Doktoravhandlinger ved NTNU, 2021:82

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Trondheim, mars 2021

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ISBN 978-82-326-5439-0 (trykt utg.)
ISBN 978-82-326-5605-9 (elektr. utg.)
ISSN 1503-8181 (trykt utg.)
ISSN 2703-8084 (online ver.)

Doktoravhandlinger ved NTNU, 2021:82

Trykket av NTNU Grafisk senter

To mum and dad

We plan, God laughs

Acknowledgements

First of all, I thank my dear parents for giving me the best opportunities I could have, which eventually led me to moving to Norway for my PhD. I thank you for your enormous support, acceptance and guidance.

I thank everyone who was a part of my PhD project team. I express my greatest gratitude to Kristian Hassel. This PhD was a one-in-a-lifetime opportunity for me, and I am endlessly thankful that you entrusted me with it. Thank you for giving me all the opportunities and freedom I had, and for all the great field trips and courses we had together. I learned so much from you, personally and scientifically. I thank Hans Stenøien for thoughtful feedback, and management and support when difficulties occurred. Working with you and the Bryo team has been such an exciting and enriching journey. I am profoundly grateful to Mike Martin for your help and support I've been receiving since day one when you joined the project. You were always there for me, finding time in your overloaded schedule to answer, help, discuss, listen and encourage. Thank you for including me in your group and for being a wonderful supervisor. I express my greatest appreciation to Péter Szövényi for his guidance during the last two years. You taught me so many things and supported me so much, which is difficult to overestimate. Your dedication to your students, and how you manage to combine brilliance and insightfulness, impresses me. I am deeply grateful for our weekly meetings, in-depth discussions, and for the fruitful research stays I had in Zurich. The participation of Kjell Ivar Flatberg in my project was a real blessing. I am deeply grateful for your kindness, feedback, support and enthusiasm, which have been helping and encouraging me since the very start of my project. Thank you for teaching me (so many) plants, skiing, persistence, and for guiding me through my cultural adaptation.

I thank the Norwegian Research Council for the funding (project no. 250541/F20), and the Department of Biology at NTNU for supporting my research stay in the University of Zurich. I thank all the co-authors who contributed to the planning and implementation of this project, in particular to Thorfinn Korneliussen for the collaboration and for kindly hosting me at the Natural History Museum in Copenhagen, and to Christian Schröck for organising our field trip to Austria and guiding us there. ForBio is gratefully acknowledged for providing highly relevant training.

I thank the Museum IT support team for their help, and the Museum administration and all the colleagues for maintaining such a wonderful working environment. In particular, I thank Renate Kvernberg for being there when I needed it, and Erik Boström for answering my labwork-related calls late in the evening, and for our great conversations in the lab. I also thank Narjes Yousefi for your guidance, and welcoming me to the Museum and the group, as well as to Trondheim and Zurich.

My sincere gratitude to everyone who I worked with at the Flouristics course. I learned so much from all of you, not only professionally, but personally and culturally. The Sletvik field courses gave me some of the fondest memories, and I thank you all for being supportive with my steep learning of the Norwegian flora and Lidsk. I also thank Sarah Martin for your persistence and enthusiasm during the labwork for my students, which made this part of my dutywork enjoyable.

These four years would be totally different if not for our PhD/PostDoc team. In particular, Malene, Marte, Anders, Vanessa, Sam, you were there at the very beginning to create the best environment I could possibly imagine. Tanja, Fabi, Sindre, Andreas, Laurène, Jaelle, Martin E., thank you for all the great activities we had together. It was a pleasure to get to know you all, to see you growing, learning, and even starting families. I deeply appreciate the support and help that many of you readily provided to me with so many times, and I cherish the memories we have together. I am looking forward to more adventures, parties, and scientific discussion with you guys.

I thank Artem for your enormous support and help in completing this PhD, which is impossible to overestimate. Your courage and persistence inspired me, and you helped me do it when I didn’t believe I could anymore. You made this happen, and you make me a better person. Дякую тобі, мій коханий!

Finally, I want to thank all my friends, who I met in Ukraine and in Norway, for standing by my side despite the fact that I spent 99% of the last 4 years working on my PhD. In particular, I thank Magni O. Kyrkjeeide for her extraordinary support within and outside of my PhD, for our great field trips together, and for stoically tolerating my Norwegian.

Last, but not least, I am endlessly grateful to my Master’s Supervisor, Prof. Dmytro Shabanov, for his enthusiasm and passion about science and evolution, which sparked my interest in this field, and for his continuous support throughout many years which led me to believe I am capable of pulling this off.

Contents

Abstract

Speciation is one of the most fundamental evolutionary processes, as it creates biodiversity. Gene flow, or introgression, can bring genetic novelty into recipient species, and hence promote adaptation, while simultaneously being antagonistic to establishment of reproductive isolation between the hybridising species. Gene flow is believed to be especially important for speciation in plants. Studying genomes of diversifying lineages enables the identification of the genomic footprints of gene flow, which facilitates disentangling its role for speciation from that of other evolutionary forces, such as selection and genetic drift. This remains challenging in non-model and nonvascular plants, where comprehensive genomic resources are lacking, and the role of gene flow for speciation remains poorly understood. In this thesis, I study speciation with gene flow on the genomic level in a bryophyte genus of peatmosses. Peatmosses (*Sphagnum*) are described by recent rapid diversification, frequent hybridisation, ancient history, phenotypic and ecological plasticity, and huge ecological importance. The combination of these features makes them an excellent model for studying the genomics of speciation in general, and the long-standing question of the evolutionary significance of introgression in particular.

First, I explored the extent of gene flow in the genus and its relation to phylogenetic divergence and variation in key life-history traits of the hybridising species, based on the published literature. I showed that hybridisation is very common in the genus, but mostly takes the form of allopolyploid hybridisation, where two haploid species produce a diploid hybrid species. I also found that species with monoicous and polyocious mating systems, high sporulation frequency and smaller spores that prefer poor habitats tend to produce more hybrids than other species. However, variation in key life-history traits and phylogenetic relatedness do not fully explain the occurrence of hybridisation in the genus. Then, I focused on the relative importance of introgression, in the form of hybridisation without change in chromosome number, for genome evolution compared to stochastic coalescent processes. I sampled populations of twelve haploid species representing all *Sphagnum* subgenera and performed low-coverage whole-genome sequencing. Contrary to expectations, I did not find evidence of widespread recent gene flow. Instead, the results suggest that ancestors of the extant subgenera exchanged genes in the past, which might have fueled rapid radiation of the genus. I also demonstrated extensive genome-wide phylogenetic discordance, which was due to incomplete sorting of ancestral polymorphism following the rapid radiation of the genus, and not due to gene flow. Finally, I tested how selection and genomic architecture influenced genome evolution in these twelve species. I described and compared the genomic distribution of diverse measures of genetic diversity, phylogenetic discordance and density of genomic features. The results suggest that genome evolution was likely constrained by conserved genomic architecture, leading to similar effects of linked selection in different species.

Overall, the findings suggest that, in contrast to many other groups with a known history of hybridisation, gene flow is not a prominent driver of genome evolution in peatmosses relative to selection and incomplete lineage sorting, at least not in the studied species. The results also corroborate the idea suggested in other studies that evolutionary processes in land plants may be universal, since rapid radiation creates very similar phylogenomic patterns across bryophytes and angiosperms. I suggest that the genome evolution in *Sphagnum* might involve strong positive divergent selection and gene flow in the ancestor populations, whereas at the later stages of speciation, their genomes became shaped mainly by purifying selection and incomplete lineage sorting, constrained by genomic architecture.

Abstrakt

Artsdannelse er en av de mest grunnleggende evolusjonære prosessene siden den skaper biologisk mangfold. Genflyt, eller introgresjon, kan gi nyskapning i de involverte artene, og dermed fremme tilpasning, samtidig som det kan hindre etablering av reproduktiv isolasjon mellom hybridiserende arter. Genflyt antas å være spesielt viktig for artsdannelse i planter. Å studere genomer hos divergerende linjer, gjør det mulig å identifisere de genomiske fotsporene av genflyt, noe som gjør det mulig å løsrive dens rolle for artsdannelse fra andre evolusjonære krefter, som seleksjon og genetisk drift. Dette er fortsatt utfordrende i ikke-modellplanter og ikke-vaskulære planter, der omfattende genomressurser mangler, og rollen som genflyt har for artsdannelse, fortsatt er dårlig forstått. I denne doktorsavhandlingen studerer jeg artsdannelse med genflyt på genomisk nivå i torvmoser. Torvmoser (*Sphagnum*) er beskrevet med nylig, rask oppsplittelse, hyppig hybridisering, lang evolusjonær historie, fenotypisk og økologisk plastisitet og enorm økologisk betydning. Kombinasjonen av disse funksjonene gjør dem til en utmerket modell for å studere genomikk av artsdannelse generelt, og det mangeårige spørsmålet om evolusjonær betydning av introgresjon, spesielt.

Først brukte jeg publisert litteratur for å utforske omfanget av genflyt i slekten, også i forhold til fylogenetisk divergens og variasjon i viktige livshistorieegenskaper hos hybridiserende arter. Jeg viste at hybridisering er veldig vanlig i slekten, som for det meste tar form av allopolypoid hybridisering, der to haploide arter produserer en diploid hybridart. Jeg fant også at arter som er monoike og polyoike, har høy sporeproduksjon og små sporer, og som foretrekker fattige habitater, har en tendens til å produsere flere hybrider enn andre arter. Imidlertid forklarer variasjon i viktige livshistorieegenskaper og fylogenetisk sammenheng ikke forekomsten av hybridisering i slekten. Deretter fokuserte vi på den relative betydningen av introgresjon, i form av hybridisering uten endring i kromosomtallet, for genomutvikling sammenlignet med stokastiske koalescerende prosesser. Jeg samlet populasjoner av tolv haploide arter som representerer alle *Sphagnum*-underslekter og utførte sekvensering av hele genomet med lav dekning. Jeg fant ikke bevis for utbredt nylig genflyt, men at forfedre til de eksisterende underslektene utvekslet gener tidligere, noe som kan ha drevet rask oppsplitting i slekten. Jeg demonstrerte også omfattende fylogenetisk uoverensstemmelse i hele genomet, som skyldtes ufullstendig sortering av forfedres polymorfisme som følge av den raske oppsplittingen, og ikke på grunn av genflyt. Til slutt testet jeg hvordan seleksjon og genomisk arkitektur påvirket genomutviklingen i disse tolv artene. Jeg beskrev og sammenlignet den genomiske fordelingen av forskjellige målinger av genetisk mangfold, fylogenetisk uoverensstemmelse og tetthet av genomiske egenskaper. Resultatene antyder at genomutvikling sannsynligvis var begrenset av bevart genomisk arkitektur, noe som førte til lignende effekter av koblet seleksjon i forskjellige arter.

Samlet sett antyder funnene mine, i motsetning til i mange andre grupper med kjent hybridiseringshistorie, at genflyt ikke er en fremtredende driver for genomutvikling i torvmoser i forhold til seleksjon og ufullstendig sortering, i det minste ikke i de studerte artene. Resultatene bekrefter også ideen om at evolusjonære prosesser i planter kan være universelle, siden rask oppslitting skaper veldig like fylogenomiske mønstre på tvers av forskjellige plantegrupper. Jeg foreslår at genomutviklingen i *Sphagnum* var drevet av sterk positiv divergerende seleksjon og genflyt hos stamformene, mens ved nylig artsdannelse er genomene formet hovedsakelig av rensende seleksjon og ufullstendig sortering, begrenset av genomisk arkitektur.

List of papers

The doctoral thesis is based on the following papers, which are hereafter referred to with their Roman numerals:

I. Meleshko O, Stenøien HK, Speed JDM, Flatberg KI, Kyrkjeeide MO, Hassel K. 2018. Is interspecific gene flow and speciation in peatmosses (*Sphagnum*) constrained by phylogenetic relationship and life-history traits? *Lindbergia* 41:1.

II. Meleshko O, Martin MD, Korneliussen TS, Schröck C, Lamkowski P, Schmutz J, Healey A, Piatkowski BT, Shaw AJ, Weston DJ, Flatberg KI, Szövényi P, Hassel K, Stenøien HK. Extensive genome-wide phylogenetic discordance is due to incomplete lineage sorting and not ongoing introgression in a rapidly radiated bryophyte genus (Accepted with minor revision, *Molecular Biology and Evolution*)

III. Meleshko O, Szövényi P, Martin MD, Flatberg KI, Stenøien HK, Hassel K. Genome-wide patterns of diversification are shaped by selection, ancient introgression and incomplete lineage sorting in a rapidly radiated genus of peatmoss (manuscript)

Author contributions

I performed all work on which this thesis is based, namely, contributed significantly to the planning of the experiments for all papers, performed all analyses and led the writing of all papers. Hans K. Stenøien (HKS) and Kristian Hassel (KH) contributed significantly to the planning of the experiments and the writing of all papers. Péter Szövényi (PS) and Michael D. Martin (MDM) contributed significantly to the planning of the experiments and the writing of Paper II and III. Kjell I. Flatberg (KIF) contributed significantly to the planning and writing of Paper I. I have conducted the data collection for Paper I together with KIF and Magni O. Kyrkjeeide (MOK). James D. M. Speed (JDMS) contributed to the analysis of the paper I. MOK and JDMS contributed to the writing of Paper I. I have performed the samples collection for Paper II and III together with HKS, KH, KIF and Christian Schröck, with contributions from Paul Lamkowski (PL) and MOK. I have performed the wet laboratory work for Paper II and III with significant contributions from MDM. Thorfinn Sand Korneliussen contributed significantly to the analysis for Paper II. The access to the reference genome sequence for Paper II and III was provided due to the contributions of Jeremy Schmutz, Adam Healey, Bryan T. Piatkowski, A. Jonathan Shaw, and David J. Weston. JS, AH, AJS, and PL contributed to the writing of Paper II.

Introduction

The role of introgression for speciation

Speciation generates biodiversity, and hence constitutes one of the most fundamental and important evolutionary processes. For many decades, the establishment of absolute reproductive isolation was viewed as crucial for subdivided populations to diverge into separate species, which was thought to be impossible without spatial separation (reviewed in Coyne and Orr 2004). In recent years, however, numerous studies have revealed speciation with past or ongoing gene flow at the same geographical scale in many taxa (reviewed by Morjan and Rieseberg 2004, Arnold 2006, and Feder et al. 2012). The idea of speciation occurring without complete geographical and reproductive isolation has eventually become more accepted (Noor and Bennett 2009; Sousa and Hey 2013; Ravinet et al. 2017), whereas incontestable evidence of true primary speciation with gene flow is still missing (reviewed by Foote 2018). Nevertheless, gene flow is a potent evolutionary force, as it enhances genetic diversity of recipient species and transfers genetic adaptations, which can reinforce adaptation and reproductive barriers (Coyne and Orr 1998; Soltis et al. 2009), and propel rapid radiations (reviewed by Marques et al. 2019). Introgressive hybridisation is particularly common and important in plants (Coyne and Orr 2004; Ellstrand 2014; Yakimowski and Rieseberg 2014), where polyploid hybridisation is one of the most common speciation mechanisms (Soltis et al. 2009; Soltis et al. 2014; Alix et al. 2017).

The development of next-generation sequencing technologies unlocked studying speciation and gene flow on the genomic level, which has drastically widened our knowledge about the processes underlying diversification (Seehausen et al. 2014; Wolf and Ellegren 2017; Jiggins 2019). In plants, however, such studies are mostly associated with crop species (e.g. Huang et al. 2012; Owens et al. 2016; Z.-Y. Ma et al. 2018), and few model species groups, most of which are vascular plants, e.g. *Arabidopsis* (Novikova et al. 2016), monkeyflowers (Stankowski and Streisfeld 2015), and poplars (T. Ma et al. 2018), but also the moss *Physcomitrella patens* (Beike et al. 2014). There is a profound lack of genomic studies of speciation and introgression in non-model and non-vascular plant species.

The speciation-with-gene-flow model

Genomic studies of speciation are often focused on genome scans, i.e. identifying genomic regions which have higher than genome-average degrees of genetic differentiation. This approach can potentially inform about processes of past and ongoing adaptation, as well as formation of barrier loci (Nosil and Feder 2012). Normally, genetic differentiation between species is highly variable across the genome, where some regions display elevated differentiation relative to the rest of the genome (see Seehausen et al., 2014 for a review). Under the so-called speciation-with-gene-flow model, such regions of accentuated differentiation are viewed as the result of speciation via divergent selection, which leads to gradual establishment of barriers to gene flow at these loci (reviewed by Feder et al. 2012). The rest of the genome remains permeable to and homogenised by gene flow (Fig. 1). This pattern has been described in many groups of closely-related species, where hybridisation is frequent, for example, in insects (Michel et al. 2010; Martin et al. 2013; Riesch et al. 2017), gastropods (Butlin et al. 2014), fish (Jones et al. 2012), marine mammals (Árnason et al. 2018), and flowering plants (Stankowski et al. 2015).

The linked selection model

It has recently been shown that the heterogeneous differentiation landscape does not always evolve in association with the speciation process (reviewed by Noor and Bennett 2009; Harrison and Larson 2016; Burri 2017). Instead, the variation in genome-wide differentiation can be conjectured by the distribution of structural features and recombination rates across the genome, which predefine the effects of selection or gene flow (Nachman and Payseur 2012; Cruickshank and Hahn 2014; Jiggins 2019). Positive and purifying (background) selection reduces genetic diversity and effective population sizes (Fig. 2A) at sites linked to its actual targets (Smith and Haigh 1974; Charlesworth et al. 1993), which also leads to a local increase of among-species differentiation (Fig. 2B, C). This linked effect of selection is amplified in genomic regions where recombination rate is low, and the density of selection targets is high (Kaplan et al. 1989; Begun and Aquadro 1992; Payseur and Nachman 2002). With time since the speciation event, selection occurs recurrently, and its effect on the linked sites accumulates and becomes even stronger (Fig. 2D). Under this linked selection model, the distribution of genetic differentiation can be predicted by variation in genomic architecture (Schrider 2020). If the latter is highly conserved across diversifying lineages, they would be experiencing similar outcomes of selection processes on the genomic landscape of diversity, which they inherited from the ancestral population (Fig. 2). Consequently, the genomic landscapes of differentiation in these lineages would be very similar to one another (Burri 2017). Such heterogeneous differentiation landscapes, highly correlated across a speciation continuum, have been described in various organisms, such as birds (Burri et al. 2015; Han et al. 2017; Delmore et al. 2018), insects (Kronforst et al. 2013; Martin et al. 2013; Edelman et al. 2019), and vascular plants (Renaut et al. 2013; Stankowski et al. 2019). Therefore, studying diversification in groups with a known history of hybridisation requires considering the genome structure in addition to introgression.

Studying the drivers of genome evolution during diversification

Gene flow leaves traces in the genome, which must be identified and quantified in order to study its role for speciation. These traces might look very similar to those resulting from incomplete lineage sorting (ILS), which describes the pattern when the most recent common ancestor of two lineages is older than the speciation event between the species from which they are sampled (Allman et al. 2011). ILS is very common in recently diverged groups, and results in retention of ancestral polymorphism, which leads to decreased differentiation. ILS can be wrongly interpreted as the effect of gene flow, therefore the effects of ILS must be taken into account when testing for introgression. Most of the robust methods developed to differentiate between the two (Green et al. 2010; Durand et al. 2011; Edelman et al. 2019) require the correct branching order among the species to be known (Fontaine et al. 2015; Edelman et al. 2019). The reconstruction of species relationships in the presence of either gene flow or ILS remains challenging (Fontaine et al. 2015; Li et al. 2019), which in turn makes it difficult to quantify the level of introgression among the species.

When its signal in the genome is identified, the most compelling question about gene flow is its relative importance for diversification in comparison with other evolutionary forces, such as selection and ILS. Insights into this question can be gained by characterising patterns of the genome-wide variation in genetic diversity and phylogenetic discordance in various species across a speciation continuum (e.g. Pease et al. 2016; Han et al. 2017; Edelman et al. 2019; Stankowski et al. 2019; Vianna et al. 2020). Speciation-with-gene-flow and the linked selection models, although not mutually exclusive, imply different relationships among various measures of genetic diversity, such as nucleotide diversity, differentiation and divergence, in relation to the distribution of phylogenetic

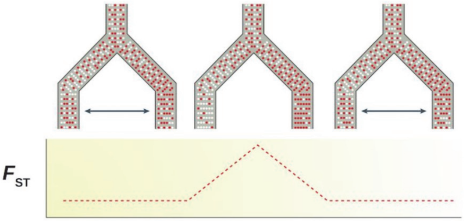

Fig. 1. The formation of a genomic region of accentuated differentiation under the speciation-with-gene-flow model. Different alleles present in the population at the corresponding locus are represented by coloured circles. These alleles segregate between the diverging populations, which is represented by branching. Gene flow (represented by arrows) leads to reduction of differentiation (F_{ST}) at the corresponding loci compared to elevated differentiation at the loci associated with barriers to gene flow, where selection is acting against gene flow. Adapted from Wolf and Ellegren (2017).

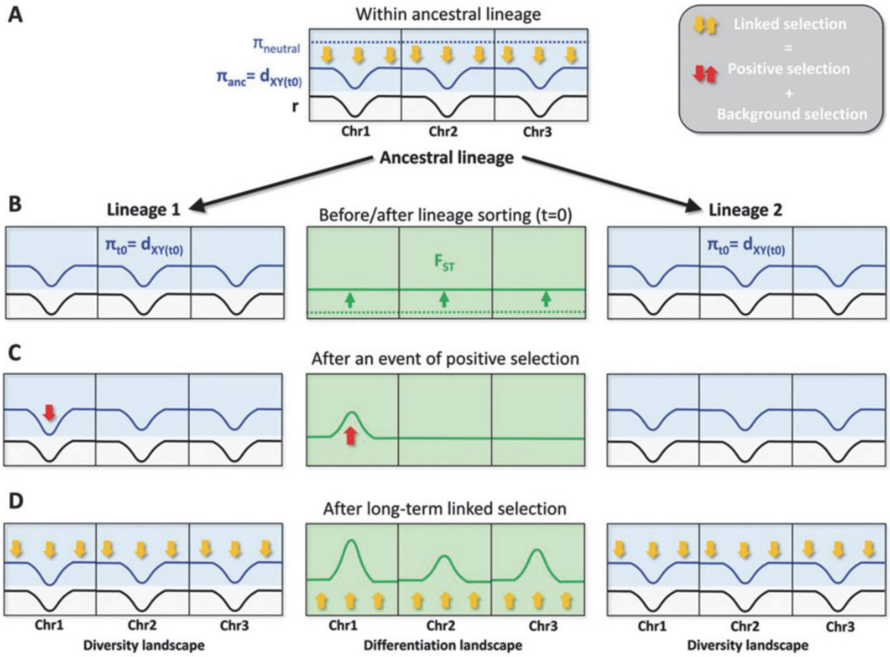

Fig. 2. Genomic landscapes of genetic diversity (π, in blue), differentiation (F_{ST}, in green), and recombination (in black) on three chromosomes of hypothetical populations at different stages of differentiation under the linked selection model. (A) Genetic diversity and heterogeneous recombination landscapes before (dashed line) and after (solid line) the action of linked selection. (B) Genomic landscapes of diversity and differentiation after a speciation event. Green arrows represent lineage sorting, dashed and solid lines represent differentiation before and after lineage sorting, respectively. Before lineage sorting, π in the descendent populations (π_{t0}) is the same as π in the ancestral population (π_{anc}) (C) Positive selection occurs in one of the populations, leading to elevated differentiation in one chromosome. (D) At the earlier stages of speciation, background selection had limited effect on diversity and differentiation. With time, long-term effects of linked selection lead to stronger increase in differentiation in regions with low recombination compared to the rest of the genome. Adapted from Burri (2017).

discordance and structural features in the genome (Burri et al. 2015; Han et al. 2017). Furthermore, under the linked selection model only, correlations can be observed in genomic landscapes of differentiation among numerous species in a group, given karyotypes and chromosome structure are conserved (Cutter and Payseur 2013; Burri 2017). Since linked effects of selection influence the rate of lineage sorting at the affected sites, the distribution of phylogenetic discordance in the genome might reflect preceding selection processes, and the strength of ILS (Pollard et al. 2006; Slatkin and Pollack 2006; Hobolth et al. 2011; Wang and Hahn 2018). Implementing this approach requires high-quality genomic data, among others. Therefore, the research on genome evolution during diversification and introgression is mostly focused on established and relatively well-studied model organisms, while little is known about how speciation with gene flow proceeds in other organisms, especially non-model plants, where interspecific hybridisation is commonly observed.

Study system

A group with high potential for studying speciation with gene flow is the peatmosses (*Sphagnum* L., Sphagnaceae, Bryophyta), a bryophyte genus comprising numerous (almost 300) species with wide geographical distributions (Michaelis 2019). Peatmosses are highly ecologically variable across their habitats and exhibit high phenotypic plasticity (Cronberg 1998; Stenøien et al. 2014; Johnson et al. 2015; Kyrkjeeide et al. 2015; Yousefi et al. 2017; Yousefi et al. 2019). This remarkable species diversity and variability originated rapidly and relatively recently (7-20 Ma, Shaw et al. 2010). Extant *Sphagnum* species play a key role in global carbon balance and climate (Weston et al. 2015), since the peatlands they form store at least 25% of all terrestrial carbon (Yu et al. 2010; Glime 2017). Genomes of peatmoss species are haploid, with relatively small, stable sizes (0.39-0.49 pg DNA, Temsch et al. 1998) and chromosome numbers (19n, Fritsch 1991), which enables their side-by-side comparison. In many peatmosses, intraspecific genetic structure across their intercontinental distributions is weak, which has been explained by past and ongoing introgression due to long-distance dispersal, as well as by ILS due to their large effective population sizes (Sundberg 2000; Szövényi et al. 2008; Stenøien et al. 2011; Karlin et al. 2013; Shaw et al. 2014; Kyrkjeeide et al. 2016). In turn, interspecific introgression is thought to cause difficulties in species delimitation and phylogenetic inference in the genus (Ricca et al. 2011; Shaw et al. 2012; Karlin et al. 2014). There is evidence of past and extant hybridisation and polyploid speciation in peatmosses (e.g. Cronberg and Natcheva 2002; Flatberg et al. 2006; Natcheva and Cronberg 2007; Karlin et al. 2009; Szurdoki et al. 2014; Yousefi et al. 2017; Kyrkjeeide et al. 2019), whereas several whole genome duplication events have likely contributed to the rapid diversification of Sphagnopsida (Devos et al. 2016). However, most genetic studies on *Sphagnum* are focused on phylogeography, adaptation, species delimitation or allopolyploid speciation, rather than interspecific introgression *per se*, and are based on a small number of genetic markers. The extent of interspecific introgression without change in chromosome number in peatmosses remains largely unknown, as are the factors promoting hybridisation in these plants. Finally, the most compelling question is the implications of gene flow for speciation in peatmosses.

Reproductive biology of peatmosses is important for understanding their evolutionary history. Mosses have a haploid-dominant life cycle with a photosynthetically autonomous, haploid gametophyte and an unbranched, diploid sporophyte, which develops on and depends on the gametophyte (see Fig. 3 for schematic illustration of the life cycle in mosses). Sexual reproductive organs develop on the gametophyte and produce gametes mitotically. In *Sphagnum*, most species are dioecious, or unisexual (Wyatt and Anderson 1984), and many are monoicous (or bisexual), exhibiting both outcrossing and self-fertilisation. As gametes of a single plant are genetically identical, offspring produced by self-fertilisation of a monoecious gametophyte are homozygous at every locus (Shaw and Goffinet 2000). In *Sphagnum*, the level of intragametophytic selfing is very high, but monoecious species are also commonly involved in mixed mating, in contrast to angiosperms (Johnson and Shaw 2015). After sexual reproduction, a diploid sporophyte develops on a mother gametophyte, where spores are produced meiotically from spore mother cells. Mature spores are explosively discharged (Nawaschin 1897; Goffinet and Shaw 2008; Sundberg 2010a), dispersed by wind, and eventually become established, producing one or more genetically identical gametophytes.

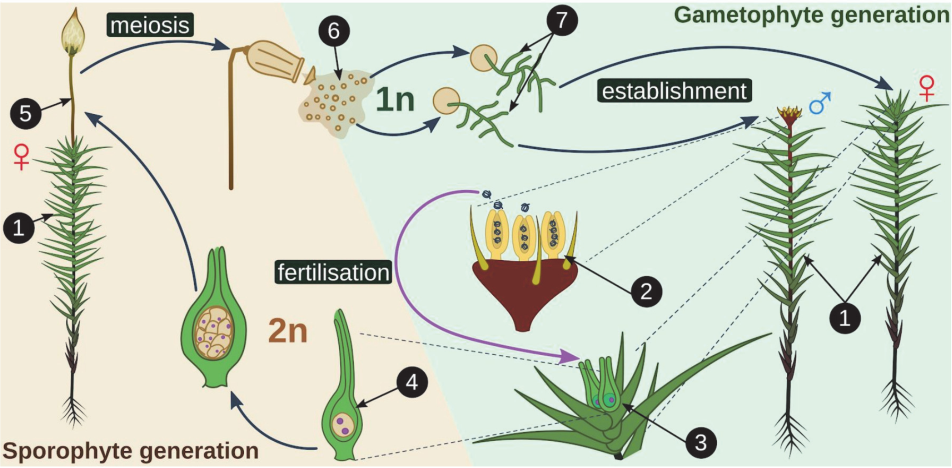

Fig. 3. Life cycle in mosses. Key: 1, haploid gametophyte, 2, male reproductive organs (antheridia) with sperm cells, 3, female reproductive organs (archegonia) with egg cells, 4, diploid zygote, 5, diploid sporophyte, 6, haploid spores, 7, spores germination into protonema. Adapted from Tomáš Kebert & umimeto.org, CC BY-SA 4.0 https://commons.wikimedia.org/wiki/File:Moss_life_cycle.svg and LadyofHats https://commons.wikimedia.org/wiki/File:Lifecycle_moss_svg_diagram.svg.

Such a life cycle accelerates the efficacy of natural selection in peatmosses, through which genes are directly exposed to selection during the haploid-dominant phase and cannot be sheltered by a dominant allele (Szövényi et al. 2013; Johnson and Shaw 2015). In addition to sexual reproduction, peatmosses often reproduce vegetatively, i.e. clonally (During 1990; Cronberg 1996; Cronberg 1998; Stenøien and Såstad 2001; Cronberg et al. 2006; Gunnarsson et al. 2007; Liu et al. 2014), which leads to decreased effective recombination rate and, hence, stronger effects of linked selection on the peatmoss genome. Altogether, strong effects of gene flow, ILS and linked selection can be expected in the peatmoss genomes.

Hypotheses about speciation-with-gene-flow in Sphagnum

Several factors, including some of the life-history traits described above, may have profound evolutionary implications in peatmosses. Firstly, phylogenetic relatedness between the hybridising species may affect the evolutionary consequences of hybridisation. The degree of divergence between the species tends to strengthen reproductive isolation between them (Coyne and Orr 1997), hence, closely related species are more likely to engage in interspecific hybridisation. Postzygotic reproductive isolation takes millions of years to develop in plants, especially in long-lived ones (Levin 2012). Since peatmoss species have long generation times, phylogenetic relatedness is not expected to be a strong constraint to gene flow in these plants. Secondly, haploid-dominant plants with a self-fertilising mating system diversify faster and purge genetic load more effectively compared to strictly outcrossing ones (McDaniel et al. 2013; Szövényi et al. 2014). Mating system can also influence the effective population size, which might facilitate population subdivision (Twyford et al. 2014). In mosses, mating system strongly influences sporulation frequency (Longton 1992), which may modulate gene flow rates (Stenøien and Såstad 1999; Stenøien and Såstad 2001). In turn, size and colour of spores influence their viability and dispersal (Sundberg and Rydin 2000; Sundberg 2010b), and therefore might affect the levels of gene flow. It is currently unclear if these and other life-history traits, as well as phylogenetic distance, are associated with the occurrence and the extent of interspecific gene flow in peatmosses.

Based on current knowledge, several hypotheses about the factors influencing genome evolution during peatmoss diversification can be put forward. One may expect gene flow to be a common and important factor for speciation in the group, and its strength to be defined by phylogenetic relatedness and/or life-history traits of the hybridising species, with several traits making introgression more likely. Therefore, the genomic landscape of diversification is expected to correspond to the predictions of the speciation-with-gene-flow model. Alternatively, given their recent rapid radiation, genome evolution in peatmosses may have been mainly influenced by ILS, with only a small role for gene flow. As another possibility, selection, namely by its linked effects, may have been the main force shaping the genomic landscape of diversification in *Sphagnum*. Finally, if the genomic architecture is highly conserved across the species, one can expect the genome evolution to follow a similar path across different species in the group. Most of these hypotheses are mutually compatible in one way or another. The papers presented in this thesis address these hypotheses, and seek to elucidate the relative importance of the factors listed above for diversification in *Sphagnum*.

Aims of the thesis

The goal of the thesis is to explore how well the speciation-with-gene-flow model explains genome evolution during diversification of a highly diverse, rapidly radiated group of peatmosses (*Sphagnum*). Specifically, I aim to answer the following questions:

1) How frequent is interspecific hybridisation in the group? (Paper I)
2) Is interspecific gene flow constrained by phylogenetic relatedness between the hybridising species? (Paper I, Paper II)
3) How is the potential for hybridisation of a peatmoss species associated with their life-history traits? (Paper I)
4) Is interspecific gene flow a prominent driver of diversification in *Sphagnum*? (Paper II, Paper III)
5) How important is gene flow for genome diversification in *Sphagnum* relative to:
    a) Incomplete lineage sorting (Paper II, Paper III)
    b) Linked selection (Paper III)
    c) Genomic architecture (Paper III)

Summary of the papers

Paper I

In this study, we summarise the current knowledge about hybridisation in peatmosses to estimate its extent and association with phylogenetic relatedness and life-history trait variation of the hybridising species. We did this by collecting published evidence of interspecific hybridisation and allopolyploid speciation in peatmoss species.

This information was then used to calculate two coefficients of hybridisation for each subgenus, providing a minimum and a maximum estimate of the extent of hybridisation. We found that there were 44 cases of hybridisation reported in peatmosses, most of which were allopolyploid hybrid species (82%). In total, 37 parental species were reported, each producing from one to four hybrids. Hybridisation is common within all and among most subgenera, with up to 21% of all peatmoss species potentially involved. Since many of the allopolyploid hybrids are of unknown origin, this number might be greatly underestimated. Next, to assess if the degree of divergence imposes constraints on hybridisation in peatmoss species, we estimated phylogenetic distance between the parental species as the average number of nodes separating them on all published phylogenetic trees. We found that parents of allopolyploid hybrids are less closely related to each other than parents of admixed haploid hybrids, albeit insignificantly.

Finally, we collected data on seven life-history traits of the parental species, such as mating system type, sporulation frequency, spore colour and sizes, position of a species along the mire water table and the nutrient gradients. We then performed factorial analysis of mixed data (FAMD) to test for association between these traits and the intensity of hybridisation, the latter calculated as the number of hybrids produced by a parental species. This analysis showed that variables such as subgenus and spore colour contribute the most to the variation in life-history traits between the parents, followed by maximum spore size, mating system and sporulation frequency. Only 2.6% of variance between species was explained by the intensity of hybridisation. We found an association between the intensity of hybridisation and key life-history traits, since the FAMD analysis showed that more hybrids are produced by species with monoicous and polyocious mating systems, high sporulation frequency and smaller spores that prefer poor habitats than by other species.

Overall, neither phylogenetic relatedness nor life-history trait variation fully explain the occurrence of hybridisation in *Sphagnum*. We then discuss the observed diverse modes of hybridisation and its potential evolutionary implications and causes, highlighting the need for more studies on the occurrence of hybridisation in peatmosses, and reproductive biology and ecology of hybridising species.

Paper II

In this study, we focus on interspecific introgression and its importance for diversification relative to incomplete lineage sorting (ILS) in peatmosses. To do this, we sampled sympatric/parapatric and allopatric populations of 12 commonly occurring haploid peatmoss species at three geographical scales in Europe (190 samples in total). We performed low-depth Illumina sequencing, and obtained whole nuclear, plastid and organellar genomes for all samples and an outgroup.

First, we explored genetic differentiation among the species based on single-nucleotide polymorphisms (SNPs) and genotype likelihoods using principal component analysis, ADMIXTURE analysis and population differentiation estimates (F_{ST}). These analyses revealed neither evidence for strong genetic structure within nor substantial admixture between species, and demonstrated that all studied species are highly differentiated from one another.

Next, we reconstructed phylogenetic relationships among the species based on concatenated nuclear SNPs, and plastid SNPs. We obtained very highly supported, but topologically conflicting, phylogenies, with each species forming a strongly supported monophyletic clade. We observed cytonuclear discordance regarding both the relationships among the subgenera, and the placement of individual species. Therefore, we used a coalescent-based method to reconstruct the species tree based on 988 arbitrary genes, which resulted in the same species tree as our concatenation-based analysis. We also reconstructed trees from 1774 100-kb consecutive sliding windows. We found extensive genome-wide discordance, with only 0.1% of the gene trees and 2.4% of the sliding window trees matching the species tree topology. The discordance was more pronounced in deeper nodes in the phylogeny. Taken together, these findings strongly suggest that the discordance results from ILS due to the rapid radiation of the genus.

Finally, we employed a suite of various tests for recent and ancient introgression, i.e. D-statistics, D_{FOIL} statistics, the $f3$ statistics, and TreeMix analysis. In addition, we used a recently described QuIBL method, which uses the distribution of internal branch lengths in triplets of species to differentiate between ILS and gene flow causing phylogenetic discordance. We found that levels of post-speciation introgression were very low, and less than 1% of discordant loci were introgressed. The D_{FOIL} analysis revealed evidence of ancient introgression among the ancestors of the subgenera.

The study demonstrates that, in contrast to many groups with a known history of hybridisation, post-speciation gene flow is not the main cause of phylogenetic discordance in *Sphagnum*. In turn, rapid radiation seems to create a phylogenomic pattern in peatmosses very similar to that in other bryophytes and angiosperms, which supports the idea of evolutionary processes among land plants suggested by earlier studies in bryophytes (Medina et al. 2018).

Paper III

In this study, we characterise the processes shaping genome evolution in 12 peatmoss species based on the sequencing data we generated in Paper II. We use the data to estimate nucleotide diversity (π), Tajima's D, and F_{ST} for each species and pairwise species comparisons based on site frequency spectra in 1774 100-kb consecutive sliding windows. We also calculated divergence (d_{XY}) for all pairwise species comparisons.

For each of the statistics, the genome-wide distributions were very similar among the species or species comparisons. Hence, we carried out principal component analyses to summarise the interspecific variation in a single genomic landscape for each statistic, and to describe the strength of the correlation among the species. This analysis was performed on the sliding-window calculations of pairwise F_{ST} and d_{XY} (66 pairwise comparisons each), and all within-species calculations of π and Tajima's D. For each of these statistics, the genomic landscapes were highly correlated across the species or pairwise comparisons, with most of the variation explained by the first principal component (73%, 73%, 56% and 57% for F_{ST}, d_{XY}, π and Tajima's D, respectively). Such correlated landscapes suggest that genome evolution in peatmosses might be constrained by conserved genomic architecture, which leads to similar effects of selection, gene flow, or ILS in different species.

To investigate the relative contributions of these processes in shaping the diversification landscapes, we assessed how the calculated statistics are distributed across the genome and co-vary in relation to gene density and phylogenetic discordance. The discordance was calculated as the number of steps required to convert a sliding-window tree into the species tree, reconstructed in Paper II. We observed a pattern where a small number of less differentiated "valleys" are present in an otherwise highly differentiated landscape, which is similar to those discovered in studies describing the late stages of speciation. In turn, π, Tajima's D, and d_{XY} followed the opposite pattern, with peaks coinciding with the F_{ST} valleys. We found no systematic difference between the distribution of F_{ST} between allopatric and sympatric comparisons, suggesting that these valleys do not originate from recent gene flow.

The patterns of covariation among the statistics strongly suggest that the genomic landscape of diversification has been shaped by recurrent linked selection, instead of recent gene flow. Namely, we found that regions with higher gene density have lower phylogenetic discordance (r_S=-0.31, p<0.0001), divergence and diversity (r_S=-0.78 and r_S=-0.25, respectively, p<0.0001), and higher differentiation (r_S=0.1, p<0.0001). We also found that d_{XY} was positively correlated with π and weakly negatively with F_{ST} (r_S=0.29 and r_S=-0.12, respectively, p<0.0001). Selection at target sites leads to reduced diversity at linked sites, and therefore to decreased divergence. This leads to locally accelerated lineage sorting, resulting in better correspondence to the species tree. Such linked effects of selection are even more pronounced in the regions with high density of selection targets and low recombination when selection occurs repeatedly. The majority of peatmosses are haploid, and therefore effective purifying selection is expected in these plants, especially in predominantly selfing species.

Finally, we found a stronger skew toward an excess of rare alleles (more negative Tajima's D) in regions with higher gene density (r_S=-0.16, p<0.0001), which might signify the traces of selective sweeps. We further tested for evidence of directional positive selection, as well as ILS, by performing autocorrelation analyses. The analyses did not reveal the blocks of spatially aggregated windows with concordant trees expected under positive selection, although it suggested that the underlying density of functional genomic features might not be detectable at the scale we used.

Based on all these findings, we conclude that genome evolution in the studied peatmosses has mainly been shaped by long-term effects of linked selection, constrained by conserved genomic architecture. We suggest that at the early stage of diversification of the studied species, positive selection and gene flow were likely more important, whereas with time, background selection and ILS became the main drivers shaping the conserved genomic landscapes of diversification across the studied species.

Discussion

Introgressive hybridisation is an important evolutionary mechanism in many organisms. Given the complexity of speciation processes, especially those accompanying rapid radiations, the role of introgression for diversification should be considered from different angles. In this thesis, patterns of interspecific hybridisation and introgression in peatmosses are summarised and characterised in relation to phylogenetic relatedness and life-history traits of the participating species, as well as to other evolutionary forces, such as selection and ILS. We showed that many peatmoss species are involved in hybridisation and allopolyploidisation, however, post-speciation introgression seems to be substantially limited in a selected set of species, representing a big part of peatmoss diversity. In these species, extensive genome-wide ILS and footprints of ancient introgression have been identified. Moreover, we demonstrated strikingly similar genome-wide distributions of genetic diversity, divergence and differentiation among these species. Together with other findings, this result strongly suggests that genome evolution in the studied species has been constrained by conserved genomic architecture, which defined the effects of selection and ILS. Finally, we found correlations among genome-wide distributions of different measures of genetic diversity, gene density, and phylogenetic discordance. These patterns are primarily attributed to recurrent linked selection and ILS. Below, the role of gene flow for speciation in *Sphagnum* is discussed in light of these findings.

Frequency of interspecific hybridisation in Sphagnum (Paper I and II)

Paper I demonstrated that interspecific hybridisation is very frequent in *Sphagnum*, but the majority of hybrids originate from allopolyploid hybridisation. Allopolyploidisation often leads to immediate postzygotic reproductive isolation of the polyploid hybrid progeny from the parents (Ricca and Shaw 2010; Abbott et al. 2013). In arctic plants, an increase in genetic diversity via polyploidisation provides polyploids with an advantage in post-glaciation colonisation of areas compared to diploids (Brochmann et al. 2004). Similar mechanisms have been suggested for the southern allotriploid peatmoss *S. falcatulum* (Karlin 2014). Recurrent polyploidisation can further increase genetic diversity of polyploid hybrids and their frequency in populations, aiding successful establishment of polyploid lineages into separate species (Ricca and Shaw 2010). This might be the case for several polyploid peatmoss species, such as *S. russowii* (Shaw et al. 2005), *S. jensenii* (Såstad et al. 1999), *S. carolinianum* (Ricca et al. 2008), *S. falcatulum* and *S. australe* (Karlin 2014). Taken together, this suggests that polyploid hybridisation is an important mechanism of speciation in *Sphagnum*.

Hybridisation without change in chromosome number, i.e. genetic admixture or introgression (see Box 1 with glossary in Paper I), is less frequently reported. There are few examples of ongoing or recent admixture in zones of contact (Cronberg 1996; Cronberg 1997; Cronberg and Natcheva 2002; Szurdoki et al. 2014; Yousefi et al. 2017), and past, likely adaptive, introgression (Thingsgaard 2001; Natcheva and Cronberg 2003). The evolutionary significance of ongoing admixture is difficult to estimate, since it is unclear if the admixed hybrids occupy different niches and are reproductively isolated from their parental species. In turn, admixed individuals often remain undetected in the field due to their morphological resemblance to one of the parents, while allopolyploid hybrids often have more distinct morphological features, which may lead to underestimation of the occurrence of admixture and introgression. The same issue applies to other bryophytes species (reviewed by Glime and Bisang 2017; and Sawangproh et al. 2020). Given how frequent polyploid hybridisation is in *Sphagnum*, one can expect similar rates of ongoing or past introgression in co-occurring peatmosses. Nevertheless, we found minimal levels of recent introgression in Paper II using twelve haploid species, representing all peatmoss subgenera. The likely explanations for this are discussed below.

Interspecific gene flow is not constrained by phylogenetic relatedness and life-history traits (Paper I, Paper II)

Based on the patterns observed in Paper I, we found that phylogenetic distance *per se* did not define the success of interspecific hybridisation in *Sphagnum*. In particular, there was no significant difference in phylogenetic relatedness of parents of allopolyploids and parents of haploid admixed individuals. For hybridisation to result in allopolyploidy, certain degrees of genetic divergence between parents may be required, which would lead to impaired meiotic chromosome pairing during spore production (Natcheva and Cronberg 2007; Karlin et al. 2014). On the contrary, we found that distantly related species were involved in admixture, while some closely-related species formed allopolyploid hybrids. In addition, we did not find significant correlation between genetic differentiation and levels of interspecific introgression in Paper II, although we did not test the most closely-related pairs in this study.

In line with theoretical predictions, Paper I showed that variation in the life-history traits, key for peatmoss dispersal, tends to be associated with the intensity of hybridisation. Specifically, polyoicous and monoicous species that frequently release small, light-coloured spores and prefer poor habitats, in terms of pH and concentration of minerals, tend to produce more hybrids than other species. High sporulation frequency can be advantageous for dispersal to longer distances, as can small spore size (Sundberg 2010b). Monoicous and polyoicous species have higher sporulation frequency (reviewed by Stenøien and Såstad 2001), which might therefore translate into higher reproductive and dispersal success, and hence higher colonisation ability, leading to more frequent hybridisation compared to dioicous species. In such a case, one can expect to see a smaller portion of dioicous species among hybridising parental species than among non-parental ones. We indeed observed this pattern; however, the difference was insignificant.

In peatmosses, variation in habitat preference, in terms of the position along the water table, seems to be phylogenetically constrained (Johnson et al. 2015), as is variation in spore colour (Flatberg 2013). Due to the high amount of missing data in our dataset, we were not able to take phylogenetic relatedness into account in our FAMD analysis. Therefore, the association between these traits and hybridisation should be tested further. From this perspective, it should be kept in mind that the relatedness between species might contribute to the observed patterns.

There is a profound lack of knowledge about most life-history traits in many parental and non-parental peatmoss species. For example, mating system is only known for 89 of 104 species listed in available floras (Chien et al. 1999; McQueen and Andrus 2007; Flatberg 2013), whereas about 300 peatmoss species are known worldwide (Michaelis 2019). In addition, peatmoss diversity is mostly described in the Northern Hemisphere, whereas tropical and Southern Hemisphere regions also harbour significant species richness (Shaw et al. 2019), which is substantially less studied. Therefore, with more knowledge about the reproductive and ecological traits of peatmosses, the importance of the studied life-history traits for the occurrence of hybridisation should be re-evaluated.

Post-speciation interspecific gene flow is very limited in Sphagnum (Paper II, Paper III)

In contrast to numerous groups of plants (e.g. Gerber et al. 2014; Stankowski et al. 2015; Pouchon et al. 2018; Roberts and Roalson 2018; Valderrama et al. 2018) and animals (e.g. Martin et al. 2013; Fontaine et al. 2015; Malinsky et al. 2018; Edelman et al. 2019; Barth et al. 2020), where hybridisation is frequent, recent admixture and post-speciation introgression do not seem to play a major role for diversification in the studied peatmoss species. Paper II demonstrated high genetic distinctiveness of the studied species, very limited post-speciation gene flow and no signs of recent admixture among them. All species formed highly supported monophyletic clades in the phylogenetic analyses. We found no evidence for isolation by distance in Paper III, suggesting that it is not geographical distance that drives reproductive isolation. It should be noted that many of the species grow side-by-side within the sampled habitats at a possible mating distance. Taken together, this strongly suggests that strong reproductive barriers have evolved in peatmosses, preventing ongoing interspecific hybridisation, if any, from translating into substantial introgression. Similar patterns are observed in several rapidly radiated plant taxa, for example, in the Neotropical genera *Begonia* and *Costus*. In *Begonia,* co-occurring species, occupying different microhabitats within their range and producing morphologically distinct hybrids, show highly limited introgression due to strong reproductive barriers (Twyford et al. 2014; Twyford et al. 2015). In *Costus*, strong prezygotic barriers have been described that maintain species distinctiveness in the face of hybridisation (Surget-Groba and Kay 2013).

The mechanisms of reproductive isolation are largely unknown in bryophytes in general, and in peatmosses in particular. There is spatial isolation due to limited distances of gamete and spore dispersal (Longton and Schuster 1983; Bisang et al. 2004; Glime and Bisang 2017), and ecological isolation within habitat (reviewed by Natcheva and Cronberg 2004). Prezygotic reproductive barriers include phenological difference, i.e. in the timing of gamete production by co-occurring species. There seem to be no gametic incompatibilities in mosses (reviewed by Natcheva and Cronberg 2004; and Sawangproh et al. 2020). Postzygotic barriers are also poorly understood, and include chemical inhibition of germination of conspecific spores or spores from an unrelated species, reported in several moss species (Rosengren and Cronberg 2015). Therefore, it is difficult to speculate which barriers could have primarily contributed to the establishment of reproductive isolation, and how these contributions occurred. Based on our findings, one can speculate that reproductive isolation evolved in sympatry, and is primarily caused by prezygotic barriers. Otherwise, we would observe a higher incidence of admixture among the studied species. In plants, dynamic structure of the genome and differences in mating systems, among others, can facilitate the establishment of reproductive isolation and divergence (Twyford et al. 2015). Paper III, however, suggested that peatmosses have highly conserved genome structure. Further research is therefore needed to describe the genetic mechanisms of reproductive isolation in peatmosses and the role of introgression in their establishment.

A single admixed individual, resulting from admixture between two closely-related species (*S. flexuosum* and *S. tenellum*), was identified in Paper II. This individual could be an infertile F_1 hybrid, signifying admixture, and not necessarily ongoing introgression, between these species. To this date, the only study confirming genetic transfer of admixed genotypes beyond F_1 generation in sympatric bryophyte populations is in the genus *Homalothecium* (Sawangproh, Hedenäs, et al. 2020).

Nevertheless, we might have underestimated the extent of recent introgression in Paper II for several reasons. Specifically, introgression from a “ghost” population and different population sizes in the tested species can bias D (Zheng and Janke 2018) and D_{FOIL} estimates (Pease and Hahn 2015). In turn, QuIBL is sensitive to recombination within the genomic windows used for the analysis (Edelman et al. 2019), which we accounted for by choosing a narrow window size of 2 kb. In contrast to D-statistic, QuIBL is robust to hybridisation among all three species in the triplet (Edelman et al. 2019). We therefore believe that the estimated levels of post-speciation gene flow are reliable.

While the findings of Paper II support limited post-speciation gene flow, they represent only a part of the vast species diversity of *Sphagnum* and do not dismiss a possibility of significant gene flow among species not included in the analysis. In this study, very closely related species were not sampled, and the most closely related species pairs in the dataset could not be included in most of our introgression analyses due to methodological constraints. Therefore, more widespread interspecific introgression may still happen between very closely related peatmosses that were not included in this study.

Ancient gene flow and peatmoss diversification (Paper II and Paper III)

Paper II showed that the studied species were highly distinct and likely reproductively isolated. In turn, the genome-wide distributions of genetic differentiation obtained in Paper III suggest that these species are at the late stage of diversification. It is possible that gene flow could have been more pronounced in the past, at the earlier stages of speciation in the group. Indeed, the results of the D_{FOIL} analysis in Paper II suggest a deep introgression event among ancestors of the extant subgenera, which should have happened early in the diversification process. We found that the values of D-statistic were much higher than the values of post-speciation introgression inferred with QuIBL and the D_{FOIL}. In paper II, we argue that instead of post-speciation introgression, the values of D-statistic represent traces of that ancient introgression, followed by genetic drift or divergent selection, which led to differential retention of ancestral polymorphism in the studied species. Accordingly, Paper II demonstrated evidence for extensive ILS, and Paper III suggested that there might have been strong effects of divergent selection on the peatmoss genome at some point in the past. Similar patterns were recently reported in rhinoceros (Moodley et al. 2020), where gene flow between the ancestral lineages subsided within up to 2 million years after their initial divergence, but nevertheless resulted in false-positive signatures of recent gene flow among the successor species due to ILS.

In certain cases, D_{FOIL} can incorrectly infer introgression as ancient instead of post-speciation (Fontaine et al. 2015; Pease and Hahn 2015). Nevertheless, we obtained significant and consistent signals for ancient introgression in most of the five-taxon phylogenies used for the analysis. Moreover, Paper II also showed that introgressed regions rarely formed the consecutive blocks in the genome expected under recent gene flow (Barlow et al. 2018; Moodley et al. 2020; Westbury et al. 2020). Recently introgressed genomic regions should form relatively long stretches in the genome, which are broken by recombination into smaller, scattered pieces with time after the introgression event (Węcek et al. 2017). This result provides strong support for the hypothesis about ancient introgression among the ancestral peatmoss lineages.

The phenomenon of rapid radiation is difficult to explain by *de novo* mutations or new ecological opportunity alone (Pease et al. 2016; Marques et al. 2019). Ancient introgressive hybridisation has been shown to be a catalyst for recent rapid radiation in many plant and animal groups, since it reshuffles old polymorphism into novel adaptive combinations (reviewed by Marques et al. 2019). In peatmosses, the last burst of diversification was associated with the Miocene cooling, which presumably prompted adaptation to novel habitats (Shaw et al. 2010; Devos et al. 2016). This rapid radiation could have been facilitated by gene flow (Shaw et al. 2010; Devos et al. 2016). Therefore, it is very likely that the ancient gene flow among the ancestors of the extant subgenera demonstrated here played an important role in peatmoss diversification. Further work is needed to reconstruct the exact timing of the introgression events and their adaptive potential.

Incomplete lineage sorting explains phylogenetic incongruence (Paper II, Paper III)

Phylogenetic relationships among species reflect their evolutionary history, whereas the distribution of phylogenetic signals across the genome can inform about evolutionary processes in the ancestral population (Pollard et al. 2006; Slatkin and Pollack 2006; Hobolth et al. 2011; Wang and Hahn 2018). Paper II demonstrated extensive genome-wide phylogenetic discordance in *Sphagnum*, which was common across sliding windows and genes in the genome, as well as between the organellar- and nuclear-based phylogenies. This discordance was also associated with deeper nodes. We showed that this pattern is best explained by extensive ILS, resulting from rapid radiation of the genus, rather than by post-speciation introgression. Introgressed loci accounted for only 0.29% of the windows, supporting discordant topologies. The patterns of distribution of phylogenetic discordance identified in Paper II are very similar to those described in other rapidly radiated groups, including recently diverged ones, such as wild tomatoes (Pease et al. 2016), wild bananas (Rouard et al. 2018), the plant genus *Jaltomata* (Wu et al. 2018), and cichlid fishes (Irisarri et al. 2018), and older radiations, such as in neoavian birds (Suh et al. 2015). It is known that short coalescent times and ILS should accompany rampant radiations (Whitfield and Lockhart 2007). In addition, peatmosses are characterised by large effective population sizes (N_e) (Stenøien and Såstad 1999; Szövényi et al. 2008) and long generation times, which intensify ILS even more (Copetti et al. 2017). This leads to (1) incongruences between the species tree and gene trees in extant lineages, reconstructed using any type, quality and quantity of the genetic markers (Pease et al. 2016; Wang and Hahn 2018), and (2) difficulties in resolving inferences involving more than four taxa (Degnan and Rosenberg 2009; Suh et al. 2015), which corresponds perfectly to our findings. We conclude that rapid diversification of peatmosses has likely caused the observed extensive phylogenetic incongruence, in accordance with other studies of rapidly diversified groups of organisms.

In Paper III, we characterise the genome-wide distribution of topological discordance, used as an estimate of phylogenetic incongruence, in relation to the distribution of the density of the genomic features. Unless N_e is significantly different between the extant lineages and the ancestral populations (Slatkin and Pollack 2006), the levels of ILS-induced discordance across the genome should be reduced in regions of low recombination under positive or purifying selection (Hobolth et al. 2011; Pease and Hahn 2013; Stankowski et al. 2019). Accordingly, we demonstrated that topological discordance was associated with lower gene density, which can serve as a proxy for recombination rate. There was also no evidence for spatial autocorrelation of regions with low phylogenetic discordance, expected under directional selection, in contrast to the neutral model with ILS (Slatkin and Pollack 2006; Hobolth et al. 2011). This further strengthens the idea that the observed discordance is primarily caused by ILS, compared to both gene flow and directional selection.

Similarly to peatmosses, many bryophyte lineages have originated through recent rapid radiation and whole genome duplication (Laenen et al. 2014; Johnson et al. 2016; Silva et al. 2017; Medina et al. 2018). It has been proposed that intrinsic and extrinsic factors underlying evolution in bryophytes are not fundamentally different from angiosperms, suggesting universality of evolutionary processes in land plants (Medina et al. 2018). Our results corroborate this idea, since the phylogenomic patterns of rapid radiation that we describe in peatmosses are very similar to those of vascular plants, and other bryophytes.

Overall, ancient gene flow followed by ILS, and highly limited post-speciation gene flow, correspond very well to all our findings. It is, however, beyond the scope of this study to determine the relative impact of ILS and introgression on the early diversification process in this group. Given the high level of ILS, a bifurcating tree might not be a realistic representation of the complex evolutionary history of this rapidly radiated group.

Correlated genomic landscapes of diversification in peatmosses

In numerous organisms, genomic landscapes of diversification are conserved in various species across the speciation continuum (e.g. Martin et al. 2013; Burri et al. 2015; Irwin et al. 2016; Vijay et al. 2016; Delmore et al. 2018; Stankowski et al. 2019). Such patterns are predicted by the linked selection model, provided that genomic architecture in diversifying lineages is highly conserved (Burri 2017). In paper III, we describe highly correlated genomic landscapes of differentiation, divergence and diversity across the studied peatmoss species. These results suggest that genome evolution in *Sphagnum* is driven by conserved genomic architecture, leading to similar outcomes of selection in different species, rather than by processes directly related to speciation (Cutter and Payseur 2013; Burri et al. 2015). In addition, we found that the genome-wide distribution of F_{ST}-based differentiation does not follow the predictions of the speciation-with-gene-flow model. Instead, it resembles the pattern describing the late stages of speciation, with a small number of less differentiated genomic islands among an otherwise highly differentiated landscape (Han et al. 2017; Riesch et al. 2017; Ravinet et al. 2018). If these valleys in the differentiation landscape originated from gene flow, they would be deeper in sympatric comparisons, in contrast to more isolated allopatric comparisons (Yamasaki et al. 2020). Conversely, we found no systematic difference between allopatric and sympatric comparisons. Our findings suggest reduced efficacy of selection acting in the F_{ST} valleys, and dismiss recent gene flow as a main force contributing to the formation of the differentiation landscape (Han et al. 2017). We suggest that recurrent linked selection is one of the major factors explaining the correlated pattern of genomic divergence, differentiation and diversity observed.

Linked selection and genomic architecture shape genome evolution

As described above, there are several factors implying a high extent of natural selection in peatmosses. Rapid radiation into various environments and niche differentiation are expected to incur divergent positive selection. Additionally, strong negative and/or positive selection is known to act on haploid gametophytes of peatmosses (Szövényi et al. 2013), especially in primarily selfing species (Szövényi et al. 2014). Recurrent linked effects of selection account for reduced neutral genetic variation and N_e, and intensified lineage sorting at linked sites (Pollard et al. 2006; Hobolth et al. 2011; Pease and Hahn 2013; Li et al. 2019), whereas the strength of these effects depends on genomic architecture (Kaplan et al. 1989; Hudson and Kaplan 1995; Cutter and Payseur 2013; Schrider 2020). Indeed, in paper III we found weak negative correlation between gene density and heterogeneously distributed phylogenetic discordance. This correlation should be stronger under recurrent linked selection at late stages of speciation, unless the recombination rate is not conserved across the species, or gene conversion occurred in the regions of low recombination (Pollard et al. 2006; Burri 2017). Recombination rate must be conserved, since we observed the correlated diversity, divergence and differentiation landscapes among the species, which would otherwise be impossible (reviewed in Burri 2017). It is therefore plausible that recombination rate variation does not fully correspond to gene density distribution in the studied species. The relationship between recombination rate and gene density distribution needs to be further investigated.

The patterns of covariation among measures of genetic diversity, phylogenetic discordance and gene density described in Paper III are predicted under long-term purifying selection (or background selection, BGS) (Burri 2017). It has been shown that cumulative linked effects of recurrently occurring BGS are mainly responsible for variation in genetic diversity along the genome and correlated landscapes of differentiation, especially at late stages of differentiation (reviewed by Burri 2017). In turn, relationships between genetic diversity, gene density and Tajima's *D* support the idea of positive selection, i.e. recurrent selective sweeps, contributing to the genome evolution in the studied species (Braverman et al. 1995; Sella et al. 2009). However, we did not find the strong spatial autocorrelation among windows with low phylogenetic discordance expected under positive selection (Slatkin and Pollack 2006; Hobolth et al. 2011). In bryophytes, gene density is distributed along the chromosomes more evenly than in angiosperms, where the chromosomes have distinct gene-rich regions at the ends and gene-sparse regions at the center (Lang et al. 2018; Diop et al. 2020; Li et al. 2020). Therefore, long blocks of spatially aggregated regions with many genes and low phylogenetic discordance might not be present in the peatmoss genome, or might be shorter and not detectable on the scale we used.

Taken together, the findings presented in Paper III strongly suggest that the combination of long-term effects of BGS and conserved genomic architecture has mainly shaped genome evolution in the studied species. Nonetheless, the relationships among differentiation, diversity and divergence also indicate strong effects of positive selection on the genome for at least some period of time in their evolutionary history. Some form of positive selection is required for strongly correlated differentiation landscapes in all species to evolve rapidly, as this is unlikely to happen just as a result of conserved genome structure or BGS alone (Burri 2017; Matthey-Doret and Whitlock 2019; Rettelbach et al. 2019; Stankowski et al. 2019). It has been shown that the effects of recurrent sweeps often accumulate with time, thereby traces of linked selection may also be explained by adaptations in ancestral populations (Munch et al. 2016; Phung et al. 2016). This explanation agrees very well with our results, since ancestral populations went through adaptation into diverse habitats during the rapid radiation of the genus (Shaw et al. 2010; Devos et al. 2016). Disentangling the relative importance of directional and background selection, ILS and gene flow for speciation is challenging (Fontaine et al. 2015; Vijay et al. 2016; Foote 2018; Stankowski et al. 2019), especially since all these processes occur recurrently during the speciation process. Moreover, at the later stages of speciation, genomic traces of earlier processes might become unidentifiable. Therefore, our findings provide evidence, rather than proof, for one or another.

Other processes affecting genome evolution

Whole-genome-duplication (WGD) represents an important mechanism in plant evolution (reviewed by Van de Peer et al. 2017, and Koenen et al. 2020). In angiosperms, WGD is very common, and provides morphological complexity, developmental innovations, and changes in important chemical pathways (reviewed by Rensing 2014). Evidence for WGD has been shown in many mosses (Rensing et al. 2007; Devos et al. 2016; Johnson et al. 2016; Lang et al. 2018), where it might have facilitated adaptation to distinct ecological environments (Gao et al. 2021) or triggered rapid radiations, as in the Hypnales (Johnson et al. 2016) and *Sphagnum* (Devos et al. 2016). The last WGD in *Sphagnum* preceded its rapid diversification burst, but might have contributed to the latter via differential retention of duplicates among species occurring in different habitats (Devos et al. 2016). In Paper II, we showed that the number of potentially mismapped duplicates regions, or paralogs, was very low in all species, and therefore would not substantially affect the phylogenetic inference and our tests for introgression. The effect of differential retention of paralogs on our analyses is less clear, since the proportion of such loci is unknown. Together with rapid diversification, WGD events might lead to ILS, and could cause phylogenetic incongruence at the deeper nodes (Koenen et al. 2020). Differential loss of gene copies might lead to longer internal branches, in which case QuIBL would overestimate gene flow (Edelman et al. 2019). Accordingly, we found higher gene flow with QuIBL than with D_{FOIL}, which is based on site patterns. Clearly, this problem should be addressed in future studies of *Sphagnum*.

Demographic events in evolutionary history are expected to broadly affect the genome as a whole, in comparison to much more narrow effects of natural selection (Stajich and Hahn 2005;

Schrider 2020). For instance, a recent bottleneck coupled with recurrent selection has been shown to strongly influence the genome in many organisms, including humans (Stajich and Hahn 2005), crucifers (Slotte et al. 2010), monkeyflowers (Stankowski et al. 2019), and poplar species (T. Ma et al. 2018), among others. During the Last Glacial Maximum, the Northern Hemisphere peatmoss species experienced dramatic bottlenecks (Kyrkjeeide et al. 2014). This must have affected the evolutionary history of the studied species, and complicates the interpretation of the results of our analyses in Paper II and III. Firstly, false-positive values may have been inferred in our D-statistic and D_{FOIL} tests due to certain population structure in the ancestral population, and different effective population sizes among the species (Zheng and Janke 2018). Secondly, the latter will also result in deviation from the expected relationships between phylogenetic discordance and the distribution of functional features in the genome (Slatkin and Pollack 2006). Finally, bottleneck events followed by population expansion can create a false signature of selection, and in particular, generate patterns resembling selective sweeps instead of BGS (reviewed in Schrider 2020). Since demographic events create deviations from the already unrealistic assumptions about evolutionary history used in most population genetic models, their effects are difficult to account for using most of the available methods. Therefore, comprehensive methods based on simulations should be used in future studies to reconstruct the demographic events in each species and their effect on genome evolution.

Conclusions and Outlook

The importance of gene flow in species diversification remains a core question in evolutionary biology and speciation research. The relative importance of gene flow, especially in rapidly radiated groups, is notoriously difficult to quantify, especially since intensive ILS muddies the detection of the gene flow signal. Peatmosses are an excellent model for addressing this question due to their recent rapid diversification, frequent hybridisation, ancient history, phenotypic and ecological plasticity, and small genome sizes. Based on our findings, the genomic landscape of diversification in peatmosses does not conform to the predictions of the speciation-with-gene-flow model. We showed that despite common interspecific hybridisation in peatmosses, there has been minimal recent gene flow among the species, suggesting that the genus has evolved strong reproductive barriers. Unless it leads to enforcing reproductive isolation, post-speciation introgression seems to play a minor role for speciation in peatmosses, in contrast to allopolyploidisation and, likely, ancient gene flow at the early stage of diversification. We described how peatmoss genomes were affected by extensive ILS, resulting from rapid radiation, which in turn might have been fueled by ancient introgression among the ancestral lineages. The presented findings contribute to the idea that evolutionary processes accompanying rapid radiation might be universal among bryophytes and other land plants. This study is therefore an important contribution to the emerging phylogenomic understanding of how speciation unfolds in hybridising, rapidly radiated species groups.

Correlated landscapes of differentiation, as described here, are another example of a growing body of evidence that genome evolution stems from an interplay between selection, ILS, and genomic architecture, and is propelled by gene exchange at its earlier stages. We hypothesise that the following is the most plausible scenario for the evolution of the diversification landscape in the studied species. The ancestor population was subjected to strong positive divergent selection, which led to recurrent selective sweeps and resulted in a heterogeneous variation landscape. Fueled by ancient gene flow, this led to diversification, and the newly formed lineages inherited the heterogeneous landscape of genetic variation. With time, signatures of positive selection were largely displaced by BGS, reproductive barriers were strengthened, and lineage sorting at linked sites with low recombination became more complete. These processes were substantially constrained by conserved genome structure, thereby leading to evolution of correlated genomic landscapes across the studied species.

There is an increasingly recognised need for applying modern genomic and phylogenomic methods in non-model plants and especially in bryophytes, which represent a basal clade in the phylogeny of land plants. The studies included in this thesis are the first example of using whole-genome sequencing data in peatmoss, and the second whole-genome-based population genomic study in bryophytes, providing valuable genomic resources for future studies of these incredibly interesting plants. There remain multiple knowledge gaps, important for understanding evolutionary processes related to introgression in peatmosses. Primarily, the genetic mechanisms of reproductive isolation in peatmosses must be characterised, to enable studying their evolution and the role of introgression in their establishment. Another important question is the timing of speciation events, as well as of past and recent introgression events and their adaptive potential. Also, reconstructing demographic history and the consequences of WGD in peatmosses can significantly facilitate population genomic analyses in this group. Answering these questions requires first and foremost obtaining high-quality genome assemblies and linkage maps in numerous species. This would also provide valuable information about the structure of the genome in different species. Finally, as we show in Paper I, expanding our knowledge about life-history traits in hybridising species can shed more light on why some species hybridise, while others do not.

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Paper I

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BioOne COMPLETE

Is interspecific gene flow and speciation in peatmosses (Sphagnum) constrained by phylogenetic relationship and life-history traits?

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Source: Lindbergia, 41(1)

Published By: Dutch Bryological and Lichenological Society and Nordic Bryological Society

URL: https://doi.org/10.25227/linbg.01107

Lindbergia 41: linbg.01107, 2018
doi: 10.25227/linbg.01107

Subject Editor and Editor-in-Chief: Nils Cronberg. Accepted 27 November 2018

Is interspecific gene flow and speciation in peatmosses (*Sphagnum*) constrained by phylogenetic relationship and life-history traits?

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Peatmosses are interesting for studies of speciation processes not only because of their frequent hybridization and recent diversification, but also their phenotypic diversity, ecological importance and ancient history. Diverse and widespread hybridization has been widely documented in the genus, but little is known about what factors underlie this phenomenon. We hypothesize that these factors include phylogenetic distance and variation in life-history traits of parental species. We summarize current knowledge about the occurrence of hybridization in peatmosses and explore how it is associated with phylogenetic distance and life-history trait variation of parental species. Possibly as much as one out of five (or more) peatmoss species hybridize, mostly producing allopolyploid hybrids. Parents of admixed haploids are more closely related to each other than parents of allopolyploids. Hybridization seems to be most frequent in 1) monoicous and polyoicous species exhibiting 2) relatively high sporulation frequency, 3) producing relatively small spores, as well as 4) growing in poor habitats. Surprisingly, neither phylogenetic proximity nor life-history trait variation explain patterns of hybridization in peatmosses, and other likely explanations for patterns observed are discussed.

Hybrid speciation has been acknowledged to be important for speciation and biological diversity in many organism groups (Levin and Kerster 1974), but has traditionally been considered to be of limited importance in explaining overall large-scale biodiversity (Mayr 1942, Ehrlich and Raven 1969, Levin 1981). More recently, accumulating evidence have revealed patterns of parapatric and sympatric speciation with past or ongoing gene flow in many taxa (Morjan and Rieseberg 2004, Arnold 2006, Feder et al. 2012). Ellstrand (2014) showed that in a diverse set of plants, interspecific gene flow is much more prevalent than what previously thought (Levin 1984), and polyploid hybridization is now acknowledged as one of the most common mechanisms of plant speciation (Soltis et al. 2009, 2014). For a glossary of genetic expressions see Box 1.

Numerous studies have demonstrated that hybridization is common across old, species-rich lineages of bryophytes and might have been one of the key factors underlying speciation in these plants (Wyatt et al. 1988, Natcheva and Cronberg 2004, Stenøien et al. 2011b, Shaw et al. 2015). One of the largest bryophyte genera, *Sphagnum* (peatmoss), has been extensively studied, and introgression, hybridization, polypoidization, reticulate evolution and cryptic speciation is common in the genus (Såstad et al. 2001, McDaniel and Shaw 2003, Natcheva and Cronberg 2007, Shaw 2008, Ricca et al. 2011).

One of the oldest known fossil remains of land plants is morphologically similar to extant peatmosses (Cardona-Correa et al. 2016), dated 455–454 Ma. Today *Sphagnum* includes almost 300 species (Michaelis 2011), often growing in peatlands which occupy in total ca 3% of terrestrial land, storing more carbon than any other plant genus (at least 25% of all terrestrial carbon, Yu et al. 2010, Glime 2017a). Peatmosses thus play a key role in global carbon balance and climate (Weston et al. 2015). Many peatmoss species are ecologically variable and exhibit high phenotypic plasticity (Stenøien et al. 2014). Genetic structure of modern peatmoss populations is shaped by past and on-going gene flow and intercontinental distributions of many species are thought to reflect high potential of dispersal in the genus (Sundberg 2000, Szövényi et al. 2008, Stenøien et al. 2011b, Karlin et al. 2013, Shaw et al. 2014, Kyrkjeeide et al. 2016b). There is a considerable species diversity in certain areas of the world (Goffinet and Shaw 2008), even though the last peak of diversification in peatmosses was surprisingly recent, only 7–20 Ma (Shaw et al. 2010). The combination of ancient history, recent diversification, high gene flow potential and

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Box 1. Genetic glossary

Gene flow: the movement of alleles between populations.
Genetic admixture: the integration of a genomic region from one population/species into the genome of another population/species, hereafter referred to as admixture.
Homoploid hybrid species: a species having resulted from homoploid hybrid speciation.
Homoploid hybrid speciation: speciation by interspecific hybridization without change in chromosome number.
Hybrid: an individual having resulted from hybridization.
Hybridization: the interbreeding of individuals from two distinct populations/species.
Introgression: gene flow between populations of different species.
Polyploidization: hybridization leading to formation of hybrid progeny with multiple sets of chromosomes.
Admixed individual: here referred to an individual showing evidence of admixture with another species of the same ploidy level, but not in itself considered as a taxonomically separate species.
Allopolyploid: a hybrid individual with ploidy level of two (or more), and having resulted from interspecific crosses.
Autopolyploid: a hybrid individual with ploidy level of two (or more), and having resulted from intraspecific crosses.

ecological variability makes peatmoss an interesting model for studying patterns and processes of speciation.

There is evidence of past and extant polyploid hybridization in peatmosses (examples discussed in details below), and possible mechanisms of polyploids formation are reviewed in detail elsewhere (Natcheva and Cronberg 2004, Såstad 2005). For instance, Devos et al. (2016) has revealed multiple whole genome duplication events in evolutionary history of Sphagnopsida, two of which could have contributed to the rapid diversification of peatmosses. Furthermore, numerous studies have described extant polyploid peatmoss species and many have emphasized the importance and relative commonness of hybridization and polyploidization within the genus (Karlin et al. 2009, Ricca et al. 2011, Shaw et al. 2012a, 2013, Karlin 2014). In contrast to angiosperms, interploidal hybridization is rather commonly observed in *Sphagnum* (Flatberg et al. 2006, Karlin et al. 2009, 2014). Nevertheless, we still do not know exactly the extent to which peatmosses experience interspecific gene flow, and even less about what factors promote the ability to hybridize in these plants.

Difference in mating system might have profound evolutionary implications in peatmosses (Stenøien and Såstad 1999, Szövényi et al. 2014, Johnson and Shaw 2015). The gametophyte, which is the dominant phase in the life cycle, carries sexual reproductive organs producing gametes mitotically. Most species are dioicous, i.e. unisexual (Wyatt and Anderson 1984), and the sexes must therefore grow in close proximity to be capable of sexual reproduction (Longton and Schuster 1983). Many species are monoicous (i.e. bisexual) and exhibit both outcrossing and intragametophytic selfing. Gametophytic sex expression seems to be a fixed trait in most peatmosses (Szövényi et al. 2009, Ricca et al. 2011), but many monoicous species may occur with separate male plants (i.e. they are andropolyoicous sensu Kyrkjeeide et al. 2018, hereafter referred to as polyoicous). Mating system might not in itself affect allelic diversity (Stenøien and Såstad 2001), but in haploid-dominant plants 'selfers' diversify faster and seem more effective in purging genetic load compared to 'outcrossers' (McDaniel et al. 2013, Szövényi et al. 2014). In addition, mating system strongly influences sporulation frequency in mosses (Longton 1992), that could in turn affect gene flow rates, since frequently sporulating monoicous and polyoicous species might have a higher gene flow potential than less frequently sporulating dioicous species (Stenøien and Såstad 1999, 2001).

As a result of sexual reproduction, a diploid sporophyte develops on a mother gametophyte, where spore mother cells undergo meiosis and produces spores. Mature spores are explosively discharged via so-called air-gun mechanism (Nawaschin 1897, Goffinet and Shaw 2008, Sundberg 2010b). Spores are easily dispersed by wind and can eventually establish by germination and production of a protonema, which gives rise to one or more genetically identical gametophytes. Peatmoss species exhibit considerable variation in spore size and colour (Sundberg and Rydin 1998). Compared to larger spores, small spores remain viable longer (Sundberg and Rydin 2000), and provide a dispersal advantage over short distances (Sundberg 2010a). Spore colour is associated with viability of spores after the dispersal event, because it might influence resistance to mutagenic effect of UV light (Sundberg and Rydin 2000). Consequently, spore size and colour might affect levels of gene flow.

It has been shown, that pre- and postzygotic isolation between lineages tends to increase with time (Coyne and Orr 1997). Interspecific hybridization should then be more likely in closely related species, which have not developed reproductive barriers. Establishment of postzygotic barriers is shown to often take very long time in plants (probably, millions of years), especially for plants with long generation times (Levin 2012). Peatmoss species are long-lived and we can therefore expect hybridization to occur even between non-sister species. High genetic divergence between parents may actually facilitate allopolyploidization by prevention of normal chromosome pairing during meiosis in hybrids (reviewed by Karlin et al. 2014).

It is currently unclear how phylogenetic distance and life-history traits influence the occurrence of interspecific hybridization in peatmosses. In this paper we aim to 1) summarize evidence of hybridization in peatmosses, 2) explore how phylogenetic distance and life-history traits are associated with hybridization and interspecific gene flow, and 3) discuss in what way interspecific gene flow can influence speciation in peatmosses. To address these questions, we use results from published literature to first identify hybrid species and their parents, and then do comparative analyses to identify how different factors contribute to the occurrence and commonness of hybridization.

Material and methods

Data collection and summarizing

We first gathered reports already known to us with evidence for interspecific gene flow and polyploidy between peatmoss species. References from those papers were checked to identify other possible papers. Then, we conducted a literature search using the Web of Science Core Collection online database (ver. 5.26.2, Web of Science, Clarivate Analytics 2017) and in Google Scholar for articles published between 1960 and 2017. We searched for different combinations of such terms as 'Sphagnum', 'peatmoss', 'introgression', 'hybridization', 'hybrid', 'polyploid' and 'admixture'. We performed the search in November 2017 but did not find new papers in addition to those we had collected earlier. To differentiate between reported cases of hybridization, we assigned the cases to the following groups: allopolyploid hybrids, admixed haploid individuals (hereafter – admixed individuals) and homoploid hybrids (see Glossary in Box 1).

Based on the collected information, we calculated a minimum coefficient of hybridization for each subgenus as the ratio of the number of identified hybridizing species to the total number of species within the subgenus. We also collected information about certain life-history traits of the identified parental species: mating system type, observed frequency of sporulation, spore colour, position of a species along the mire water table ('hummock–hollow') and the nutrient ('poor–rich') gradients (Eddy 1985, McQueen and Andrus 2007, Flatberg 2013, Johnson 2013, Kyrkjeeide et al. 2018), and maximum and minimum spore size (Suzuki 1958, McQueen and Andrus 2007, Kyrkjeeide et al. 2018). Mire is here used in a wide sense, also including moist heaths and forests.

Estimation of phylogenetic distance between the parents

We found no published phylogenetic tree including all species of interest that matched our objectives. In order to summarize the phylogeny of parental species, we constructed a composite cladogram using all available published phylogenetic trees containing species of interest. The cladogram was visualized with Dendroscope (ver. 3.5.8, Huson and Scornavacca 2012). In several cases, one or both parents could not be unambiguously identified. For example, there are 22 observed cases of species from subgenus *Subsecunda* being involved in hybridization, but parental species were only determined to subgenus in 11 cases, and to a species complex in two cases. As no information about the specific position in the phylogeny is available in these cases, we combined them for each subgenus into one 'unknown species' and placed it within the subgenus on the composite cladogram in order to visualize all reported evidence of hybridization simultaneously. Assuming, that all these unknown species represent different species, we added these cases to the number of unequivocally identified parental species in a subgenus. We then calculated a maximum hybridization coefficient by dividing this number by the total number of species in a subgenus. In this way, we can get an overview of the possible upper extent of hybridization for each subgenus.

The composite cladogram unites a broad spectrum of species from different subgenera, but it does not include many species within subgenera. Parental species might thus seem to be more related within subgenera than they actually are. Due to this, we counted the number of nodes separating parental species in each possible tree, and calculated the average number for each parental species pair as a measure of phylogenetic distance between the parents (Vellend et al. 2010). Because not all parents were identified, we estimated phylogenetic distances for 22 parental species pairs. The portion of the inter-subgeneric hybrids among these species pairs was the same as in the general sample.

Comparative analysis

We were interested in testing for associations between occurrence of hybridization on one hand, and life-history traits of the parental species on the other. Hence, we combined a dataset with seven life-history traits of parental species listed above with two additional factors: subgenus and intensity of hybridization, which corresponds to the number of hybrid species produced by each individual parental species. *Sphagnum australe*, *S. irritans*, *S.* 'sp-3' (Shaw et al. 2015) and *S.* 'sp-4' (Shaw et al. 2015) were excluded from the analysis because most of their life-history traits are unknown. As our data set contained both categorical and continuous variables, we explored it with factorial analysis of mixed data (FAMD) using the FactoMineR package in R (Lê et al. 2008), and used the missMDA package in R (Josse and Husson 2016) to account for missing trait values within some species. All analyses were conducted and visualized in the R statistical environment (ver. 3.4.1, <www.r-project.org>).

Results

Occurrence of interspecific hybridization

There are 36 documented allopolyploid hybrids, seven cases of genetic admixture and one case of homoploid hybridization in our data set, respectively (Table 1, Fig. 1). Peatmoss autopolypoids have not been registered, although Shaw et al. (2012b) discuss potential autopolyploidy of diploid *Sphagnum tescorum* based on registered genetic admixture between parental *S. fimbriatum* and *S. girgensohnii*, which in turn might be the second evidence of homoploid hybridization for the genus. So far, we treat the latter as an example of admixture. The parentage is completely unknown for five allopolyploid hybrids and partially unknown for 18 allopolyploid and admixed hybrids. In total, there are 37 parental species, each producing from one to four hybrids (Fig. 2A, Table 2). Some species are involved in both admixture and polyploid hybridization (Table 2). Hybridization events often occur within subgenera, but as many as 13 out of 39 hybrids are the results of inter-subgeneric crosses (Table 1, Fig. 1).

Hybridization is common in all subgenera, and the fraction of species hybridizing varies from 9 to 20% (Fig. 2B). The maximum coefficient of hybridization is of the same magnitude and reaches 27% in *Cuspidata*, while the lowest coefficient is observed in subgenus *Sphagnum*, but here parentage is unknown for half of the registered hybrid species. In general, up to one out of five (21%) of peatmoss species potentially hybridize.

Table 1. Polyploid hybrids and admixed haploid individuals registered in *Sphagnum*. Phylogenetic distance calculated as a number of nodes separating species in published phylogenetic trees (see 6, References). We refer to all studies which include information about 1) taxonomic status, 2) parentage, 3) ploidy level and/or 4) phylogenetic trees with the species of interest, which were used to obtain phylogenetic distance estimates. * – homoploid hybrid, NA – data is not available.

1. Subgenus	2. Hybrid species	3. Ploidy level	4. Parental species	5. Phylo-genetic distance	6. References
Sphagnum	*S.* × *alaskense*	2	unknown	NA	Kyrkjeeide et al. 2016a
	S. × *centrale*	2	unknown	NA	Temsch et al. 1998, Karlin et al. 2010a
	S. × *cristatum*	2	unknown	NA	Karlin et al. 2008
	S. × *palustre* (including *S. henryense)*	2	unknown	NA	Bryan 1955, Temsch et al. 1998, Shaw et al. 2008, Karlin et al. 2010a
	S. × *papillosum*	2	unknown	NA	Temsch et al. 1998, Karlin et al. 2010b
	S. austinii × *S. affine*	1	*S. austinii* × *S. affine*	2	Shaw and Goffinet 2000, Thingsgaard 2002, Johnson 2013, Johnson et al. 2015
	S. medium × *S. divinum*	1	*S. medium* × *S. divinum*	1.3	Kyrkjeeide et al. 2016a, Yousefi et al. 2017, Hassel et al. 2018
Sphagnum × *Rigida*	*S.* × *australe*	2	*S.* cf. *strictum* (subgenus *Rigida*) × subgenus *Sphagnum* (unknown species)	NA	Karlin et al. 2009, Karlin 2014, Shaw et al. 2016
Sphagnum × *Acutifolia*	*S.* × *australe*	3	*S. australe* (2n) × *S. fimbriatum*	5.9	Karlin et al. 2009, Karlin 2014
Sphagnum × *Subsecunda*	*S.* × *cucculiforme*	?	unknown *Sphagnum* (Neotropical, maternal) × uknown *Subsecunda*	NA	Crum 1987, Shaw and Goffinet 2000, Karlin et al. 2010b
Cuspidata	*S.* × *jensenii*	2	*S. balticum* × *S. annulatum*	6.5	Såstad et al. 1999, Johnson 2013, Johnson et al. 2015
	S. × *majus*	2	*S. cf. cuspidatum* × unknown *Cuspidata*	NA	Såstad et al. 2000
	S. × *torreyanum*	2	*S. cuspidatum* × unknown *Cuspidata (S. recurvum?)*	NA	Shaw et al. 2009, Karlin et al. 2014
	S. × *troendelagicum*	2	*S. balticum* × *S. tenellum*	4	Såstad et al. 2001, Stenøien et al. 2011a
	S. angustifolium × *S. flexuosum*	1	*S. angustifolium* × *S. flexuosum*	3.4	Såstad et al. 1999, 2001, Johnson 2013, Szurdoki et al. 2014, Karlin et al. 2014, Johnson et al. 2015
	S. × *irritans*	2	unknown *Cuspidata* × unknown *Subsecunda* (maternal)	NA	Karlin et al. 2009, 2013, Karlin and Robinson 2017
	S. × *falcatulum*	3	*S. irritans* × *S. cuspidatum*	5.2	Karlin et al. 2009, Karlin 2014
	S. × *mendocinum*	2	unknown *Cuspidata* × unknown *Subsecunda*	NA	Shaw and Goffinet 2000, Karlin et al. 2010b
Cuspidata × *Subsecunda*	*S.* × *slooveri*	2	*S. cf. recurvum* × *Subsecunda (S. africanum* complex)	7	Shaw 2000, Karlin et al. 2014, Karlin 2014
	S. × *planifolium 1*	3	*S. slooveri* × *Subsecunda (S. capense* complex*)*	4	Karlin et al. 2014
	S. × *planifolium 2*	3	*S. slooveri* × *S. cuspidatum*	5	Karlin et al. 2014
	S. × *lenense*	2	*S. lindbergii* × unknown *Subsecunda*	NA	Shaw et al. 2016
	S. × *contortum**	1	unknown *Cuspidata* × unknown *Subsecunda*	NA	Shaw et al. 2016
	S. contortum × *S. subsecundum*	1	*S. contortum* × *S. subsecundum*	NA	Ricca and Shaw 2010, Shaw et al. 2012a
	S. × *carolinianum*	2	*S. lescurii* × unknown *Subsecunda*	NA	Ricca et al. 2008, Shaw et al. 2012a
	S. × *guwassanense*	2	*S. inexspectatum/orientale* (female) × unknown *Subsecunda*	NA	Shaw et al. 2013

(Continued)

Table 1. Continued

1. Subgenus	2. Hybrid species	3. Ploidy level	4. Parental species	5. Phylo-genetic distance	6. References
	S. × *inundatum*	2	*S. auriculatum* × *S. subsecundum*	1	Ricca et al. 2008, Shaw et al. 2012a, b, Karlin et al. 2013
	S. × *missouricum*	2	*S. lescurii* × *S. subsecundum*	5	Ricca and Shaw 2010, Shaw et al. 2012a
	S. × *triseriporum*	2	*S. inexspectatum/orientale* (maternal) × unknown *Subsecunda*	NA	Shaw et al. 2013
Subsecunda	*S.* × *perfoliatum*	2	*S. orientale/inexspectatum* × unknown *Subsecunda*	NA	Shaw et al. 2015
	S. ×*"microporum"*	2	*S. kushiroense/microporum* × *S. miyabeanum*	4.7	Shaw et al. 2015
	S. ×"sp-5"	2	*S.* 'p-3' × *S.* 'sp-4'	1.3	Shaw et al. 2015
	S. × *platyphyllum* 2n	2	S. *platyphyllum* × unknown *Sphagnum*	NA	Ricca and Shaw 2010, Shaw et al. 2012a
	S. × *missouricum* × *S. lescurii*	3, 4	*S.* × *missouricum* × *S. lescurii*	1	Ricca and Shaw 2010, Ricca et al. 2011
Acutifolia × *Subsecunda*	*S.* sp. nov.	3	*S. incundum* × unknown *Subsecunda*	NA	Kyrkjeeide et al. 2018
	S. × *arcticum*	2	*S. incundum* × unknown *Acutifolia*	NA	Greilhuber et al. 2003, Shaw et al. 2005, Kyrkjeeide et al. 2018
	S. × *olafii*	2	*S. incundum* × unknown *Acutifolia*	NA	Greilhuber et al. 2003, Shaw et al. 2005, Kyrkjeeide et al. 2018
	S. russowii	2	*S. girgensohnii* × *S. rubellum*	7.8	Cronberg 1996a, Temsch et al. 1998, Shaw 2000, Shaw et al. 2005, 2016, Kyrkjeeide et al. 2018
	S. × *girgensohnii* × *S. russowii*	3	*S. girgensohnii* × *S. russowii*	6.6	Shaw et al. 2005, Flatberg et al. 2006, Karlin 2014, Kyrkjeeide et al. 2018
Acutifolia	*S.* × *skyense*	2	*S. quinquefarium* × *S. subnitens*	4.4	Shaw 2000, Shaw et al. 2005, Karlin 2014, Kyrkjeeide et al. 2018
	S. × *tescorum*	2	*S. girgensohnii* × *S. fimbriatum*	2	Shaw 2000, Shaw et al. 2005, 2012b, Karlin 2014, Kyrkjeeide et al. 2018
	S. capillifolium × *S. rubellum*	1	*S. capillifolium* × *S. rubellum*	3.4	Cronberg 1997, 1998, Shaw and Goffinet 2000, Natcheva and Cronberg 2003, Shaw et al. 2005, 2016, Johnson 2013, Johnson et al. 2015, Kyrkjeeide et al. 2018
	S. capillifolium × *S. warnstorfii*	1	*S. capillifolium* × *S. warnstorfii*	4	Cronberg 1997, Shaw and Goffinet 2000, Natcheva and Cronberg 2003, Shaw et al. 2005, Johnson 2013, Johnson et al. 2015, Kyrkjeeide et al. 2018
	S. capillifolium × *S. quinquefarium*	1	*S. capillifolium* × *S. quinquefarium*	3.2	Shaw 2000, Natcheva and Cronberg 2007, Karlin 2014, Kyrkjeeide et al. 2018

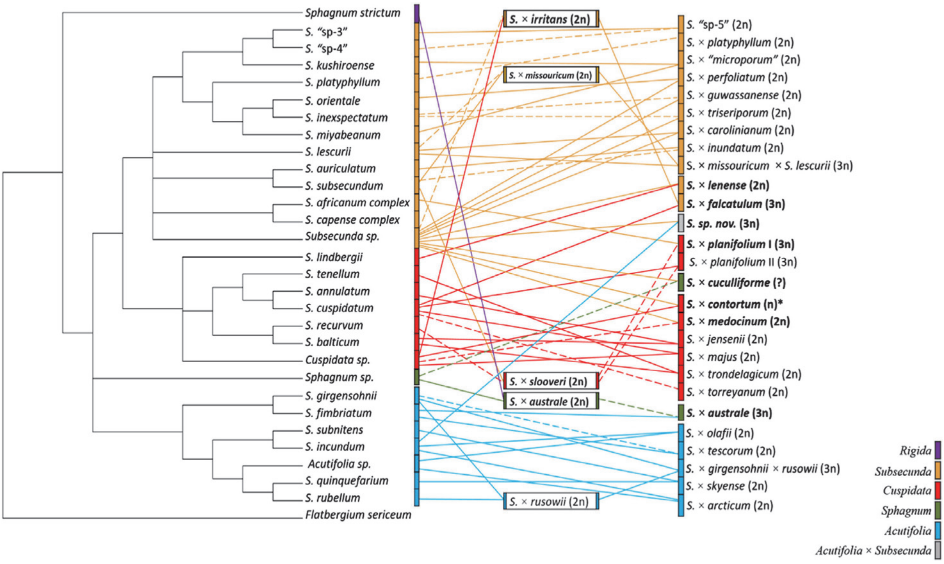

Figure 1. Hybridization in *Sphagnum*. All cases of allopolyploid and homoploid hybridization (species to the right) when at least one parent was identified (species to the left). Other cases, including admixture, are listed in Table 1. Coloured bars indicate subgenera as showed in the lower right corner. Dashed lines correspond to maternal parents, solid lines – to paternal or unidentified parents. Ploidy level is stated in brackets and otherwise is 1n, * – homoploid hybrid. Intersubgeneric hybrids are in bold, some of these hybrids are assigned to that subgenus, which their maternal plant belongs to. For references see Table 1.

Phylogenetic distance of parental species and life-history trait analysis

The majority of allopolyploid hybrids are produced by non-sister species, with a mean phylogenetic distance of 4.68 (SE = 0.56) nodes between parental species (Fig. 3). Distributions of phylogenetic distances between parents do not deviate from normal distribution (Shapiro test, p = 0.43 and p = 0.36 for parents of the allopolyploid hybrids and the admixed individuals, respectively). The average phylogenetic distance between parents of admixed individuals seems lower than between parents of allopolyploids, albeit insignificantly so (2.88 (SE = 0.41) versus 4.68 (SE = 0.56) nodes, respectively, Student's t-test, p = 0.06).

The FAMD based on the collected life-history trait information (Table 2) shows that subgenus and spore colour contribute the most to the variation in characters between parental species, followed by maximum spore size, mating system and sporulation frequency (Table 3). The contribution of spore colour to axis 1 is 23.1%, and contribution of the maximum spore size variable to axis 2 is 23.6% (Table 3). Contribution of subgenus variable to axis 1 and axis 2 is 23.4% and 16.7%, respectively (Table 3). The intensity of hybridization explains 2.6% of variance between species. Although we distinguish several groups, species producing different number of hybrids are scattered evenly across all of them (Fig. 4A). The FAMD individual factor plot shows that intensity of hybridization tends to be associated with polyoicous and monoicous reproductive systems, high sporulation frequency, poor habitats (low pH and few minerals), small spore sizes and high position along the water table (Fig. 4B). Data on spore sizes and sporulation frequency is unavailable for many parental species, because they are rarely or never observed with sporophytes.

Discussion

Occurrence and a potential role of interspecific gene flow in speciation of peatmosses

The majority of hybrids in peatmosses result from allopolyploid hybridization (82%). Polyploidy represents a very important mechanism of speciation in these plants, and this seems primarily related to immediate postzygotic reproductive isolation between hybrid progeny and parents (Ricca and Shaw 2010, Abbott et al. 2013). Despite this, complete reproductive isolation is sometimes not established, and polyploids are able to backcross with their parents, preventing the establishment of new 'distinct evolutionary lineages' and also increasing the genetic diversities of both polyploid and parental species. In peatmosses, several allopolyploids are reported to undergo interploidal backcrossing with haploid parents (e.g. *Sphagnum russowii, S. troendelagicum, S. missouricum*, Flatberg et al. 2006, Ricca et al. 2011, Stenøien et al. 2011a).

It has been suggested that high levels of fixed heterozygosity can increase ecological amplitudes in hybrid plant taxa, even beyond the habitat and niche limitations of the parents (Levin 2002). Well-established allopolyploid species are relatively often found in habitats which parental species do not occupy. From this perspective, it seems that environmental heterogeneity can promote and contribute to the establishment of new hybrid species (Brochmann et al.

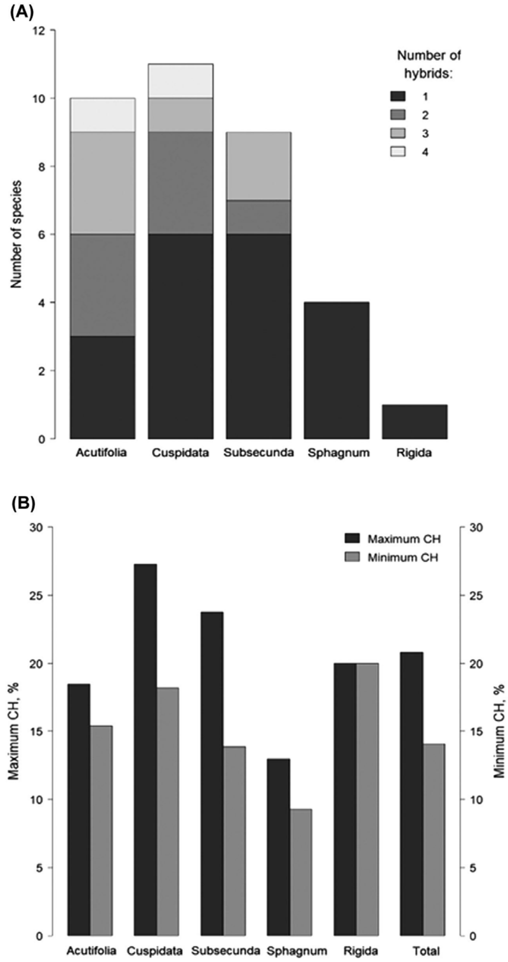

Figure 2. Characteristics of hybridization across *Sphagnum* subgenera. (A) Intensity of hybridization across *Sphagnum* subgenera. Intensity of hybridization corresponds to the number of hybrids produced by an individual parental species. Bars on the X-axis represent subgenera, coloured according to the number of hybrid species produced by individual parental species as shown on the right. Y-axis represent number of parental species of each category within subgenera. Inter-subgeneric hybrid parents are assigned to that subgenus, which their maternal plants belongs to. (B) Occurrence of hybridization across *Sphagnum* subgenera. Maximum CH – the maximum coefficient of hybridization counted as the ratio of the maximum possible number of parental species to the total number of species in a subgenus. Minimum CH – the minimum coefficient of hybridization counted as the ratio of the number of the identified parental species to the total number of species in a subgenus.

2004, Abbott et al. 2013). This might be the case for several peatmoss allopolyploids, for example *S. missouricum* and *S. australe* (Shaw et al. 2012a, Karlin et al. 2014). It could also be the other way around, when ecological divergence originates after the establishment of new species (Abbott et al. 2010). Polyploid plants are often characterized by greater vigour compared to their diploid progenitors, possibly facilitating their dispersal to and establishment in new habitats (Grant 1981). Brochmann et al. (2004) suggested that polyploid arctic plants might have been more successful in colonizing areas after the last glaciation than diploids, because fixed highly heterozygous duplicated genomes of polyploids contain much of the ancestral diversity. In peatmosses, an increase of genetic diversity through polyploidization has been hypothesized to facilitate successful colonization of new habitats in allotriploid *S. falcatulum* (Karlin et al. 2014). Genetic diversity and frequency of polyploids in populations can also be increased via recurrent polyploidization, which thus may play an important role in the successful establishment of polyploid lineages (Ricca and Shaw 2010). This is probably the case for several peatmoss polyploids which have originated more than once, e.g. *S. russowii* (Shaw et al. 2005), *S. jensenii* (Såstad et al. 1999), *S. carolinianum* (Ricca et al. 2008), *S. falcatulum* and *S. australe* (Karlin 2014).

Registered admixture between peatmoss species might result from hybrid speciation sensu stricto, but introgression in itself is not evidence of successful speciation. In order for speciation to take place, more complete reproductive isolation between newly formed admixed lineages and parental species must subsequently develop (Abbott et al. 2013). Nonetheless, extensive genomic admixture clearly indicates an early phase in speciation. In peatmosses, one case of admixture (*S. girgensohnii* and *S. fimbriatum*) presumably resulted in polyploidization and subsequent establishment of a separate species, *S. tescorum* (Shaw et al. 2012b). In other cases, however, observed admixture is an ongoing process in zones of contact, which does not affect distinctiveness of parental gene pools, as for *S. capillifolium* × *S. warnstorfii* (Cronberg 1997), *S. capillifolium* × *S. quinquefarium* (Cronberg and Natcheva 2002), *S. capillifolium* × *S. rubellum* (Cronberg 1996b), *S. angustifolium* × *S. flexuosum* (Szurdoki et al. 2014), or is a consequence of secondary contact, as for *S. magellanicum* expanse × *S. magellanicum* margin (cf. Yousefi et al. 2017, *S. divinum* and *S. medium*, respectively, in Hassel et al. 2018). There are also examples of past hybridization events, e.g. *S. rubellum* × *S. capillifolium* (Natcheva and Cronberg 2003) and *S. austinii* × *S. affine* (Thingsgaard 2001). The latter has been suggested to represent an example of past adaptive introgression (Thingsgaard 2001). Comparing to allopolyploid hybridization, admixture and homoploid hybridization in peatmosses might be underestimated since hybrid individuals remain undetected because of their morphological resemblance to one of the parents.

The age of admixed taxa can be important for distinguishing hybrid speciation from more or less "neutral" admixture (Abbott et al. 2013). Yet, there is modest information available about the age of hybrid taxa in peatmosses, particularly for admixed hybrids. Several allopolyploid species seem to have originated before the last glaciation maximum, e.g. *S. troendelagicum* (Stenøien et al. 2011a); *S. guwassanense*, *S. triseriporum* (Shaw et al. 2013); *S. alaskense* (Kyrkjeeide et al. 2016a), while others probably are of more recent origin, e.g. *S. jensenii* (Såstad et al. 1999), *S. falcatulum* (Karlin et al. 2013) and both the diploid and

Table 2. Reproductive and microhabitat characteristics of identified parental species. Key to the columns abbreviations: 5 – Number of hybrid species produced by the parental one (Table 1); 6 – Reproductive system: m – monoicous, d – dioicous, p – polyoicous (including andro-polyoicous species sensu Kyrkjeeide et al. 2018, i.e. which are reported with separate male plants, but with certainty not with pure female plants); 7 – Sporulation frequency: F – frequent, R – rare; 8 – Position along the water table ('hummock–hollow') mire gradient: H – hummock, L – lawns/carpets, I – intermediate (both in hummocks and lawns/carpets); 9 – Position along the nutrient ('poor–rich') mire gradient: R – rich fen habitat, P – poor fen and bog habitat, I – intermediate fen; 10 – Spore colour, sources: Eddy 1985, McQueen and Andrus 2007, Flatberg 2013, Johnson 2013, Hassel et al. 2018, Kyrkjeeide et al. 2018; 11 – Maximum spore size, µm; 12 – Minimum spore size, µm, sources: Suzuki 1958, McQueen and Andrus 2007, Kyrkjeeide et al. 2018; * – homoploid hybrid; ♂ – male parent of the hybrid, ♀ – female parent of the hybrid; NA – data is not available. Mire is here used in a wide sense, also including moist heaths and forests.

1. No	2. Parental Species	3. Subgenus	4. Produced hybrid species	5	6	7	8	9	10	11	12
1	*Sphagnum strictum*	*Rigida*	*S.* × *australe* (2n)	1	m	F	I	P	yellow-brown	31	43
2	*S. medium*	*Sphagnum*	*S. medium* × *S. divinum* (n)	1	d	R	I	P	yellow-brown	NA	NA
3	*S. divinum*	*Sphagnum*	*S. medium* × *S. divinum* (n)	1	d	R	H	P	yellow-brown	21	31
4	*S. austinii*	*Sphagnum*	*S. austinii* × *S. affine* (n)	1	d	R	H	P	light-brown	23	28
5	*S. affine*	*Sphagnum*	*S. austinii* × *S. affine* (n)	1	d	F	I	I	yellow-brown	27	31
6	*S. annulatum*	*Cuspidata*	*S.* × *jensenii* (2n)	1	d	R	L	I	light-brown	25	32
7	*S. balticum*	*Cuspidata*	*S.* × *jensenii* (2n) *S.* × *troendelagicum* (2n) ♂	2	d	F	I	P	yellow	25	33
8	*S. tenellum*	*Cuspidata*	*S.* × *troendelagicum* (2n) ♀	1	p	F	L	P	yellow	27	44
9	*S. cuspidatum*	*Cuspidata*	*S.* × *falcatulum* (3n) *S.* × *planifolium* (3n) ♂ *S.* × *majus* (2n) *S.* × *torreyanum* (2n)	4	d	R	L	P	light-brown	29	38
10	*S. recurvum*	*Cuspidata*	*S.* × *slooveri* (2n)	1	d	R	I	P	light-brown	22	28
11	*S.* × *slooveri*	*Cuspidata*	*S.* × *planifolium1* (3n) ♀ *S.* × *planifolium2* (3n) ♀	2	d	NA	NA	NA	NA	NA	NA
12	*S. lindbergii*	*Cuspidata*	*S.* × *lenense* (2n)	1	p	F	L	P	yellow-orange	22	40
13	*S. angustifolium*	*Cuspidata*	*S. angustifolium* × *S. flexuosum* (n)	1	d	F	I	I	light-brown	21	25
14	*S. flexuosum*	*Cuspidata*	*S. angustifolium* × *S. flexuosum* (n)	1	d	R	I	I	light-brown	23	25
15	*S. lescurii*	*Subsecunda*	*S.* × *carolinianum* (2n) *S.* × *missouricum* (2n) ♀ *S.* × *missouricum* × *S. lescurii* (3n, 4n)	3	d	R	L	I	NA	27	34
16	*S. inexspectatum*	*Subsecunda*	*S.* × *guwassanense* (2n) ♀ *S.* × *triseriporum* (2n) ♀	2	d	NA	I	I	NA	36	39
17	*S. auriculatum*	*Subsecunda*	*S.* × *inundatum* (2n) ♂	1	d	R	I	I	light-brown	NA	NA
18	*S. subsecundum*	*Subsecunda*	*S.* × *inundatum* (2n) ♀ *S.* × *missouricum* (2n) ♂ *S.* × *contortum* ♀ × *S. subsecundum* (n)	3	d	R	I	R	light-brown	30	35
19	*S. orientale*	*Subsecunda*	*S.* × *perfoliatum* (2n)	1	d	R	I	R	light-brown	NA	NA
20	*S. kushiroense*	*Subsecunda*	*S.* × *'microporum'* (2n)	1	d	R	L	NA	NA	NA	NA
21	*S. miyabeanum*	*Subsecunda*	*S.* × *'microporum'* (2n)	1	d	R	L	NA	NA	NA	NA
22	*S.* × *missouricum*	*Subsecunda*	*S.* × *missouricum* × *S. lescurii* (3n, 4n)	1	d	R	I	I	NA	NA	NA
23	*S. platyphyllum*	*Subsecunda*	*S.* × *platyphyllum* (2n) ♀	1	d	R	L	R	brownish	23	35
24	*S.* × *contortum**	*Subsecunda*	*S.* × *contortum* × *S. subsecundum* (n)	1	d	R	I	R	light-brown	22	28
25	*S. fimbriatum*	*Acutifolia*	*S.* × *australe* (3n) ♂ *S.* × *tescorum* (2n) *S. fimbriatum* × *S. girgensohnii* (n)	3	p	F	I	R	yellow-brown	20	27
26	*S. rubellum*	*Acutifolia*	*S.* × *rusowii* (2n) *S. capillifolium* × *S. rubellum* (n)	2	d	R	I	P	yellow-brown	18	33
27	*S. girgensohnii*	*Acutifolia*	*S.* × *rusowii* (2n) *S.* × *girgensohnii* × *S. rusowii* (3n) *S.* × *tescorum* (2n) ♀ *S. fimbriatum* × *S. girgensohnii* (n)	4	d	R	H	P	yellow-brown	21	27
28	*S. russowii* 2n	*Acutifolia*	*S.* × *girgensohnii* × *S. rusowii* (3n)	1	d	R	I	P	yellow-brown	18	33
29	*S. quinquefarium*	*Acutifolia*	*S.* × *skyense* (2n) *S.* × *capillifolium* × *S. quinquefarium* (n) ♀	2	p	F	H	P	yellow-brown	19	27
30	*S. subnitens*	*Acutifolia*	*S.* × *skyense* (2n)	1	m	F	I	I	yellow-brown	22	32
31	*S. incundum*	*Acutifolia*	*S.* × *artcticum* (2n) *S.* × *olafii* (2n) S. sp. nov. (3n)	3	p	R	I	R	yellow-brown	24	29
32	*S. capillifolium*	*Acutifolia*	*S.* × *capillifolium* × *S. quinquefarium* (n) ♂ *S. capillifolium* × *S. warnstorfii* (n) *S. capillifolium* × *S. rubellum* (n)	3	p	F	H	P	yellow-brown	20	28
33	*S. warnstorfii*	*Acutifolia*	*S. capillifolium* × *S. warnstorfii* (n)	1	d	R	I	R	light-brown	17	26

triploid *S. australe* cf. Karlin et al. (2009). For admixed hybrids the age is only estimated for those formed between *S. divinum* and *S. medium*, which seem to be around 20 000 years old (Yousefi et al. 2017).

Abbott et al. (2013) point out that admixed individuals resulted from secondary contact can evolve into a separate species by occupying a niche not yet occupied by its parents. Early homoploid hybrid plant lineages are characterized

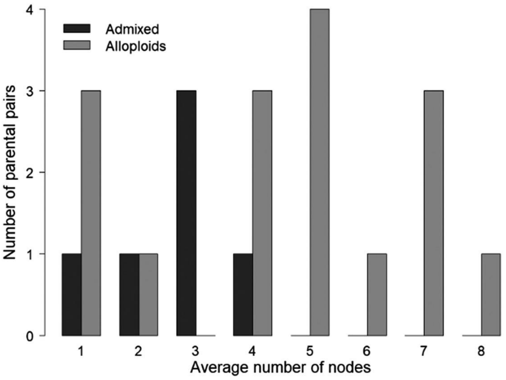

Figure 3. Phylogenetic distance between parental species in *Sphagnum*. X-axis represents averaged rounded number of nodes separating identified parental species pair in published phylogenetic trees, Y-axis represents counts of parental species pairs with the corresponding number of nodes. Dark grey bars represent counts for parents of admixed haploid individuals, light-grey bars – parents of allopolyploid hybrids as showed on the right. n = 22 species pairs.

by rapid and sometimes large-scale changes in gene expression patterns, which might increase phenotypic novelty and facilitate differentiation into new species (Abbott et al. 2010). Even if reproductive barriers are not complete at the initial stage of speciation, environmental based (exogenous) selection can maintain the distinctness of hybrid species. It is, however, not clear whether admixed peatmoss hybrids occupy different ecological spaces and are reproductively isolated from parents at any level. In addition, their morphological distinctiveness has not been examined in the majority of cases. Further research is thus needed to assess evolutionary significance of admixture observed in peatmosses and to define their taxonomical status.

Does phylogenetic distance explain occurrence of interspecific hybridization within the genus?

It has been suggested that certain degrees of genetic divergence between parents is required in order for allopolyploidization to occur as a result of impaired meiotic chromosome pairing in peatmosses (Natcheva and Cronberg 2007, Karlin et al. 2014). Although the only recorded homoploid hybrid species in peatmosses (*S. contortum*) is not included in our analysis because of unknown parentage, we do observe that parents of allopolyploids are less related compared to parents of haploid admixed individuals. At the same time, several allopolyploid hybrids are formed by closely related species, while several distantly related species are involved in admixture, which is not expected assuming that divergence ultimately leads to problems in meiosis during spore production. Patterns observed in allopolyploids and admixed species indicates that phylogenetic distance in itself does not define the success of interspecific crosses. It is worth noting that the homoploid *S. contortum* is thought to be an inter-subgeneric species, whose parents are rather distantly related. *Sphagnum contortum* also hybridizes inter-subgenerically with *S. subsecundum*, producing admixed individuals. But it cannot be ruled out that instead of being a homoploid hybrid, this species could have originated through polyploidization followed by chromosome number reduction, or also through introgression of genes between the subgenera and subsequent divergent speciation (Shaw et al. 2016).

Levin (2013) argues that low divergence between parents leads to formation of homoploids, whereas strong and modest divergence result in strict and segmental polyploids (i.e. allopolyploids whose chromosomes are partially homologous), respectively. These patterns are observed in vascular plants (Chapman and Burke 2007), and might also explain formation of allopolyploid hybrids by closely related parents in peatmosses. It is unclear whether these hybrids are strict or segmental polyploids since strict disomic inheritance usually serves as a null-hypothesis in revealing allopolyploids (Karlin and Smouse 2017). So far, evidence of recombination between parental genomes has only been registered in two allopolyploids: *S. tescorum* (Shaw et al. 2012b) and *S. palustre*, the latter a hybrid species with unknown parentage (Stenøien et al. 2014). Otherwise, recombination between parental genomes has only been reported for admixed haploid individuals (Natcheva and Cronberg 2007).

Do life-history traits explain intensity of interspecific hybridization?

We show that intensity of hybridization tends to be associated with polyoicous and monoicous reproductive systems, high sporulation frequency, poor habitats (low pH and low concentration of minerals), small spore size and light spore

Table 3. Contribution of the variables to the axes in the FAMD. * – Number of species produced by individual parental species.

Variable	Type	Contribution of a variable to the axes				
		Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Subgenus	categorical	23.66	16.76	26.30	46.78	32.11
Spore colour	categorical	23.18	12.34	12.97	4.17	9.51
Minimum spore size	continuous	13.23	6.42	1.16	0.13	7.02
Water gradient	categorical	12.68	5.08	14.11	6.58	22.65
Reproductive system	categorical	8.83	15.59	31.81	6.49	1.01
Nutrient gradient	categorical	8.25	4.87	3.33	27.07	6.15
Spore frequency	categorical	5.28	13.63	0.00	0.00	7.25
Maximum spore size	continuous	3.32	24.52	0.04	0.01	4.71
No_sp_prod*	continuous	1.59	0.80	10.28	8.78	9.59

colour. The latter is in line with theoretical expectations, as small spores and high sporulation frequency can give an advantage of dispersal to longer distances. More frequent hybridization found in monoicous and polyoicous species might result from their higher reproductive and dispersal success, and hence colonization ability, compared to dioicous species. Consequently, we can expect the portion of dioicous species to be smaller among hybridizing species than among non-parental species. This is indeed what we observe, even though we find that the difference is insignificant. Yet, one of the two species that have produced the highest observed number of hybrids is *S. cuspidatum*, a dioicous species which have the largest spores within the genus and rarely sporulate (Glime 2017b). According to the conducted FAMD, intensity of hybridization only explains about 2.6% of the total variance in life-history traits between species. Thus, other factors might certainly be more important in explaining the observed contradictions.

Johnson et al. (2015) showed a considerable phylogenetic signal for interspecific variation along the hummock–hollow gradient in peatlands. Based on this finding, we treat the position along the water table as a phylogenetically constrained trait and do not interpret how it is associated with intensity of hybridization. The same apparently applies to spore colour (Flatberg 2013). Phylogenetic constraints imply that traits of related species cannot be considered as

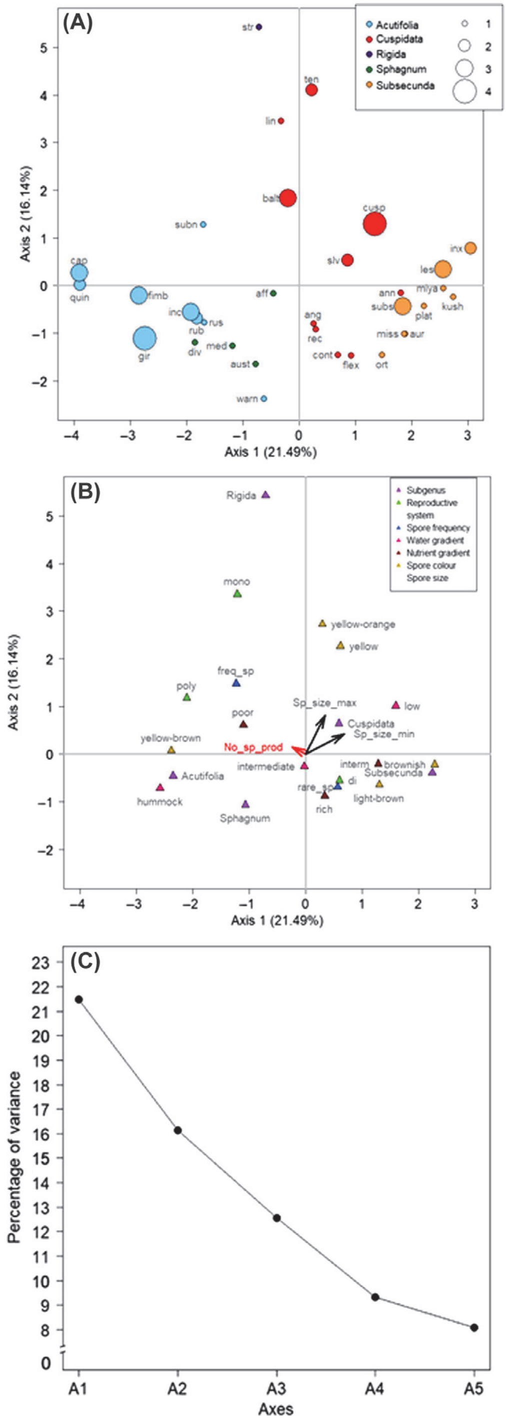

Figure 4. Two-dimensional FAMD plots for 33 parental species. Based on seven life-history variables (Table 2, column 6–12), as well as subgenus and intensity of hybridization as factors (Table 2,

Figure 4. Continued

column 3 and 5, respectively). Percentage of the variance explained by the axis is given along each axis. (A) Individual species plot. Size and colour of point markers corresponds to the number of hybrids produced by the species and to the subgenus, respectively, as showed on the upper right corner. Key to the species abbreviations: aff - *S. affine*, ang - *S. angustifolium*, ann - *S. annulatum*, aur - *S. auriculatum*, aust - *S. austinii*, balt - *S. balticum*, cap - *S. capillifolium*, cont - *S. contortum*, cusp - *S. cuspidatum*, div - *S. divinum*, fimb - *S. fimbriatum*, gir - *S. girghensonii*, inc - *S. incundum*, inx - *S. inexspectatum*, kush - *S. kushiroense*, les - *S. lescurii*, lin - *S. lindbergii*, med - *S. medium*, miss - *S. missouricum*, miya - *S. miyabeanum*, ort - *S. orientale*, pla - *S. platyphyllum*, quin - *S. quinquefarium*, rec - *S. recurvum*, rub - *S. rubellum*, rus - *S. russowii*, slv - *S. slooveri*, str - *S. strictum*, sub - *S. subnitens*, subs - *S. subsecundum*, warn - *S. warnstorfii*, ten - *S. tenellum.* (B) Individual factor plot for quantitative and qualitative variables. Shape and colour of point markers correspond to different variables used in analysis as showed on the upper right corner. Key to the factor abbreviations: Reproductive system: *di* – dioicous, *mono* – monoicous, *poly* – polyoicous (including andro-polyoicous species sensu Kyrkjeeide et al. 2018, i.e. which are reported with separate male plants, but with certainty not with pure female plants); Spore frequency: *freq_sp* – frequent sporulation, *rare_sp* – rare sporulation; Water gradient (i.e. position along the water table ('hummock–hollow') mire gradient): *hummock* – hummock, *low* – lawns/carpets, *intermediate* – intermediate (both in hummocks and lawns/carpets); Nutrient gradient (i.e. position along the nutrient ('poor–rich') mire gradient): *rich* – rich fen habitat, *poor* – poor fen and bog habitat, *interm* – intermediate fen. Mire is here used in a wide sense, also including moist heaths and forests. Black arrows correspond to maximum and minimum spore sizes, and the red arrow – to the number of species produced by individual parental species, according to the labels. (C) A scree plot from the FAMD: X-axis represents Axis 1–5 according to the labels, Y-axis represents the percentage of variance explained by the axis.

independent and identically distributed, by that violating assumptions of most of the statistical tests (Sober and Orzack 2001). Because of the amount and incompleteness of the available data, we were not able to account for relatedness in the FAMD. In light of this, it should be kept in mind that the relatedness between species might contribute to the patterns we observe.

Nevertheless, the association between more intensive hybridization and monoicous and polyoicous reproductive system, high sporulation frequency and smaller spores in peatmosses makes biological sense and provides a rationale for further testing. Unfortunately, there is lacking knowledge about mating system and other life-history traits in many parental and non-parental species. Available floras (Chien et al. 1999, McQueen and Andrus 2007, Flatberg 2013) list 104 *Sphagnum* species out of 289 species known worldwide (McQueen and Andrus 2007, Michaelis 2011), mostly describing the peatmoss diversity in the Northern Hemisphere. In particular, mating system is only known for 89 of the listed species, and the fraction of polyoicous species might be generally underestimated (Kyrkjeeide et al. 2018). To that end, it is likely that with more knowledge about the reproductive biology of peatmosses, we will be able to show the importance of these life-history traits for the occurrence of hybridization.

What other factors can potentially affect interspecific gene flow in *Sphagnum*?

There are other factors that might explain occurrence and intensity of interspecific hybridization in peatmosses, including levels of intraspecific gene flow. Generally, interspecific gene flow has been viewed insignificant compared to intraspecific rates of gene exchange (Mayr 1942, Ehrlich and Raven 1969). However, recent meta-analyses of a range of different organism groups show that distribution of interspecific and intraspecific rates of gene flow sometimes overlaps (Hey and Pinho 2012). Substantial intraspecific gene flow and frequent mating could in itself lead to frequent introgression between highly dispersing species in plants (Levin and Kerster 1974, Levin 1979), leading to a positive correlation between intra- and interspecific gene flow rates. Despite the high number of studies linking patterns of inter- and intraspecific gene flow and speciation in plants (Currat et al. 2008, Zhou et al. 2010), this has not been studied in bryophytes. Because of high ability of long-distance dispersal, peatmosses have high levels of intraspecific gene flow between populations, located even on different continents (Kyrkjeeide et al. 2016b, Désamoré et al. 2016). Therefore, intraspecific gene flow can potentially be important in explaining levels of interspecific introgression between species.

It was shown, that interaction of genetic and demographical factors, such as population size, time of season and relatedness, is important for explaining gene flow rates in plants (Goodell et al. 1997). Thus, studying speciation by gene flow in peatmosses primarily requires clarification of the relationships between inter- and intraspecific gene flow using genomic data and accounting for possible interaction between different factors.

Conclusion

Interspecific introgression is very common in peatmosses. Allopolyploidization seems to be a prominent process for speciation in the genus, while evaluation of the evolutionary significance of admixture requires further research. Up to 21% of all peatmosses are involved in intra- and intersubgeneric hybridization, producing mainly allopolyploid species, but also homoploid species and haploid admixed hybrids. This number might be substantially underestimated, since many parents of described allopolyploid hybrids are still unknown.

Parents of allopolyploids are on average less related than parents of admixed hybrids. Key life-history traits tend to be associated with intensity of hybridization as monoicous and polyocious species with high sporulation frequency and smaller spores preferring poor habitats produce more hybrids than other species. Overall occurrence of hybridization, however, is not constrained by phylogenetic distance and life-history traits of the parents. We suggest that differences in levels of intraspecific gene flow and/or interaction of population genetics and demographical history factors have a high potential in explaining occurrence and level of interspecific introgression. Finally, more studies are needed to determine the actual occurrence of hybridization in nature, as well as more detailed comparative data regarding reproductive biology and ecology of parental and hybrid species.

Acknowledgements – We thank Nils Cronberg for the comments on the manuscript. Vanessa C. Bieker is gratefully acknowledged for help during the work on the manuscript.

Funding – The study was supported by Norwegian Research Council (project no. 250541/F20).

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Paper II

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ARTICLE
Discoveries Section

Extensive genome-wide phylogenetic discordance is due to incomplete lineage sorting and not ongoing introgression in a rapidly radiated bryophyte genus

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Abstract

The relative importance of introgression for diversification has long been a highly disputed topic in speciation research and remains an open question despite the great attention it has received over the past decade. Gene flow leaves traces in the genome similar to those created by incomplete lineage sorting (ILS), and identification and quantification of gene flow in the presence of ILS is challenging and requires knowledge about the true phylogenetic relationship among the species. We use whole nuclear, plastid and organellar genomes from 12 species in the rapidly radiated, ecologically diverse, actively hybridizing genus of peatmoss (*Sphagnum*) to reconstruct the species phylogeny and quantify introgression using a suite of phylogenomic methods. We found extensive phylogenetic discordance among nuclear and organellar phylogenies, as well as across the nuclear genome and the nodes in the species tree, best explained by extensive ILS following the rapid radiation of the genus rather than by post-speciation introgression. Our analyses support the idea of ancient introgression among the ancestral lineages followed by ILS, whereas recent gene flow among the species is highly restricted despite widespread interspecific hybridization known in the group. Our results contribute to phylogenomic understanding of how speciation proceeds in rapidly radiated, actively hybridizing species groups, and demonstrate that employing a combination of diverse phylogenomic methods can facilitate untangling complex phylogenetic patterns created by ILS and introgression.

Key words: phylogenomics, introgression, incomplete lineage sorting, rapid diversification, speciation, peatmoss.

Introduction

After a long history of rejecting the plausibility of speciation with gene flow in sympatry, it is now generally accepted that speciation does occur without complete geographical and reproductive isolation (Morjan and Rieseberg 2004; Sousa and Hey 2013; Ravinet et al. 2017). Indeed, mounting evidence for post-speciation introgression between closely related species has shifted the discussion towards a debate of the relative importance of gene flow for speciation. How important is gene flow *per se* in speciation, in comparison with other evolutionary forces? Case studies show that gene exchange between closely related species can trigger adaptive radiation (e.g. Dasmahapatra et al., 2012; Fontaine et al., 2015), whereas selective processes are more important for the divergence of lineages into separate species (e.g. Ma et al., 2018). As the magnitude of gene flow changes over the course of speciation-with-gene-flow (Feder et al. 2012), the relative role of introgression might depend on the stage of speciation.

It is well-known that identifying the genomic footprints of gene flow is difficult in the presence of incomplete lineage sorting (ILS) among the diversifying species (Pinho and Hey 2010; Ravinet et al. 2017). ILS describes the pattern in which lineages fail to coalesce during speciation events due to stochasticity of the coalescent process (Degnan and Rosenberg 2009; Zwickl et al. 2014). Therefore, ILS represents the retention of ancestral polymorphism, which may become fixed in the descendant lineages after speciation events due to stochastic genetic drift (Suh et al. 2015). Similarly to gene flow, ILS obstructs reconstruction of true evolutionary history and generates discordant phylogenetic signals among loci across the genome (Pollard et al. 2006; Avise and Robinson 2008; Suh et al. 2015; Pease et al. 2016). Several methods have been developed to differentiate between the two (Green et al. 2010; Durand et al. 2011; Edelman et al. 2019), but they require knowledge of the correct branching order among the species (Fontaine et al. 2015; Edelman et al. 2019). Despite recent advances in relevant analytical methods, the reconstruction of species relationships in the presence of gene flow and/or ILS remains challenging (Fontaine et al. 2015; Li et al. 2019), which in turn makes it difficult to quantify the level of introgression among them. However, the problem can be approached using independent phylogenomic methods on numerous genetic markers in hybridizing species across a speciation continuum, which has been accomplished in several organism groups (e.g. Pease et al. 2016; Irisarri et al. 2018). Comparing phylogenetic signals among genetic markers with differential inheritance (e.g. Zhou et al. 2017; Westbury et al. 2020) or in windows across the genome (e.g. Copetti et al. 2017; Edelman et al. 2019; Stankowski et al. 2019) can also further the inference and its interpretation. In addition, the distribution of phylogenetic discordance in the genome can inform about different selection processes in the ancestral population (Pollard et al. 2006; Slatkin and Pollack 2006; Hobolth et al. 2011; Wang and Hahn 2018).

Peatmoss (*Sphagnum* L.), a species-rich genus of non-vascular haploid plants, offers a potential for studying the relative importance of introgression and ILS in diversification. Peatmosses typically grow in peatlands, where they serve as ecosystem engineers (van Breemen 1995) and sequester carbon, thereby making peatlands the largest terrestrial carbon sink (Yu et al. 2010). Numerous peatmoss species normally disperse over wide geographical distributions (Szövényi et al. 2008; Sundberg 2013; Mikulášková et al. 2015; Kyrkjeeide et al. 2016) across which they co-occur and often hybridize. At least 20% of all species potentially engage in interspecific admixture or allopolyploid hybridization (for a review, see Meleshko et al., 2018). Difficulties in species delimitation and phylogenetic reconstruction in this genus are often attributed to interspecific introgression (Ricca et al. 2011; Shaw et al. 2012; Karlin et al. 2014). However, genetic studies on peatmosses have been performed mostly using a small number of genetic markers and focusing on phylogeography, species delimitation or allopolyploid speciation rather than mere interspecific introgression. Hybridization does not seem to be constrained by phylogenetic relatedness in *Sphagnum*, and is common even between distantly related species from different subgenera (Meleshko et al., 2018). Yet, the extent of how often it translates into introgression is unknown. In many eukaryotes, introgression occurs more readily in genomic regions with high recombination rate (Begun and Aquadro 1992; Schumer et al. 2018). Recombination rates are negatively correlated to genome size in eukaryotes (Lynch 2006; Tiley and Burleigh 2015), thus the relatively small peatmoss genomes might exhibit high recombination rates that could facilitate interspecific introgression.

Several features make peatmoss an excellent model for studying the long-standing question of evolutionary implications of ILS and introgression. Northern Hemisphere peatmoss species exhibit vast variability and plasticity in morphology, ecology and life-history (Stenøien et al. 2014; Johnson et al. 2015). This remarkable species diversity and variability originated rapidly and relatively recently (7-20 Ma, Shaw et al. 2010). Typically, rampant radiations are accompanied by ILS (Whitfield and Lockhart 2007), especially if the effective population size of the ancestral population is large (Slatkin and Pollack 2006), leading to differential retention of polymorphisms that were present in the ancestral population (Pollard et al. 2006). Considering the large effective population sizes of peatmoss species, the effect of ILS might be exacerbated in the group (Stenøien and Såstad 1999). Indeed, in addition to gene flow, the retention of shared ancestral polymorphism due to ILS has been invoked to explain the low levels of among-population divergence across wide geographical distributions observed in several peatmoss species (Stenøien and Såstad 1999; Szövényi et al. 2008; Stenøien et al. 2011). Finally, it has been hypothesized that species diversity in peatmosses originated through adaptation to diverse habitats facilitated by gene flow (Yousefi et al. 2017) and differential paralog retention after the last whole-genome-duplication event preceding the radiation of the group (Devos et al. 2016). Gene duplication and loss often lead to intensified genome-wide phylogenetic discordance and ILS (Rasmussen and Kellis 2012).

Here, we explore the genome-wide patterns of phylogenetic discordance in relation to gene flow and ILS in several more or less closely related peatmoss species pairs at different geographical scales. Specifically, we produced low-depth whole-genome shotgun sequencing data for 12 widely distributed, co-occurring, haploid peatmoss species representing different subgenera within the genus. We use these data to: (i) reconstruct phylogenetic relationships in the group based on genomic markers, (ii) quantify levels of interspecific introgression, (iii) identify signatures of ILS among the species, and (iv) estimate genome-wide variation in phylogenetic discordance. Our analyses show that levels of post-speciation gene flow were surprisingly low and that ILS has mainly been responsible for shaping the genomic landscape of diversification in this diverse group of plants.

Results

Sequencing summary, mapping, SNP calling and filtering

We generated whole-genome shotgun sequencing data for 12 peatmoss species representing all five subgenera within *Sphagnum*, as well as an outgroup non-*Sphagnum* peatmoss species (Devos et al. 2016), *Flatbergium sericeum* (Müll. Hal.) A.J. Shaw (Table 1). For each of the 12 species, we collected one to four individuals from at least two geographically separated populations (Fig. 1A, Table 1). In total, we performed shotgun whole-genome sequencing on 191 individuals (Table S1). The sequencing reads were mapped to the *S. angustifolium* (formerly *fallax*) draft reference genome (v0.5, DOE-JGI, http://phytozome.jgi.doe.gov/). After quality filtering of the raw sequencing reads, we retained 65±45M (SD) reads per sample, of which 16±0.09% (SD) were PCR duplicates, 38±16% (SD) mapped uniquely to the *S. angustifolium* nuclear reference genome, and 1% and 2% mapped uniquely to the *S. fallax* mitochondrial and chloroplast genomes, respectively. Mean sequencing coverage varied from 1.6 to 14.36 (6.25±2.6 SD) for the nuclear genome, while the mitochondrial and the chloroplast genome exhibited a sequencing coverage of 300±170 SD and 830±530 SD, respectively (Table S2). We did not observe any substantial difference in mapping rates among the species from different subgenera (Table S1).

Genetic differentiation among the species

We first explored the relationship of the species using principal component analysis (PCA) performed on the genetic covariance matrix among all individuals based on 16.3 million (M) biallelic sites. The PCA demonstrated a considerable level of interspecific differentiation with most of the species forming distinct point clusters in the space of the first three principal components (Proportion of total variance explained: *PC1* 12%, *PC2* 10%, *PC3* 10%, Fig. 1). Individuals of the three species, *S. capillifolium, S. fuscum* and *S. subnitens*, that appeared unresolved in the space of *PC1-PC3,* were well-separated in a PCA carried out only on the subset of these individuals (Fig. S2).

We further estimated individual ancestry assignment and admixture using ADMIXTURE (Alexander et al. 2009) to detect recent introgression among the species. The analysis based on 23,560 independent SNPs both supported *K*=12 (cross-validation error 0.06, Fig. S3) and did not reveal either evidence for strong genetic structure within or substantial admixture between species, with the exception of one *S. flexuosum* individual whose genome may be shared with *S. tenellum* (30%) (Fig. 1D).

To estimate the level of differentiation among the species, we calculated genome-wide F_{ST} based on 121±10M (SD) biallelic sites for each species pair taking into account genotyping uncertainty (see Materials and Methods). The values of F_{ST} vary from 0.75 to 0.98 among the species pairs (Fig. 2). Together with the results of the PCA and ADMIXTURE analysis, this suggests that all studied species are highly differentiated from one another which is in accordance with other studies showing high level of genetic distinctiveness in *Sphagnum* (Shaw, Shaw, Johnson, et al. 2015; Kyrkjeeide et al. 2016; Yousefi et al. 2017; Yousefi et al. 2019).

Phylogenetic relationships between the species

To infer the phylogenetic relationship among the species, we first used the filtered nuclear SNP dataset (455K SNPs, see Materials and Methods) to perform a maximum-likelihood analysis in RAxML. We also carried out the very same analysis on the chloroplast (1.9K SNPs) and on the mitochondrial (1K SNPs) SNP datasets. Organellar genomes are believed to be maternally inherited and non-recombining, as shown in some peatmosses (Natcheva and Cronberg 2007). Assuming no genetic exchange among taxa and complete lineage sorting, nuclear and organellar phylogenies should resolve the very same relationships. However, the analyses of organellar and nuclear SNPs provided very well-resolved, but topologically conflicting, phylogenies with each species forming a strongly supported monophyletic clade (Fig. 3). The relationships inferred using plastid and mitochondrial markers are congruent to the most comprehensive organellar-based phylogenies of the genus (Shaw et al. 2016; Shaw et al. 2019) and to each other, except that the admixed *S. flexuosum* individual (ND4) is resolved either within *S. flexuosum* or *S. tenellum* in the chloroplast-based and in the mitochondrion-based phylogeny, respectively (in red on Fig. S5). The nuclear and organellar markers led to conflicting phylogenies regarding both the relationships among the subgenera and the placement of individual species, namely, *S. lindbergii*, *S. compactum, S. divinum, S. platyphyllum* and *S. squarrosum* (Fig. 3).

In all phylogenies, there was no evidence for geographical structure within species, with the exception of *S. compactum,* for which samples from Norway, Germany and Austria form distinct clades (Fig. S5D). This suggests weak genetic structure within peatmoss species across the sampled distribution, corroborating previous observations in many *Sphagnum* species (Szövényi et al. 2008; Stenøien et al. 2011; Szövényi et al. 2012; Szurdoki et al. 2014; Mikulášková et al. 2015; Shaw, Shaw, Stenøien, et al. 2015; Kyrkjeeide et al. 2016).

Coalescent-based analysis

It is well known that phylogenetic analysis using concatenated data sets does not take into account the stochasticity of the coalescent process and often fails to recover the true species tree (Kubatko and Degnan 2007). Therefore, we also used a coalescent-based phylogenetic method to infer the species tree from a set of gene trees by explicitly taking into account the inherent stochasticity associated with the coalescent process (Rabiee et al. 2019). Our coalescent-based analysis of 988 genes (1.7±1.2 kb [SD], Table S4) recovered the very same highly supported species tree as our RAxML analysis with an ASTRAL quartet score of 79% (Fig. 4A). This suggests that the incongruence between the organellar and nuclear phylogenies is real and not simply due to phylogenetic error using concatenated data sets (Wang and Hahn 2018).

To explore the distribution of discordance across the species tree, we calculated the concordance factor, which corresponds to the number of gene trees recovering a particular node. The results show that the deeper nodes describing the split among taxa and taxon groups are supported by only a small fraction, while the monophyly of all species is recovered by the majority of the gene trees (Fig. 4B and S6B). We also found that the poorly-supported nodes corresponded to those causing incongruence between the nuclear- and the organellar-based phylogenies. In particular, only 12% of the trees recover the node uniting all species in the clade sister to the *Cuspidata* species (Table 1), and only 12% of the trees resolve *S. divinum* and *S. compactum* as sister species. Most of the trees recover the species tree branching order within *Cuspidata* and *Acutifolia* species, while the positions of *S. squarrosum* and *S. platyphyllum* within the *Acutifolia* clade were recovered in 13 and 28% of the trees, respectively. Similarly, the placement of *S. lindbergii* was supported in only 20% of the trees. We observed that the branch length at the node was positively correlated to the node recovery (r_S=0.77, $p<0.0001$, Fig. S6A), and, despite low recovery by the gene trees, all deep nodes received very high posterior support in ASTRAL (Fig. 4A). We also compared the among-species topology of each gene tree to the species tree topology and found that 99% of the gene trees had different topologies, and only 1 of 988 gene trees had the species tree topology (Fig. 4C). Short branches at the deeper nodes suggest ILS as the cause of the observed incongruences, but gene flow among the species can also distort the phylogenetic signal across the genome.

Because our coalescent-based analysis was based on 988 genes randomly sampled across the genome, we extended our analysis to many more sites by estimating phylogenetic trees in 100-kb non-overlapping windows across all genomic scaffolds longer than 2-Mb. In total, the resulting trees contained 141M distinct site patterns and 19M parsimony informative sites compared to 1.5M and 118K, respectively, found in the gene trees (Table S5 and S4). Similarly to the pattern we observed with the gene trees, only 2.4% out of the 650 different topologies identified in the 1774 sliding window trees matched the species tree topology (Fig. 4D). Concordance factor estimates confirmed our previous estimates based on genes, nevertheless, the node recovery was higher for the sliding window trees than for the gene trees (31.5% [SE=2.4] versus 12.7% [SE=1.7], respectively, Wilcoxon rank sum test, $p<0.0001$).

D-statistics

To assess whether the observed phylogenetic incongruences are mainly due to interspecific gene flow, we calculated Patterson's *D*-statistic (hereafter referred to as *D*) implemented in ANGSD, which uses the ABBA-BABA test for introgression among a quartet of species (Soraggi et al. 2018). To carry out the test, we used all phylogenetically correct quartet topologies as $(((P_1,P_2),P_3)$,outgroup) to test for evidence of excess of derived sites shared by P_3 and P_1 or P_2 versus shared by P_1 and P_2 defining *F. sericeum* as an outgroup (Table S6). Three species pairs could not be tested (*S. tenellum* and *S. flexuosum*, *S. capillifolium* and *S. fuscum*, *S. compactum* and *S. divinum*, designated with empty squares on Fig. 5) since they are sister species in our dataset. Our block jack-knife analysis supports the view that *D* is significant in many of the triplets (80%, 175 out of 220 triplets, $p<0.002$, Table S6). Our estimates of *D* and number of sites assessed varied widely depending on the third species in the triplet (P_1 or P_2, Fig. S7), thus a mean value of absolute *D* for a species pair was calculated from all triplets in which these species had significant values of *D*. The absolute *D* was significant in most of the pairwise species comparisons (81%, 51 out of 63 pairwise comparisons based on 22-41K sites, Table S7), and varied from 0.02 to 0.18 (Fig. 5). For some species pairs, *D* was not significantly different from zero (Fig. 5). Our analysis was insensitive to the size of the genomic window used for the analysis (1 Mb and 5 Mb, Fig. S7E). The species showing incongruent placement across the phylogenies have low, yet significant, values of *D* with species of subgenus *Cuspidata* and *Acutifolia* (Fig. 5), which suggest that gene flow might have contributed to the observed phylogenetic discordance.

Assuming that gene flow is on-going or recent, it might be restricted to closely-related species as reproductive barriers accumulate with time since divergence (Coyne and Orr 2004). Therefore, one might expect *D* to be negatively correlated with differentiation between the species. In contrast, *D* was positively correlated with F_{ST} ($r_S=0.32$, $p=0.02$, Fig. S7D). Given that our ADMIXTURE analysis did not reveal recent genomic exchange among the species, this suggests that the introgression inferred with *D* happened earlier in the diversification process, and likely among the ancestral lineages (see this hypothesis explicitly addressed under "Testing for ancient introgression" below).

We additionally performed tests for admixture using 23,560 independent SNPs with TreeMix (Pickrell and Pritchard 2012) and calculated the f_3 statistics (Keinan et al. 2007). We did not find evidence for recent gene flow with the f_3 statistics (Table S8), while the results of the TreeMix analysis were ambiguous with different models being equally supported. Namely, the inferred migration events were inconsistent, and the likelihood of the estimated tree model did not greatly differ among replicates with the same number of migration events allowed and among the best supported replicates (Fig. S8). This might suggest a complex rather than tree-like evolutionary history of the studied species (Foote and Morin 2016).

QuIBL analysis

Because we observed that phylogenetic discordance can be potentially associated with both ILS and introgression, we made use of a recently developed tree-based method, QuIBL (Edelman et al. 2019), to differentiate between these two processes. QuIBL estimates the distribution of internal branch length in discordant topologies for triplets of species, and then calculates the likelihood that this distribution corresponds to the model with introgression and ILS or with ILS only. QuIBL therefore only estimates post-speciation gene flow for a set of three species at a time. For the analysis, we kept one sample with the highest coverage per species and, since the method is sensitive to recombination (Edelman et al. 2019), generated 3,195 trees (Table S11) based on small windows (2 kb) considerably distant from each other (20-kb steps). Because *S. compactum* showed pronounced geographic structure, we used samples from two different populations in the analysis and obtained the same results for both samples (not shown). Three closely-related species pairs could not be tested as they are sister species in our dataset (marked with empty squares on Fig. 5A).

The QuIBL analysis revealed that only 22% of the tested triplets showed significant evidence for introgression (48 of 220 triplets, BIC>10, Table S9). For the rest of the triplets, adding introgression did not improve the fit of the ILS-only model. Furthermore, we found that only 0.29% of loci supported discordant topologies and were introgressed (Fig. S9), suggesting limited overall interspecific introgression among the studied species (Fig. 5A, Table S10). QuIBL analysis suggests ILS, rather than post-speciation introgression, is the main factor behind phylogenetic discordance among the species.

Testing for ancient introgression

Our D-statistic based analysis revealed significant, albeit relatively low, levels of recent gene flow among species. Nevertheless, the degree of introgression between taxa (*D*-statistic) was positively correlated with between-species genetic differentiation (F_{ST}) suggesting that ancient introgression could have been more frequent than post-speciation gene exchange. Therefore, we further explored this hypothesis with the D_{FOIL} statistic (Pease and Hahn 2015). The method uses a group of four species and an outgroup as (((P_1,P_2),(P_3,P_4)),O) to quantify introgression among non-sister tips, as well as ancient introgression. D_{FOIL} performs well in the presence of ILS, and at low rates of introgression (Pease and Hahn 2015). We used one sample per species with the highest coverage (Table S1), *F. sericeum* as the outgroup, and computed D_{FOIL} for all phylogenetically correct five-taxon combinations (Table S12) in 100-kbp non-overlapping windows across the scaffolds longer than 1 Mb (Pease and Hahn 2015). D_{FOIL} analysis showed that 98% of five-taxon phylogenies (180 out of 183, Table S12) showed evidence for introgression. In accordance with the results of the traditional *D*-statistic and QuIBL, the analysis revealed very low levels of post-speciation gene flow among the extant species (<0.1% of all windows, Table S13, Fig. 5B), whereas up to 19% of the windows showed evidence of ancient introgression between (P_1,P_2) and P_3, and up to 1.3% between (P_1,P_2) and P_4 (Table S13, Fig. 5B). We found 11 five-taxon phylogenies which had >10% windows introgressed from (P_1,P_2) into P_3 (Fig. 5C). In agreement with the D-statistic test, these results support genomic exchange between the ancestor of the species of subgenus *Cuspidata* (*S. flexuosum*, *S. riparium*, *S. tenellum*, *S. lindbergii*) with the ancestor of the species of subgenus *Acutifolia* (*S. fimbriatum*, *S. subnitens*, *S. fuscum*, *S. capillifolium*), as well as with the ancestors of *S. compactum* and *S. divinum*.

The length of consecutive introgressed regions can be used to infer the relative timing of introgression (Barlow et al. 2018; Moodley et al. 2020; Westbury et al. 2020). Assuming recent introgression, longer stretches of introgressed genomic segments are expected to be found in the genome, which with time get broken into smaller pieces due to recombination (Węcek et al. 2017). We therefore investigated if the windows showing any evidence for introgression formed consecutive regions. We found that most of the introgressed windows were singletons, with occasional blocks of 2-4 consecutive introgressed windows (Fig. S10, Table S14). For instance, in the five-taxon phylogeny with the highest number of introgressed windows (Fig. 5C), 87% of the windows were singletons, and 10% were arranged in blocks of two consecutive windows. Taken together, these results strongly support the hypothesis of ancient introgression among the ancestral *Sphagnum* species.

Discussion

In this study, we focused on the genome-wide pattern of phylogenetic discordance and its relationship to interspecific introgression and ILS in 12 peatmoss species, representing all subgenera within the genus, sampled at different geographical scales. Our analyses show that all species are highly genetically differentiated from one another, and most show no evidence for population genetic structure across the sampled distribution. At the same time, phylogenetic discordance was common both across the genome and between the organellar- and nuclear-based phylogenies. We found evidence for ancient introgression among the ancestral population likely followed by ILS, whereas levels of post-speciation gene flow were surprisingly low. Our analyses show that ILS, and not extensive introgression, has mainly been responsible for shaping the genomic landscape of diversification in this diverse group of plants. In the following paragraphs, we discuss how these two processes may have shaped the diversification of *Sphagnum* mosses.

Genomic signatures of rapid radiation

Sphagnum is known for a recent rapid burst of diversification 7-20 Ma associated with the Miocene cooling, which presumably triggered adaptation to diverse, novel habitats (Shaw, Devos, et al. 2010). Rampant radiation should lead to short coalescent times and ILS among newly formed lineages (Whitfield and Lockhart 2007). Consequently, phylogenetic studies of extant lineages in such a case would infer hemiplasy (Avise and Robinson 2008), i.e. topological incongruences between the species tree and gene trees, irrespectively of type, quality and quantity of the markers used in the analysis (Pease et al. 2016; Wang and Hahn 2018). This is precisely the pattern we observed in both gene and sliding-window tree analyses, as well as in organellar genome phylogenies in peatmosses. Additionally, rapid speciation often results in the anomaly zone phenomenon, in which the true species tree topology is difficult to resolve for inferences involving more than four taxa (Degnan and Rosenberg 2009; Suh et al. 2015). This explains the numerous conflicting topologies of the gene and sliding window trees and the low recovery of deep nodes, but strong support of the species tree topology inferred with ASTRAL, which is robust to the presence of the anomaly zone (Allman et al. 2011) as it takes a quartet of leaves at a time under the multispecies coalescent model (Mirarab et al. 2014). Similar extent and distribution of discordance among loci in the genome and across the nodes in the species tree has been found in rapidly radiated groups, both recently diverged, such as in wild tomatoes (Pease et al. 2016) and cichlid fishes (Irisarri et al. 2018), and at a deeper timescale, such as in neoavian birds (Suh et al. 2015). Altogether, rapid diversification of peatmosses has likely significantly contributed to the extensive phylogenetic incongruence observed, which is in line with findings of previous studies investigating the genomic signatures of rapid radiations in various groups of organisms.

When time after divergence increases, so does the probability that parallel evolution has occurred in the diverged lineages (Suh et al. 2015). Therefore, one could argue that some or most incongruences are due to parallel evolution rather than ILS. Considering that in *Sphagnum* the last diversification peak is relatively recent, it is less likely that the observed deep-node incongruences occur due to homoplasy rather than hemiplasy derived from ILS (sensu Suh et al. 2015). While the radiation of peatmosses was clearly sudden (Shaw, Devos, et al. 2010; Devos et al. 2016), there is some uncertainty about its timing, which might have been much older than previously thought (Shaw et al. 2019). Nevertheless, no alternative date has been suggested, and the strong negative relationship between incongruence at a node and the internode length in our gene tree concordance factor analysis further supports the idea that high levels of ILS, and not homoplasy, substantially contribute to the observed genome-wide phylogenetic signal (Zwickl et al. 2014; Pease et al. 2016; Irisarri et al. 2018).

Recent introgression or incomplete lineage sorting?

Based on the results of the phylogenetic analyses, we expect ILS to be the main factor explaining the observed phylogenetic discordance. However, these analyses do not differentiate between ILS and introgression, both of which can create similar phylogenetic signals (Fontaine et al. 2015). Considering that all species are highly supported as monophyletic clades and that no signs of recent admixture were found in the ADMIXTURE analysis, a potential explanation is that while interspecific introgression is currently constrained by strong reproductive isolation among the species, gene flow was more prominent in the past, during the speciation process, facilitating *Sphagnum*'s known rapid diversification into diverse habitats (Shaw, Devos, et al. 2010; Devos et al. 2016). It has been suggested that ancient admixture of ancestral variation is a powerful means for rapid radiations to occur (Marques et al. 2019). The results of our introgression and QuIBL tests support this idea.

We did not find significant evidence for introgression using ADMIXTURE and the f_3 statistics, which are suited to detect recent introgression (Alter et al. 2017). Levels of post-speciation interspecific gene exchange inferred with QuIBL and D_{FOIL} were very low, whereas the D-statistic showed considerable introgression among species pairs with deeper nodes and generally low values in more recent species pairs. For instance, the D-statistic shows that *S. lindbergii* and *S. riparium* share 4-18% of the derived sites with other studied species. *Flatbergium sericeum*, which was used as an outgroup in our D test, has a smaller genome size and number of chromosomes than *Sphagnum* (Shaw, Cox, et al. 2010) and represents a family of non-*Sphagnum* peatmosses that diverged from *Sphagnum* peatmosses ca 34-105 Ma (Shaw, Devos, et al. 2010). Using a distantly related outgroup does not in itself affect the robustness of D (Zheng and Janke 2018), but our estimates in this test are tied to the sites where the outgroup sequence reads can be mapped to the *S. angustifolium* reference genome, likely covering the more conserved part of the genome. Consequently, the observed D values likely represent retained traces of ancient introgression events among ancestors of the extant species followed by genetic drift or divergent selection. This is further supported by the results inferred with D_{FOIL} for different combinations of the species, which suggest that gene flow likely happened between the ancestors of the species from subgenus *Cuspidata* and the ancestors of other subgenera. Despite that D_{FOIL} cannot infer introgression between the two ancestral lineages in a five-taxon topology (Pease and Hahn 2015), the results inferred using different combinations of species from these two subgenera can only be explained by a deep introgression event, which should have happened early in the diversification process, followed by differential retention of ancestral polymorphism in the studied species due to subsequent genetic drift and/or divergent selection. A similar pattern has been recently described in rhinoceros, where gene flow between the ancestral lineages ceased within 2 million years after initial divergence, but resulted in false-positive signatures of introgression among the subsequently diverged subspecies due to random coalescent processes (Moodley et al. 2020).

Alternatively, the D and D_{FOIL} tests may have inferred false-positive values due to certain population structure in the ancestral lineage or differences in the effective population size among the lineages (Zheng and Janke 2018), which is plausible given the recent bottleneck documented in extant peatmoss species (e.g. Thingsgaard 2001; Kyrkjeeide et al. 2012; Yousefi et al. 2017). D_{FOIL} can incorrectly infer ancient introgression between (P_1,P_2) and P_3 or P_4 if introgression happened shortly after the split of (P_1,P_2) (Pease and Hahn 2015) or if P_3/P_4 exchanged genes with both P_1 and P_2 at equal rate since their split (Fontaine et al. 2015). In our case, however, the majority of different five-taxon phylogenies demonstrated significant and consistent signals for ancient introgression deep in the species phylogeny. In addition, the prevalence of singleton introgressed windows we observe with D_{FOIL} also suggests that these windows indeed represent signatures of ancient, rather than recent, introgression (Barlow et al. 2018; Moodley et al. 2020; Westbury et al. 2020).

We have to note that recent introgression might have been underestimated in our tests for various reasons detailed below. Introgression from a "ghost" unsampled population or difference in population sizes among the species can also bias D (Zheng and Janke 2018) and D_{FOIL} estimates (Pease and Hahn 2015) which are possible sources of errors we could not account for. The QuIBL analysis can also provide biased estimates: it will likely overestimate introgression if the windows used for the analysis contain recombination breakpoints (Edelman et al. 2019). We took this into account in our test by choosing a narrow window size of 2 kb to minimize the risk of including many recombination breakpoints. Accordingly, we believe that our QuIBL estimates are reliable. Unlike the D-statistic, QuIBL provides robust estimates when all three species in the triplet hybridize, which likely occurs, but will not lead to further biases (Edelman et al. 2019).

While our results imply that post-speciation gene flow is minimal, they do not exclude the possibility of significant interspecific gene-flow among selected peatmoss species. *Sphagnum* includes about 300 species distributed worldwide (Michaelis 2019), and we did not sample very closely related species (sister species) in this study, and could not test the most closely related species pairs in most of our introgression analyses. It is therefore possible that recent, and more significant interspecific introgression may take place between very closely related species pairs that were not included in this study. Hence, our finding of minimal contemporary post-speciation gene flow among peatmoss species applies only to the set of species used in this study. In turn, the single admixed individual identified in our study, resulting from admixture between two sister species (*S. flexuosum* and *S. tenellum*), could be an F_1 hybrid, which does not necessarily imply ongoing introgression between these species, but simply hybridization. Considering that the known widespread interspecific hybridization in *Sphagnum* is mostly happening in the form of allopolyploidization (reviewed in Meleshko et al., 2018), our findings may indicate that the group has evolved strong reproductive barriers, which prevent homoploid hybridization from translating into substantial introgression.

Ancient introgression and subsequent ILS, together with very limited post-speciation introgression, agree very well with all our findings and with the extensive discordance we identified in our phylogenomic analyses. This scenario explains the inconsistent placement of *S. lindbergii*, *S. compactum*, *S. divinum*, *S. platyphyllum* and *S. squarrosum* within the gene and sliding-window phylogenies, as well as the incongruences among the nuclear and the organellar phylogenies. It is, however, beyond the scope of this study to determine the relative impact of these two processes on the early diversification process in this group. There were 53 triplets in our QuIBL analysis for which the most common topology (supported by the highest number of trees) did not correspond to the species tree topology (Table S11). In particular, for the triplet (*S. lindbergii*, (*S. divinum*, (*S. squarrosum*))), all three possible topologies were nearly equally supported by the trees. Other such triplets consistently showed discordance in placement of *S. squarrosum*, *S. compactum*, and *S. divinum* relative to the backbone *Acutifolia* species (*S. capillifolium*, *S. fuscum*, *S. subnitens*, *S. fimbriatum*) and to *Cuspidata* species. None of these triplets showed significant evidence for post-speciation introgression, and average levels of ancient introgression inferred with D_{FOIL} were moderately low (Fig. 5B). These are the same incongruences we detected in our gene and sliding-window trees analyses, suggesting that the species tree topology might itself have originated from ILS (Edelman et al. 2019). With this high level of ILS, a bifurcating tree might therefore be an oversimplification of the true evolutionary history of this rapidly radiated group.

Conclusions

Our analyses suggest the following hypothesis about the evolutionary history of peatmoss. When *Sphagnum* started to diversify, effective population sizes were large and gene flow extensive among the emerging species, which resulted in plenty of shared polymorphism among species. This great diversity was then sorted out following rapid diversification, triggered by whole-genome duplication (Devos et al. 2016), into diverse habitats, newly formed as a consequence of rapid climate change (Shaw, Devos, et al. 2010). Finally, reproductive isolation and/or restricted gene flow gave rise to the current species diversity.

Our findings demonstrate that rapid radiation creates a phylogenomic pattern in bryophytes similar to that observed in angiosperms, which corroborates the suggested idea of universality of evolutionary processes among land plants (Medina et al. 2018). In contrast to many recently rapidly radiated, actively hybridizing groups, post-speciation gene flow is not prominent in creating phylogenetic discordance in *Sphagnum*, at least not in the species studied here. Based on our results, the evolutionary history of peatmoss might be too complex to be modelled as a simple bifurcating tree, and reconstructed using a single type of genetic markers. This needs to be taken into account in further studies of this and other rapidly radiated bryophyte groups.

Materials and Methods

Sampling. We sampled 12 common haploid species with no known hybrid origin and contrasting life-history traits that represent different subgenera within *Sphagnum* (Table 1). The sampling was carried out in three metapopulations from central Norway, Austria and Germany (Fig. 1). For each of the 12 species, we sampled 2-3 populations in each of two European regions and, for most species, one population in Germany. Two to four individuals were collected at each population for a total of 11 to 20 individuals per species (a total of 190 individual sampled shoots, Table 1). Vegetative reproduction is common in peatmosses, so to avoid sampling clones within possible mating distance, we collected only conspecific shoots growing approximately 1 m apart. The accessions and the voucher specimens were air-dried and deposited at the Trondheim Herbarium (TRH). Additionally, we included a sample of *Flatbergium sericeum* (Müll. Hal.) A.J. Shaw from the TRH to use as an outgroup in various analyses. For a list of voucher specimens, see Table S1.

DNA extraction. DNA was extracted from cleaned dried capitula tissue and fragmented to a mean length of 400 bp as described in detail in the Supplementary Materials (Section SMM1).

Library preparation and sequencing. Our study provides the first investigation using whole-genome sequencing in peatmosses. Therefore, we tested the performance of the library preparation and sequencing method on a subset of 11 samples (one accession per species). Individual whole-genome DNA libraries were prepared as described in detail in the Supplementary Materials (Section SMM2) and sequenced at the Functional Genomics Center Zurich (FGCZ, Switzerland) on a single lane of an Illumina HiSeq 4000 in 150 bp paired-end mode. The rest of the libraries were prepared and pooled into 16 pools based on the estimated per-library endogenous content as described in detail in the Supplementary Materials (Section SMM3). The negative library build and indexing PCR controls were included into one of the pools. Sequencing was performed at the Genomics Core Facility, Faculty of Medicine, NTNU (Trondheim, Norway) on two flowcells of an Illumina HiSeq 4000 in 150 bp paired-end mode.

Sequencing data processing. The raw sequencing reads were processed using the Paleomix pipeline v1.2.13.4 (Schubert et al. 2014). Adapter contamination was trimmed using AdapterRemoval v2.2.0 (Schubert et al. 2016), and trimmed reads shorter than 25 bases were discarded. The remaining reads were mapped to a reference genome assembly of *Sphagnum angustifolium* (formerly *fallax*, v0.5, DOE-JGI, http://phytozome.jgi.doe.gov/), using the mem algorithm of BWA v0.7.15 (Li and Durbin 2009). Aligned reads with a mapping quality (MAPQ) score below 30 were discarded. PCR duplicates were marked with PicardTools v2.9.1 (http://broadinstitute.github.io/picard). We performed realignment around indels using the Genome Analysis Toolkit (GATK) v3.7 (McKenna et al. 2010) to reduce the number of alignment artifacts, and validated the resulting bam files with PicardTools v2.9.1. We used SAMtools v0.1.19 for sorting, converting and generating summary statistics for the bam files (Li et al. 2009). The raw reads were also aligned to *Sphagnum fallax* chloroplast and mitochondrion genome sequences (GenBank accession codes KU725463 and KU725501, respectively) in the same manner as described above.

SNP calling and filtering. The variants were called with '-ploidy 1' tag using the GATK v3.7 'HaplotypeCaller' for each sample separately. Next, the samples were divided into the sets of 20 to 25, and each set was genotyped with the GATK v3.7 tool 'GenotypeGVCF'. Following the best practices pipeline

(Van der Auwera et al. 2013), we extracted SNPs from the call sets and performed hard-filtering with the recommended parameters: QualByDepth < 2.0, FisherStrand > 60.0, RMSMappingQuality < 40.0, MappingQualityRankSumTest < -12.5, ReadPosRankSumTest < -8.0. The SNPs meeting any of these criteria were excluded from the dataset. We tested different filtering parameters for missingness and depth using VCFtools (Danecek et al. 2011). As the dataset included 12 different species, strict missingness criteria led to a dramatic decrease in the number of SNPs. Therefore, we kept the SNPs that were present in at least 20% of all individuals, also filtering these for minimum mean depth of 5, maximum mean depth of 100 and minimum minor allele frequency of 0.05. The resulting dataset is referred to as the filtered nuclear SNP dataset. Plastid and mitochondrial genome alignments were treated in the same manner, except that we kept the SNPs that were present in 100% or in at least 50% of all individuals for the chloroplast and mitochondrial alignments, respectively, and no maximum mean depth was used to filter the SNPs. The resulting datasets are referred to as the chloroplast SNP dataset and the mitochondrial SNP dataset, respectively. When applying the software sensitive to linkage between the SNPs, we randomly selected 1 SNP per 2000 bp from the filtered nuclear SNP dataset. This dataset is referred to as the thinned SNP dataset. A summary of the number of genetic markers used in each of the analyses described below can be found in Table S3. Given that the ploidy level was set to 1, no heterozygous variants were called. Therefore, we calculated the percentage of potentially heterozygous variants, which could have potentially been called from mismapped paralogous genomic regions, as described in detail in the Supplementary Materials (Section SMM6). We found a very low number of sites showing heterozygous signals in our SNP dataset (mean 0.43% ±0.18% SD across samples, Supplementary Materials, Section SMM6, Fig. S11), which is in line with our assumption that mismapping of paralogous copies don't have a considerable effect on the number of SNPs called.

PCA. We computed the covariance matrix between individuals using ANGSD v0.931-8-g1ed4245 by sampling a random base from each individual at each position for biallelic sites (Korneliussen et al. 2014) to exclude bias introduced by differences in sequencing depth. First, we performed per-base alignment quality (BAQ) computation implemented in ANGSD to adjust quality scores around indels in the mapped reads used as an input (Li 2011), and adjusted MAPQ score to 50 for reads with excessive mismatches. Then, those reads with poor quality (flag>=256), low MAPQ score (<=30), low base quality score (<=20), or with unmapped mate and secondary alignments were discarded. These reads filtering procedures were also used for other analyses performed in ANGSD and are hereafter referred to as “read quality filtering in ANGSD”. Minor alleles were inferred by picking the two most frequently observed bases across individuals (Li et al. 2010). Then, sites were filtered based on minimum minor allele frequency (>=0.05) and sample size (>=⅓ of individuals). Following (Patterson et al. 2006), we generated eigenvectors for the covariance matrix in R and performed a Tracy-Widom test to determine the significance of the eigenvalues using the package ‘AssocTest’ (Wang et al. 2017).

Admixture analysis. ADMIXTURE v1.3.0 was used to estimate individual assignment and admixture (Alexander et al. 2009). We excluded the outgroup from the thinned SNP dataset and used bcftools (samtools.github.io/bcftools) and PLINK v1.90b6.9 (Chang et al. 2015) to convert the VCF into a binary PLINK file to be used in ADMIXTURE. Due to limitations of PLINK, we kept the 95 longest scaffolds during the conversion that equal to 63% (249.6M bases) of the total length of the reference. To infer the best number of *K*, 10-fold cross-validation procedure was used, testing *K* = 1 to *K* = 16. For each *K*, 20 independent runs were performed, and the mean cross-validation error among all replicates for each *K* was calculated and compared to identify the replicate with the lowest error.

Test for ancestral admixture. In order to reconstruct major migration events in the group, we performed a TreeMix v1.13 (Pickrell and Pritchard 2012) analysis which uses allele frequency data to reconstruct the relationships among the species as a bifurcating ML tree that corresponds to the estimated degree of genetic drift among the species. We calculated allele frequencies per species with PLINK using the same input file as for the ADMIXTURE analysis above, and imported these into TreeMix. TreeMix was run with bootstrap without incorporating migration and with allowing from 1 to 5 migration events. For each scenario, 100 independent runs were performed, and runs with the highest log likelihood for each scenario were selected. From the covariance matrix estimated from the data in the best runs, we calculated the total standard error and the amount of variance in species relatedness explained by the model using an R script by Daren Card (2015). We also used TreeMix to calculate the f_3 statistics on the same dataset (Keinan et al. 2007).

Phylogenetic analyses. Using a custom python script and SeqKit (Shen et al. 2016), the filtered SNP datasets including variant positions with depth of 5 to 100 and the outgroup sample were converted into a concatenated multiple sequence alignment in fasta format. For the chloroplast and mitochondrial SNP datasets, RAxML v8.2.11 (Stamatakis 2014) was used to perform 100 rapid bootstrap inferences and 10 subsequent maximum-likelihood (ML) searches using a GTRGAMMA model of nucleotide substitution. For the nuclear markers, which were located primarily in genic regions (76.2% of 455.7K SNPs), RAxML was used with 200 rapid bootstrap inferences and 20 ML searches under the same model.

Population genomic analyses. We used ANGSD v0.931 (Korneliussen et al. 2014) to calculate F_{ST} and D-statistic without calling individual genotypes. First, we performed read quality filtering in ANGSD. Individuals were discarded from a site based on individual filtered read depth (2-100) at that site. One *S. flexuosum* individual admixed with *S. tenellum* was excluded. We used the Empirical Bayes method implemented in ANGSD to calculate F_{ST} using a site frequency spectrum (SFS) to take into account genotyping uncertainty (Fumagalli et al. 2013; Korneliussen et al. 2013). To estimate the SFS, we used ANGSD specifying ploidy level with the command-line argument *-isHap 1* to compute genotype likelihoods (GL) using the SAMTools method (Li et al. 2009) without calling individual genotypes. Allele frequencies were calculated based on GLs using biallelic sites, and minor alleles were inferred from GLs using ML approach (Skotte et al. 2013). Sites were filtered based on the sample size (>=⅓ of individuals). Assuming Hardy-Weinberg equilibrium, we further used ANGSD to estimate site allele frequency likelihood (SAF) jointly for all individuals within each species as well as within each population. Using this estimate, we performed optimization using the expectation maximization (EM) algorithm, and polarization to obtain an ML estimate of the SFS for each species (Nielsen et al. 2012) and an ML estimate of the 2D (pairwise) SFS for each species pair. This SFS was then folded, and weighted F_{ST} was calculated for each species pair using an extended version of the method-of-moments estimator (Reynolds et al. 1983) implemented in ANGSD (Fumagalli et al. 2013). We kept the scaffolds longer than 1M bases equal to 70.3% (278.6) of the total length of the reference.

To compare the estimates based on GLs and on SNP data, the filtered SNP dataset was imported into the R statistical environment v3.6.3 (R Core Team, 2020) using the package 'vcfR' (Knaus and Grünwald 2017) and converted into a genlight object with the package 'adegenet' (Jombart and Ahmed 2011). The genlight object was imported into the package 'hierfstat' (Goudet 2005) using the package 'radiator' (Gosselin 2019), and F_{ST} (Weir and Cockerham 1984) was calculated for each species pair. The F_{ST} estimates were highly correlated with those calculated in ANGSD for each pairwise comparison ($r_s = 0.81$, $p<0.0001$, Fig. S4), and we hereafter used the estimates inferred with ANGSD.

D-statistic. We used the multiple-sample version of Patterson's *D*-statistic (Green et al. 2010) implemented in ANGSD (Soraggi et al. 2018) to calculate genome-wide estimates of introgression. The method is described in detail in the Supplementary Materials (Section SMM4). Significant deviation of *D*-statistic from 0 rejects the null hypothesis about absence of gene flow (Green et al. 2010; Martin et al. 2015). First, we performed read quality filtering in ANGSD and discarded sites missing in more than 10 individuals. Individuals were discarded from a site based on individual filtered read depth (2-100) at that site. We kept the scaffolds longer than 1M bases that equal to 70.3% (278.6M bases) of the total length of the reference genome. Next, we performed Abbababa2 analysis sampling all bases at biallelic sites in each individual for every phylogenetically correct triplet of 12 species using *Flatbergium sericeum* (Müll. Hal.) A.J. Shaw as the outgroup. The significance of *D*-statistic was accessed by performing Weighted Block Jack-knife method (Busing et al. 1999) using large (1-Mb) blocks to ensure that there is no linkage disequilibrium between the blocks, and that the number of sites within the blocks is big enough to allow the *D*-statistic to be approximated by a normal distribution (Soraggi et al. 2018). Following (Barlow et al. 2018), we chose 1-Mb windows instead of commonly used 5-Mb windows to include scaffolds shorter than 5 Mb into the analysis. The reliability of this approach is confirmed by strong and statistically significant correlation between the *D*-statistic obtained using 5-Mb and using 1-Mb windows ($r_s = 0.85$, $p<0.0001$, Fig. S7E). We used a threshold of $|Z|>3$ to reject the null hypothesis which corresponds to $p<0.002$. The triplets included various triplet combinations of the same species meaning multiple *D*-statistic values were obtained for the same species pairs. Thus, we calculated mean *D*-statistic for species pairs using P_2 and P_3 as a pair if *D* for the triplet was significant and positive, and P_3 and P_1 as a pair if *D* for the triplet was significant and negative.

Coalescent-based analysis. We reconstructed the coalescent-based phylogeny of the studied species. First, we used ANGSD to generate nuclear genome consensus sequences from aligned reads for each sample. For this, we performed read quality filtering in ANGSD and discarded sites based on filtered read depth (5-100) at that site keeping the scaffolds longer than 1 Mb. The filtered reads were used to generate fasta files for each sample keeping the base with the highest effective base depth (EBD) at each position as implemented in ANGSD. EBD is a product of mapping quality and base quality scores for each base, and it enables more precise base calling for low-coverage sequencing data (Wang et al. 2013). Using the gffread utility (https://ccb.jhu.edu/software/stringtie/gff.shtml#gffread), we extracted spliced genic sequences (CDS) for each sample and used a custom bash script to convert the sequences into multiple sequence alignment fasta files for each gene. For big datasets, the robustness of species tree reconstruction under the coalescent model is not affected by the high degree of missing data when more than one sample per species is sampled (Hovmöller et al. 2013). We kept the first coding sequence in each gene sequence, and filtered the sequences based on the number of missing bases (<50%) and length (>150 bases), and then randomly sampled 1000 alignments. There were only 1,366 sites in the concatenated nuclear SNP dataset that overlapped with the sites located within the resulting gene alignments (0.3% of the SNP dataset, 0.08% and 1.2% of the total number of distinct sites and parsimony-informative sites within the gene alignments, respectively). For each of these genes, we used IQ-TREE v1.6.12 (Nguyen et al. 2015) to determine the best substitution model (Kalyaanamoorthy et al. 2017), estimate the best ML tree and perform 1000 ultra-fast bootstraps (Hoang et al. 2018). We used a coalescent-based phylogenetic method to infer the species tree from a set of the successfully inferred ML gene trees (988 trees) implemented in ASTRAL (Mirarab et al. 2014). ASTRAL is based on the multispecies coalescent model and uses a set of unrooted gene trees, taking a quartet of leaves at a time, to estimate the species tree (Mirarab et al. 2014). We conducted the analysis of the best supported ML gene trees in the multi-individual version of ASTRAL v5.7.3 (Rabiee et al. 2019) to estimate a species tree annotated with posterior probabilities as nodes support. We also estimated a species tree for each bootstrap replicate of each gene tree, and used these species trees to estimate a consensus species tree annotated with node support based on the bootstrap trees. We calculated the concordance factor, i.e. the percentage of gene trees recovering the nodes in the species tree, using IQ-TREE v2.0-rc1 (Minh et al. 2020).

Sliding window analyses. To explore the spatial distribution of incongruence across the genome, we generated phylogenetic trees in sliding windows. We generated fasta alignments in the same manner as at the previous step for our Coalescent-based analysis, but based on filtered read depth of 2-100, and extracted sequences for 100-kb non-overlapping windows for each sample using 49 scaffolds longer than 2M bases that equal to 44% (175.6M bases) of the total length of the reference. We then used a custom bash script to convert the sequences into the multiple sequence alignment fasta files for each sliding window. We discarded one sample based on the high number of missing bases. We reconstructed the best ML tree for each window in IQ-TREE v1.6.12 (Nguyen et al. 2015) using GTRGAMMA model allowing for a proportion of invariable sites with 1000 ultra-fast bootstrap replicates (Hoang et al. 2018). Using the resulting sliding window trees and the species tree, we calculated the concordance factor in IQ-TREE v2.0-rc1 (Minh et al. 2020) to infer the number of sliding window trees recovering the nodes in the species tree. To estimate how many sliding window trees recovered the species tree topology, we compared the inferred sliding window consensus tree topologies to the species tree topology using the script ‘findCommonTrees.py’ from Edelman et al. (2019). Given that the monophyly was strongly supported for all species in all analyses, we randomly selected and kept one sample per species in all trees for this analysis using the package ‘ape’ (Paradis and Schliep 2019: 2019) in the R statistical environment v3.6.3. We used Dendroscope 3 (Huson and Scornavacca 2012), FigTree v1.4.4 (Rambaut 2018) and the packages ‘ape’, ‘dendextend’ (Galili 2015), ‘phangorn’ (Schliep 2011: 2011), and ‘phytools’ (Revell 2012) in the R statistical environment v3.6.3 (R Core Team, 2020) to visualize and manipulate the results of the sliding window, coalescent-based and phylogenetic analyses.

QuIBL. We made use of QuIBL, a new tree-based method (Edelman et al. 2019), to differentiate between the models with ILS+introgression and with ILS only, and to obtain localized information on introgression. The method is described in detail in the Supplementary Materials (Section SMM5). To carry out the QuIBL analysis, we used the fasta alignments we generated for our sliding window analyses and kept one sample per species that had the highest sequencing coverage (Table S1). Because *S. compactum* showed strong genetic structure among the populations, we used two samples from two different populations in this analysis. We used 49 scaffolds longer than 2 Mb that equal to 44% (175.6M bases) of the total length of the reference. Since QuIBL is sensitive to recombination (Edelman et al. 2019), we extracted small 2-kb windows separated by 20 kb from each sample with Seqkit (Shen et al. 2016) to decrease the probability of sampling a window containing a recombination breakpoint (Edelman et al. 2019). We then discarded all windows that had samples with 100% of missing data and generated sliding window trees for the resulting 3,222 windows in the same manner as for our Sliding window tree analysis. We filtered the inferred ML-trees based on the number of parsimony-informative sites (>=10), and used the resulted 3,195 trees as an input for QuIBL (https://github.com/michaelmiyagi/QuIBL). The QuIBL output was analyzed in the R statistical environment v3.6.3 (https://github.com/michaelmiyagi/QuIBL/tree/master/analysis), and we used the species tree topology to assign the outgroup to each triplet. We also calculated the percentage of loci supporting discordant topologies and showing significant evidence for introgression. We used the package 'lattice' (Sarkar 2008), 'corrplot' (Wei and Simko 2017), and 'ggplot2' (Wickham 2016) to visualize the results of this analysis and the D-statistic tests.

D_{FOIL} analysis. To test for ancient introgression among the species, we used the D_{FOIL} statistic (Pease and Hahn 2015). This extended version of *D*-statistic allows estimating of gene flow direction, and inference of gene flow between the ancestor of a species pair and extant species, and has been widely used to infer recent and ancient introgression, often in combination with the traditional *D*-statistic (Fontaine et al. 2015; Pease et al. 2016; Árnason et al. 2018; Moodley et al. 2020; Vianna et al. 2020). We generated 100-kbp fasta alignments for one sample with the highest sequencing coverage per each species (Table S1) in the same manner as described above under "Sliding window analyses", except that we included all the scaffolds longer than 1M bases. The window size of 100-kb has been suggested as being sufficiently large to keep the proportion of false-positives very low (Pease and Hahn 2015; Pease et al. 2016; Vianna et al. 2020). We then converted the fasta alignments into D_{FOIL} input files (https://github.com/jbpease/dfoil), and performed the test for all phylogenetically correct, given our species tree, symmetrical five-taxon combinations with one ingroup clade older than another and *F. sericeum* as the outgroup. We filtered the windows based on minimum total number of sites (>1000) and minimum number of site counts for any of the D_{FOIL} components (>100) per window. We used a χ^2 goodness-of-fit test with a cutoff of p<0.001 to determine the significance of the inferred introgression signal (Pease and Hahn 2015; Pease et al. 2016). We then estimated the number of consecutive windows showing significant signal of any introgression for each five-taxon combination in the R statistical environment v3.6.3 (R Core Team, 2020).

Data availability

The raw sequencing reads generated in this study are available in the European Nucleotide Archive, and can be found under study PRJEB39751. The samples and the voucher specimens used in this study are deposited at the Trondheim Herbarium (TRH). Information on the samples can be found in Table S1.

Acknowledgements

This study was supported by The Research Council of Norway (project no. 250541/F20) to K.H. We thank the Nature Conservation Departments of the provinces of Salzburg and Tyrol for issuing sampling permits, and the Genomics Core Facility (GCF) at NTNU University and the Functional Genomics Center Zurich for sequencing our libraries. The GCF is funded by the Faculty of Medicine and Health Sciences (NTNU) and the Central Norway Regional Health Authority. This work was also supported by Swiss National Science Foundation grants 160004, 131726 and 184826, the EU's Horizon 2020 Research and Innovation Programme (PlantHUB   No. 722338), the Georges and Antoine Claraz Foundation, the Forschungskredit and the University Research Priority Program 'Evolution in Action' of the University of Zurich to P.S, the Research Council of Norway (project no. 287327) to M.D.M., and by the Carlsberg Foundation Young Researcher Fellowship (CF19-0712) to T.S.K. We thank the Department of Energy Joint Genome Institute for pre-publication access to the *Sphagnum angustifolium* (formerly *fallax*) genome sequence. The work conducted by the US DOE Joint Genome Institute is supported by the Office of Science of the US Department of Energy under Contract no. DE-AC02-05CH11231. Seydina I. Diop, Vanessa C. Bieker and Marcin Górny are gratefully acknowledged for assistance with bioinformatic processing of the data, and Tommy Prestø for assistance with depositing the collected accessions at the TRH Herbarium. We also thank Erik Boström and Narjes Yousefi for technical support in the molecular laboratory, and Andrew D. Foote for helpful comments during the progression of the study. At last, but not the least, we thank the editors and the two anonymous reviewers for their helpful comments on the manuscript.

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Tables

Table 1. Sampling summary. Number of samples collected from each of the allopatric populations for each of the 12 studied species.

Species	Subgenus	Sample size, Norway	Sample size, Austria	Sample size, Germany	Total number of samples
S. capillifolium	*Acutifolia*	8	7	2	17
S. compactum	*Rigida*	8	3	2	13
S. divinum	*Sphagnum*	9	9	0	18
S. fimbriatum	*Acutifolia*	4	4	3	11
S. flexuosum	*Cuspidata*	9	3	2	14
S. fuscum	*Acutifolia*	8	9	2	19
S. lindbergii	*Cuspidata*	9	3	2	14
S. platyphyllum	*Subsecunda*	8	4	0	12
S. riparium	*Cuspidata*	8	5	1	14
S. squarrosum	*Acutifolia*	9	8	2	19
S. subnitens	*Acutifolia*	8	9	2	19
S. tenellum	*Cuspidata*	12	6	2	20

Figure captions

Fig. 1. Sampling locations for and genetic differentiation among the individuals investigated. (A) Sampling locations. The symbols represent sampling locations for all 12 species, most collected from two parapatric populations in Austria (Tamsweg district [Austria 1] and Upper Austria [Austria 2]) and Norway (Namsos area [Norway 1] and Trondheim [Norway 2]), as well as from two populations in Germany (Table S1). (B) PCA of all individuals in the space of the first two principal components and (C) in the space of the first and the third principal components. All principal components were statistically significant ($p<0.001$, Fig. S1). (D) Individual assignment for each of the 190 individuals to well-defined species for the most-supported model with $K=12$ genetic clusters (ADMIXTURE analysis).

Fig. 2. Global pairwise weighted F_{ST} among the *Sphagnum* species investigated.

Fig. 3. Phylogenetic relationships among the species inferred using concatenated genetic markers (mitochondrial and nuclear dendrograms). The coloured lines connect samples of the same species on the two dendrograms, the colour code is shown on the left.

Fig. 4. The coalescent- and sliding-window based phylogenies. (A) The coalescent-based species tree. The node colour represents ASTRAL local posterior support according to the scale shown on the left. Colour of branches refers to the species as on (B), length of the branches is in coalescent units as shown at the bottom. (B) Cladograms of the coalescent-based species tree (heavy black lines) and of 500 gene trees (in green) randomly sampled from 988 inferred gene trees. Each species is downsampled to one sample (Table S1). The node colour represents node recovery (concordance factor), i.e. the fraction of all gene trees recovering a particular node, according to the scale shown on the left. (C) The most common topologies in gene trees and (D) in 100-kb sliding-window trees, the number represents the percentage of trees with the given topology.

Fig. 5. Tests for introgression. (A) Mean pairwise D per species pair (upper diagonal) and the mean total proportion of introgressed loci per species pair inferred through the QuIBL analysis (lower diagonal). Empty squares correspond to the pairs that have not been tested since they are sister species in our dataset, and 0 values correspond to non-significant values. The nuclear-based cladogram is shown on the left, red cross symbols designate the species that are placed in disagreement with the plastid-based phylogenies. The colour of boxes and branches represents the subgenus as shown on the top left. The cladogram includes lines schematically representing interspecific introgression events based on summarized results of the D_{FOIL} analysis. The colour and shape of the lines indicate the average portion of windows supporting introgression between the branches as shown on the top. (B) Schematic summary of results of D_{FOIL} analysis on a five-taxon phylogeny with four in-group taxa (P_1−P_4) and an outgroup (O), P_{12} is an ancestral branch. The numbers correspond to the proportion of introgressed windows for the corresponding type of introgression ($P_1 \Longleftrightarrow P_3$, $P_2 \Longleftrightarrow P_3$, $P_2 \Longleftrightarrow P_4$, $P_{12} \Longleftrightarrow P_3$, $P_{12} \Longleftrightarrow P_4$) averaged in all tested five-taxon topologies followed by its standard deviation. (C) Fixe-taxon phylogenies with the highest proportion of introgressed windows inferred with the D_{FOIL} analysis. The phylogenies include lines, which represent introgression events as in (A), the numbers represent the corresponding proportion of windows showing ancient introgression to the total number of windows analyzed for the phylogeny. Colour of species names highlights represents the subgenus the species belongs to as in (A).

Fig. 1

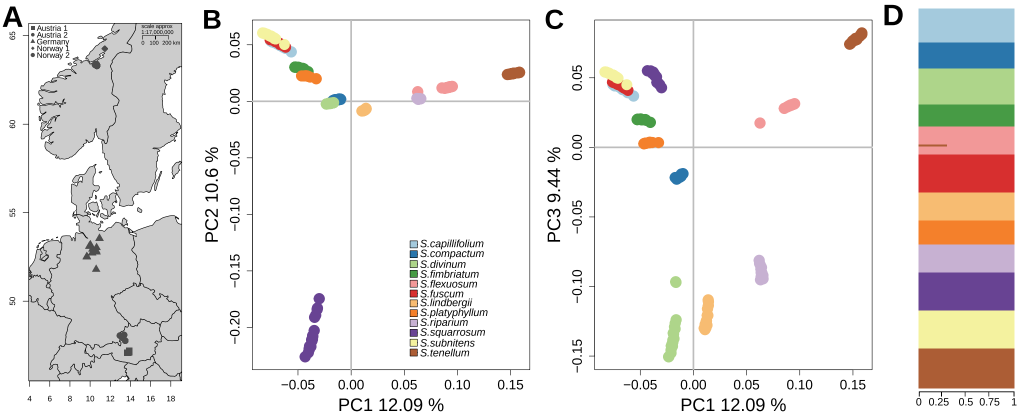
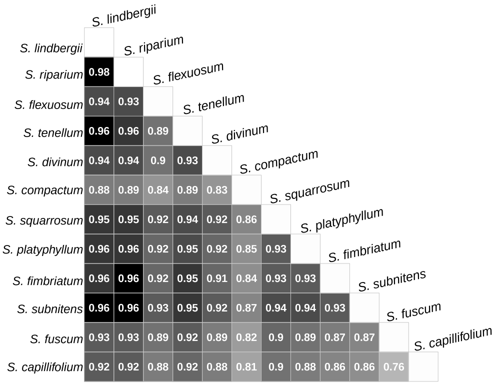


Fig. 2



	S. lindbergii	*S. riparium*	*S. flexuosum*	*S. tenellum*	*S. divinum*	*S. compactum*	*S. squarrosum*	*S. platyphyllum*	*S. fimbriatum*	*S. subnitens*	*S. fuscum*	*S. capillifolium*
S. lindbergii												
S. riparium	0.98											
S. flexuosum	0.94	0.93										
S. tenellum	0.96	0.96	0.89									
S. divinum	0.94	0.94	0.9	0.93								
S. compactum	0.88	0.89	0.84	0.89	0.83							
S. squarrosum	0.95	0.95	0.92	0.94	0.92	0.86						
S. platyphyllum	0.96	0.96	0.92	0.95	0.92	0.85	0.93					
S. fimbriatum	0.96	0.96	0.92	0.95	0.91	0.84	0.93	0.93				
S. subnitens	0.96	0.96	0.93	0.95	0.92	0.87	0.94	0.94	0.93			
S. fuscum	0.93	0.93	0.89	0.92	0.89	0.82	0.9	0.89	0.87	0.87		
S. capillifolium	0.92	0.92	0.88	0.92	0.88	0.81	0.9	0.88	0.86	0.86	0.76	

Fig. 3

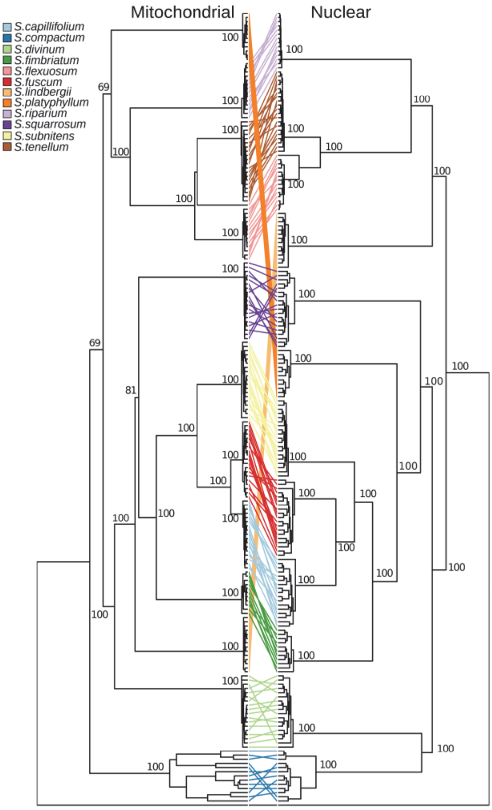

S.capillifolium
S.compactum
S.divinum
S.fimbriatum
S.flexuosum
S.fuscum
S.lindbergii
S.platyphyllum
S.riparium
S.squarrosum
S.subnitens
S.tenellum
Mitochondrial
Nuclear
69
69
81
100

Fig. 4

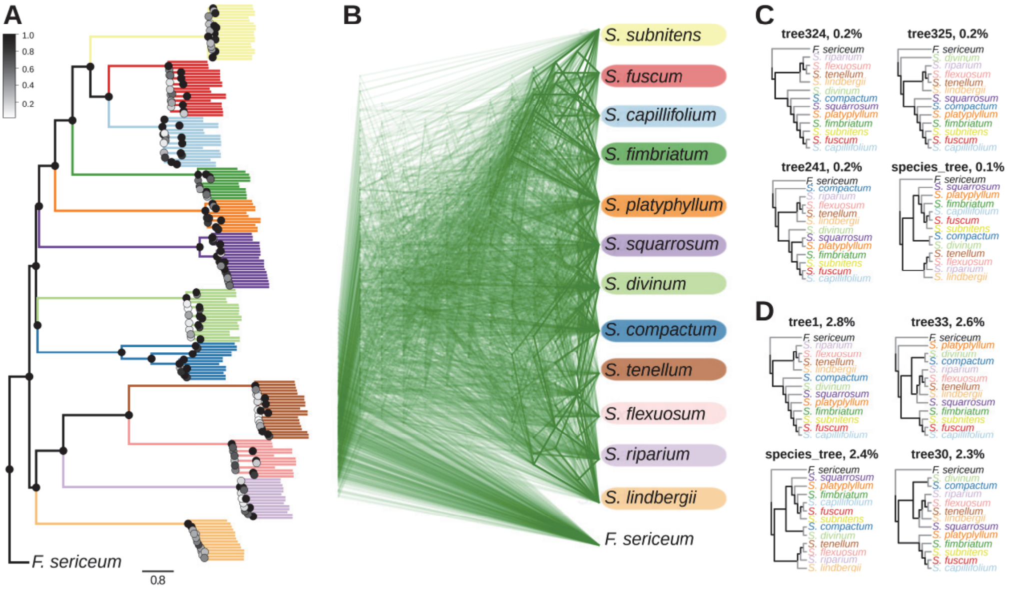
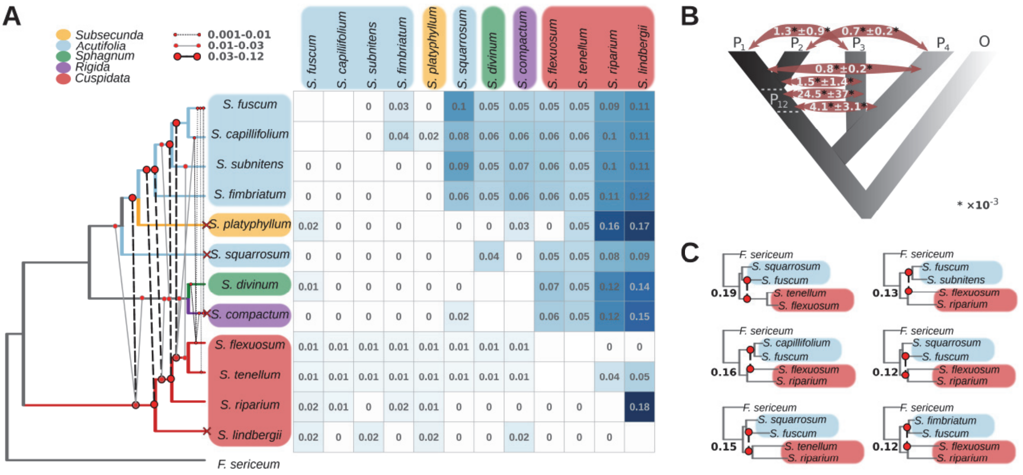

A
B
C
D
1.0
0.8
0.6
0.4
0.2
F. sericeum
0.8
S. subnitens
S. fuscum
S. capillifolium
S. fimbriatum
S. platyphyllum
S. squarrosum
S. divinum
S. compactum
S. tenellum
S. flexuosum
S. riparium
S. lindbergii
F. sericeum
tree324, 0.2%
tree325, 0.2%
tree241, 0.2%
species_tree, 0.1%
tree1, 2.8%
tree33, 2.6%
species_tree, 2.4%
tree30, 2.3%

Fig. 5



	S. fuscum	S. capillifolium	S. subnitens	S. fimbriatum	S. platyphyllum	S. squarrosum	S. divinum	S. compactum	S. flexuosum	S. tenellum	S. riparium	S. lindbergii
S. fuscum			0	0.03	0	0.1	0.05	0.05	0.05	0.05	0.09	0.11
S. capillifolium			0	0.04	0.02	0.08	0.06	0.06	0.06	0.06	0.1	0.11
S. subnitens	0	0		0	0	0.09	0.05	0.07	0.06	0.05	0.1	0.11
S. fimbriatum	0	0	0		0	0.06	0.05	0.06	0.06	0.05	0.11	0.12
S. platyphyllum	0.02	0	0	0		0	0	0.03	0	0.05	0.16	0.17
S. squarrosum	0	0	0	0	0		0.04	0	0.05	0.05	0.08	0.09
S. divinum	0.01	0	0	0	0	0			0.07	0.05	0.12	0.14
S. compactum	0	0	0	0	0	0.02			0.06	0.05	0.12	0.15
S. flexuosum	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01			0	0
S. tenellum	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01			0.04	0.05
S. riparium	0.02	0.01	0	0.02	0.01	0	0	0	0	0		0.18
S. lindbergii	0.02	0	0.02	0	0.02	0	0	0.02	0	0	0	

Supplementary Materials for

Extensive genome-wide phylogenetic discordance is due to incomplete lineage sorting and not ongoing introgression in a rapidly radiated bryophyte genus

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This PDF file includes:
Supplementary Materials and Methods
References
Figures S1 to S11
Tables S1 to S13

Supplementary Materials and Methods

SMM1, DNA extraction. Individual capitula of the dried samples were manually cleaned from visible exogenous contamination under a stereo microscope. In order to minimize contamination with the peatmoss ectomicrobiome and environmental DNA, the capitula were thoroughly washed in distilled water and air-dried. The dried tissue was lysed using the Qiagen Tissue Lyser II (Qiagen) for 120s at 30Hz, and total DNA was extracted from cleaned capitulum tissue following the protocol for dried tissue with RNase of the E.Z.N.A. HP Plant DNA Kit (Omega Bio-tek). DNA concentration was measured with the Qubit 2.0 Fluorometer (Thermo Fisher Scientific), and the length of the extracted DNA fragments was quantified on an agarose gel for a subset of the samples. Extracted DNA was fragmented to a mean length of approximately 400 bp via sonication using the Bioruptor Pico (Diagenode) with the following procedure: 5 or 6 cycles of 15 sec 'on' followed by 90 sec 'off'. The fragmentation was confirmed by visualizing the samples on an agarose gel.

SMM2, Testing the library preparation and sequencing. A subset of 11 samples, one sample for each species (except for *S. riparium*), was selected to perform a test library build and sequencing. Individual whole-genome DNA libraries were prepared using customized adapters (Meyer and Kircher 2010) following the Blunt-End-Single-Tube method by (Carøe et al. 2017). The method was developed for application to degraded DNA, but has been successfully used for modern data (e.g. Ribeiro et al. 2019; Bieker et al.) due to its simplicity and low cost. To attach sample-specific dual-indexing barcodes to the fragments, an indexing PCR was performed in 50 µL reactions with 5 µL of library template using custom indexed primers following the protocol for AmpliTaq Gold polymerase (Applied Biosystems) by (Kircher et al. 2012). The thermocycling profile was 10min at 95°C, n cycles of 30s at 95°C, 1min at 60°C and 45s at 72°C, and a final extension step of 5min at 72°C. To avoid the excess of PCR duplicates in the sequencing data, we determined the optimal number of cycles for each library with RT-PCR prior to indexing PCR. Amplified libraries were purified, and quantification and size estimation were performed with the Qubit 2.0 Fluorometer (Thermo Fisher Scientific) and the Bioanalyzer 2100 (Agilent). The libraries were pooled equimolarly based on the molarity of each library within the size range of 420-580 bp, and the pool was size-selected to a mean size of 450 bp using the BluePippin (Sage Science). The quality of the size-selected pool was checked with the Bioanalyzer 2100 (Agilent).

SMM3, Library preparation and estimation of the endogenous DNA content. The rest of the samples were prepared as described above, except that indexing PCR was carried out following the protocol for Herculase II Fusion polymerase (Agilent) by Dabney and Meyer (2012). Number of amplification cycles varied from 12 to 24 between the libraries based on the RT-PCR results. Negative extraction, library build and PCR controls were included in each run. The test sequencing run revealed DNA contamination of various degrees in the samples. Thus, we performed small-scale sequencing for the rest of the libraries to estimate per-sample endogenous DNA content. The libraries were pooled equimolarly into 2 pools (containing 156 and 62 samples) that were size-selected and quality-checked as described above and sequenced at the NTNU University Museum (Trondheim, Norway) on an Illumina MiniSeq in 150 bp paired-end format. The raw reads were treated in the same manner as described in "Sequencing data processing" in the main text, and for each sample, the ratio between the number of reads aligned to the reference genome and the total number of reads retained after trimming and filtering was used as the endogenous content estimate. Based on this estimate, 16 pools with 7 to 20 libraries each were prepared, size-selected and quality-checked as described above.

SMM4, D-statistics. Based on a phylogenetically correct topology for a triplet as (((P1,P2),P3),P4), D-statistic compares the number of derived and ancestral sites shared between P1 and P3 and between P2 and P3: D=(nABBA-nBABA)/(nABBA+nBABA) where nABBA is the number of sites for which P1 has an ancestral allele while P2 and P3 share a derived allele, and nBABA is number of sites for which P1 and P3 share a derived allele and P2 has an ancestral allele

(Green et al. 2010). Even under a scenario of incomplete lineage sorting, given that the (((P1,P2),P3),P4) topology is the true topology, P3 should share the same number of sites with both P1 and P2 if there is no gene flow between P3 and P1 or P3 and P2, so *D* is equal to 0 (Green et al. 2010; Martin et al. 2015). The null hypothesis about no gene flow between the species is rejected when D-statistic significantly deviates from 0 (Green et al. 2010; Martin et al. 2015). D-statistic can detect ancient and recent gene flow and is robust to different mutation rates and demography in P1 and P2 since their divergence, as well as to the effects of ILS (Green et al. 2010; Durand et al. 2011; Patterson et al. 2012; Martin et al. 2015). Traditional Patterson's D-statistic uses information from 1 individual per population. We used Abbababa2 algorithm implemented in ANGSD which extends D-statistic to use multiple individuals per species by using a weighted sum of the estimated allele frequencies for each individual in every population without calling genotypes (Soraggi et al. 2018). The method provides more accurate estimates of introgression compared to traditional Patterson's D-statistic (Green et al. 2010), and performs the best at low and medium-coverage data (1–10x) with sample size of 10 and more (Soraggi et al. 2018).

SMM5. QuIBL. QuIBL provides estimates of introgression proportion and of the likelihood that a locus falls into the model with introgression or with ILS only. For a triplet of species, topologies discordant to the true species tree should have exponentially distributed internal branch length given there is no gene flow among the species. If gene flow took place, the internal branch length distribution will in addition include an element corresponding to the time between the introgression event between the two species and the speciation event of all three species in the triplet (Edelman et al. 2019). QuIBL first estimates the distribution of internal branch length at each locus for a triplets of species. Using the genome-wide distribution, it then uses the expectation maximization algorithm to estimate which distribution each locus falls into, the parameters of the distribution and the likelihood that this distribution corresponds to the model with ILS and introgression (*K*=2) or with ILS only (*K*=1). The model that has the lowest Bayesian Information Criterion value is preferred, and a conservative threshold of BIC(>10) is used as a significance criterion (Edelman et al. 2019).

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Fig S1. Statistics for nuclear PCA. (A) Variance explained by the principal components and (B) Tracy-Widom statistics for each principal component.

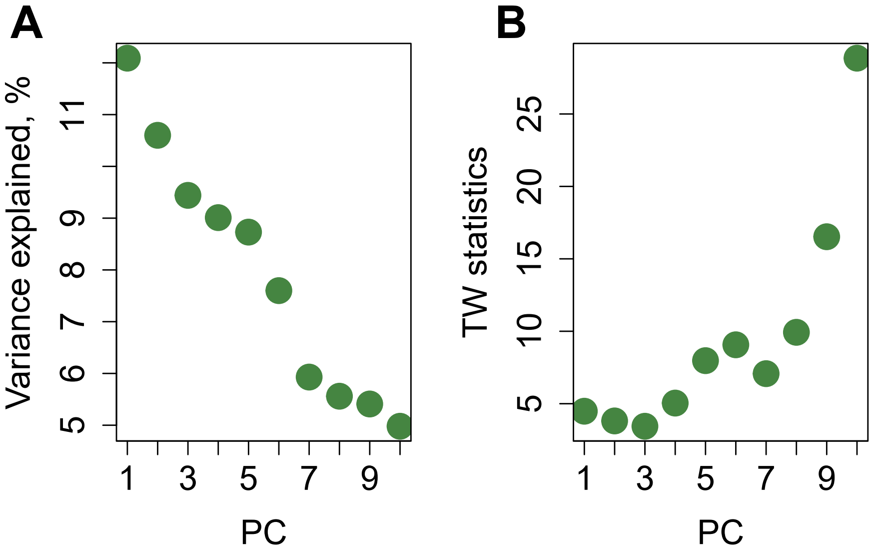


Fig. S2. PCA of *S. capillifolium, S. fuscum* and *S. subnitens* individuals (A) PCA of all individuals in the space of the first two principal components and (B) in the space of the first and the third principal components. (C) Variance explained by the principal components. (D) Tracy-Widom statistics for each principal component.

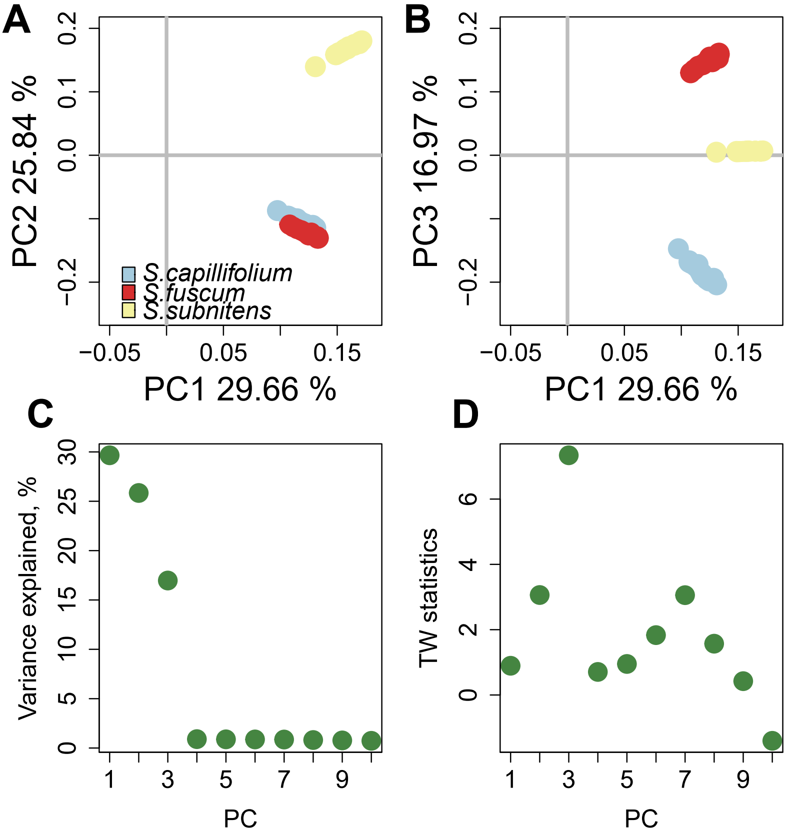


Fig. S3. ADMIXTURE results summary. (A) Boxplot with 10-fold cross-validation error (y axis) in all replicates with the corresponding number of *K* (x axis). (B) Replicates with the lowest 10-fold cross-validation error.

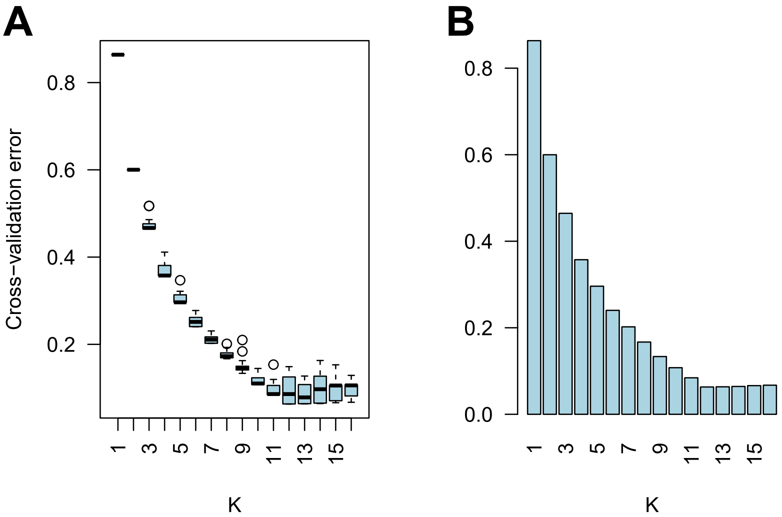
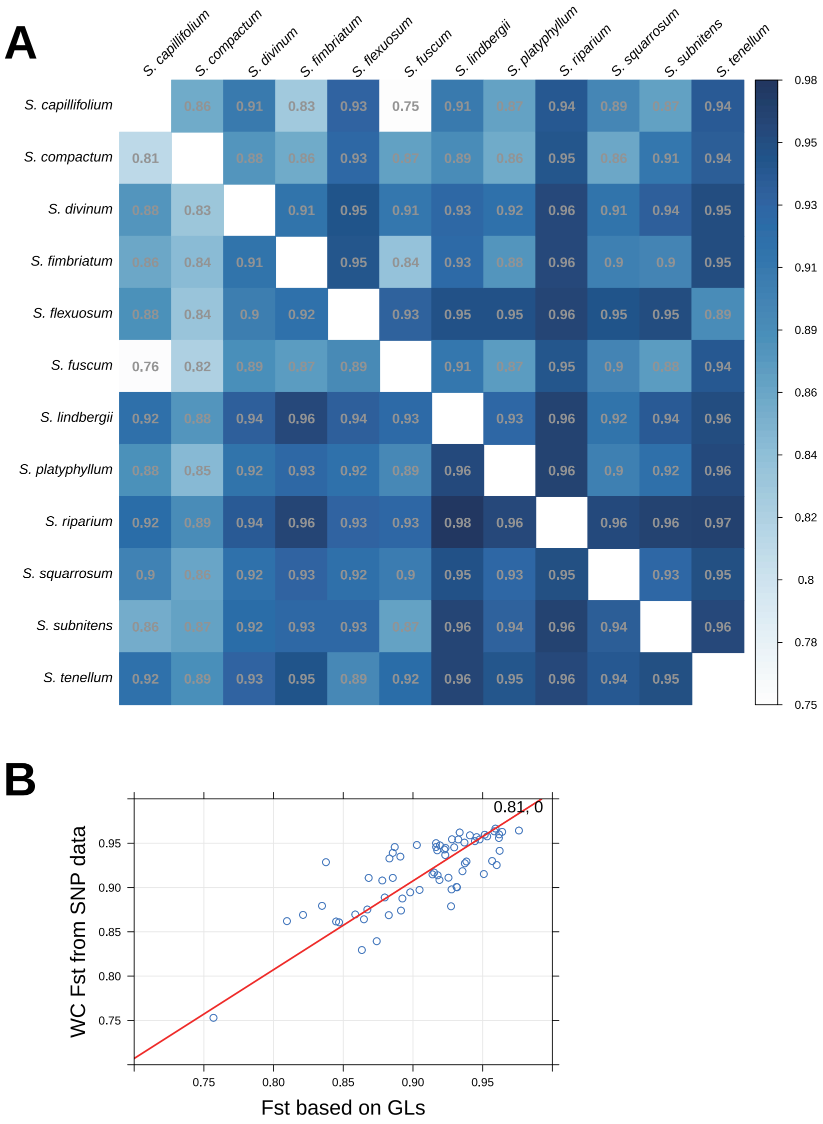
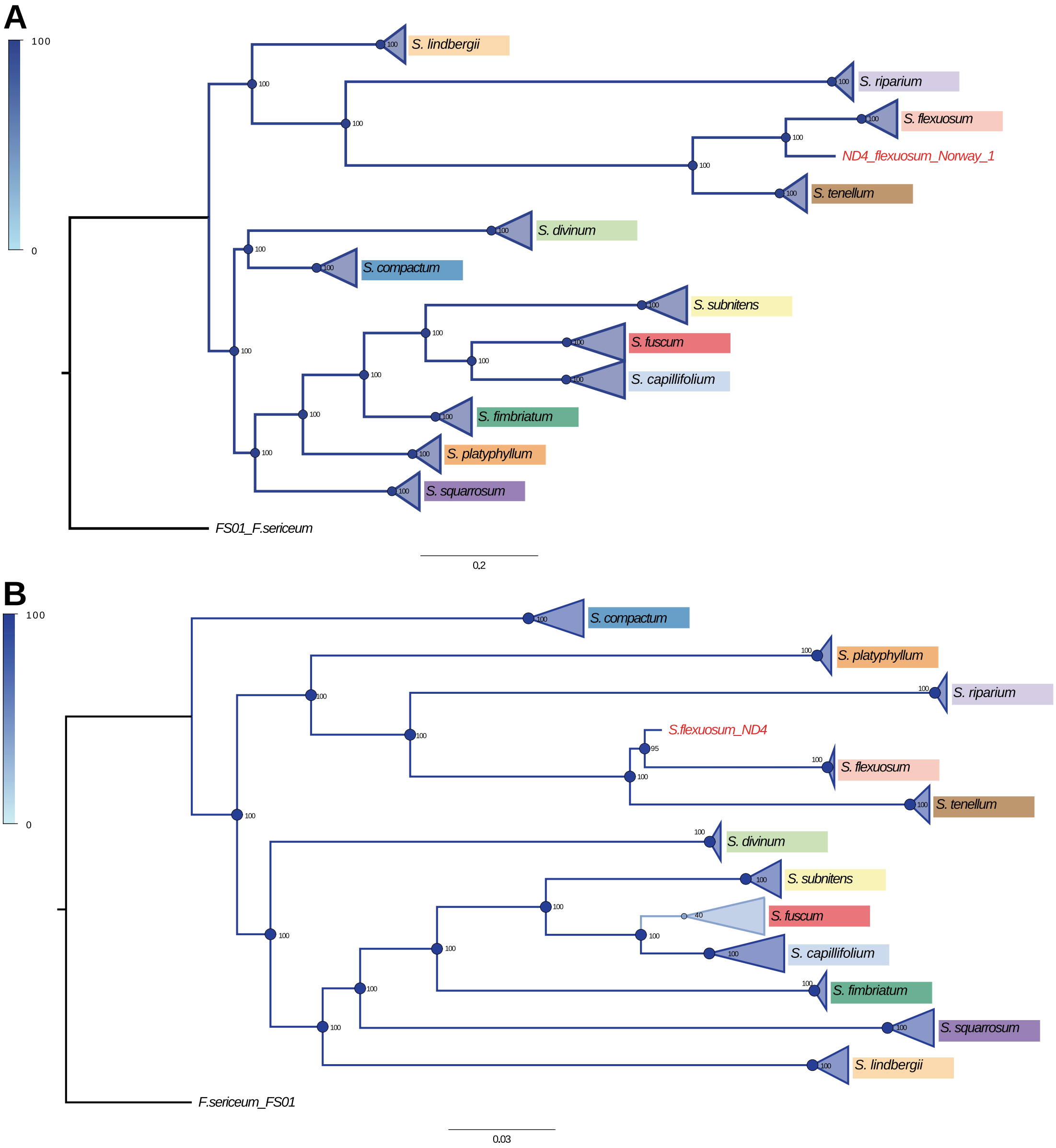


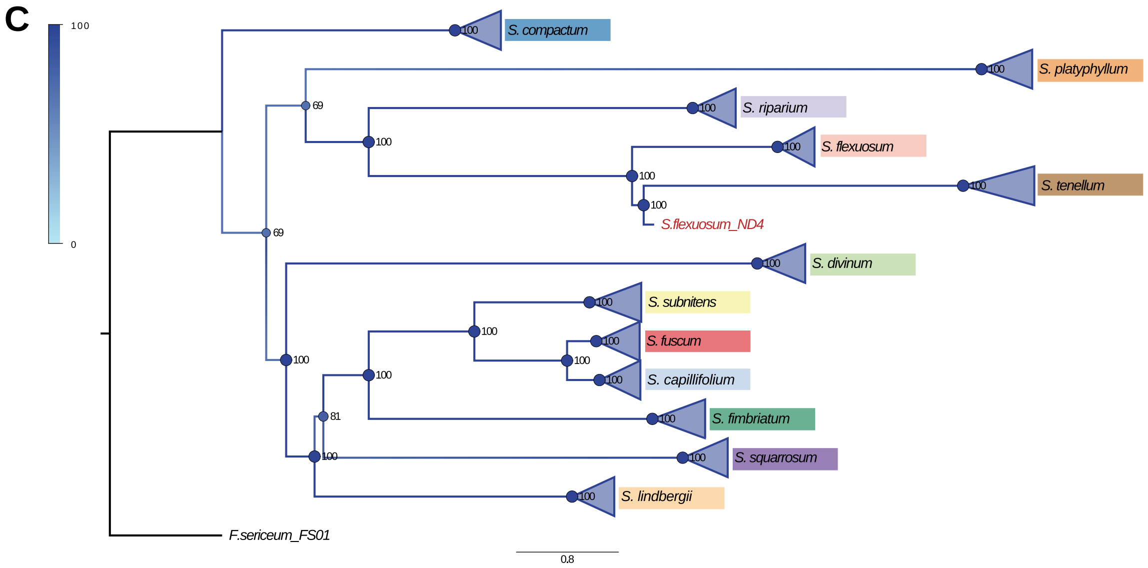
Fig S4. Pairwise F_{ST} among the species (A) based on the SNP data (upper triangle, GATK) and on genotype likelihoods (lower triangle, ANGSD). (B) Relationships between SNP-based and genotype likelihoods based pairwise F_{ST}, the numbers in the right corner correspond to r_S followed by the probability value.



	S. capillifolium	*S. compactum*	*S. divinum*	*S. fimbriatum*	*S. flexuosum*	*S. fuscum*	*S. lindbergii*	*S. platyphyllum*	*S. riparium*	*S. squarrosum*	*S. subnitens*	*S. tenellum*
S. capillifolium		0.86	0.91	0.83	0.93	0.75	0.91	0.87	0.94	0.89	0.87	0.94
S. compactum	0.81		0.88	0.86	0.93	0.87	0.89	0.86	0.95	0.86	0.91	0.94
S. divinum	0.88	0.83		0.91	0.95	0.91	0.93	0.92	0.96	0.91	0.94	0.95
S. fimbriatum	0.86	0.84	0.91		0.95	0.84	0.93	0.88	0.96	0.9	0.9	0.95
S. flexuosum	0.88	0.84	0.9	0.92		0.93	0.95	0.95	0.96	0.95	0.95	0.89
S. fuscum	0.76	0.82	0.89	0.87	0.89		0.91	0.87	0.95	0.9	0.88	0.94
S. lindbergii	0.92	0.88	0.94	0.96	0.94	0.93		0.93	0.96	0.92	0.94	0.96
S. platyphyllum	0.88	0.85	0.92	0.93	0.92	0.89	0.96		0.96	0.9	0.92	0.96
S. riparium	0.92	0.89	0.94	0.96	0.93	0.93	0.98	0.96		0.96	0.96	0.97
S. squarrosum	0.9	0.86	0.92	0.93	0.92	0.9	0.95	0.93	0.95		0.93	0.95
S. subnitens	0.86	0.87	0.92	0.93	0.93	0.87	0.96	0.94	0.96	0.94		0.96
S. tenellum	0.92	0.89	0.93	0.95	0.89	0.92	0.96	0.95	0.96	0.94	0.95	

Fig. S5. Phylogenetic relationships among the species inferred using concatenated genetic markers (A) using the nuclear genome, (B) using the chloroplast genome, (C) using the mitochondrial genome. Color of the nodes refers to the bootstrap support of the respective node according to the scale bar shown on the left, all the branch tips within each species were collapsed (triangle symbols). (D) Full nuclear-based tree, color of the nodes and branches refer to the bootstrap support of the respective node according to the scale bar shown on the left.




C
100
0
S. compactum
S. platyphyllum
S. riparium
S. flexuosum
S. tenellum
S.flexuosum_ND4
S. divinum
S. subnitens
S. fuscum
S. capillifolium
S. fimbriatum
S. squarrosum
S. lindbergii
F.sericeum_FS01
69
81
100
0.8

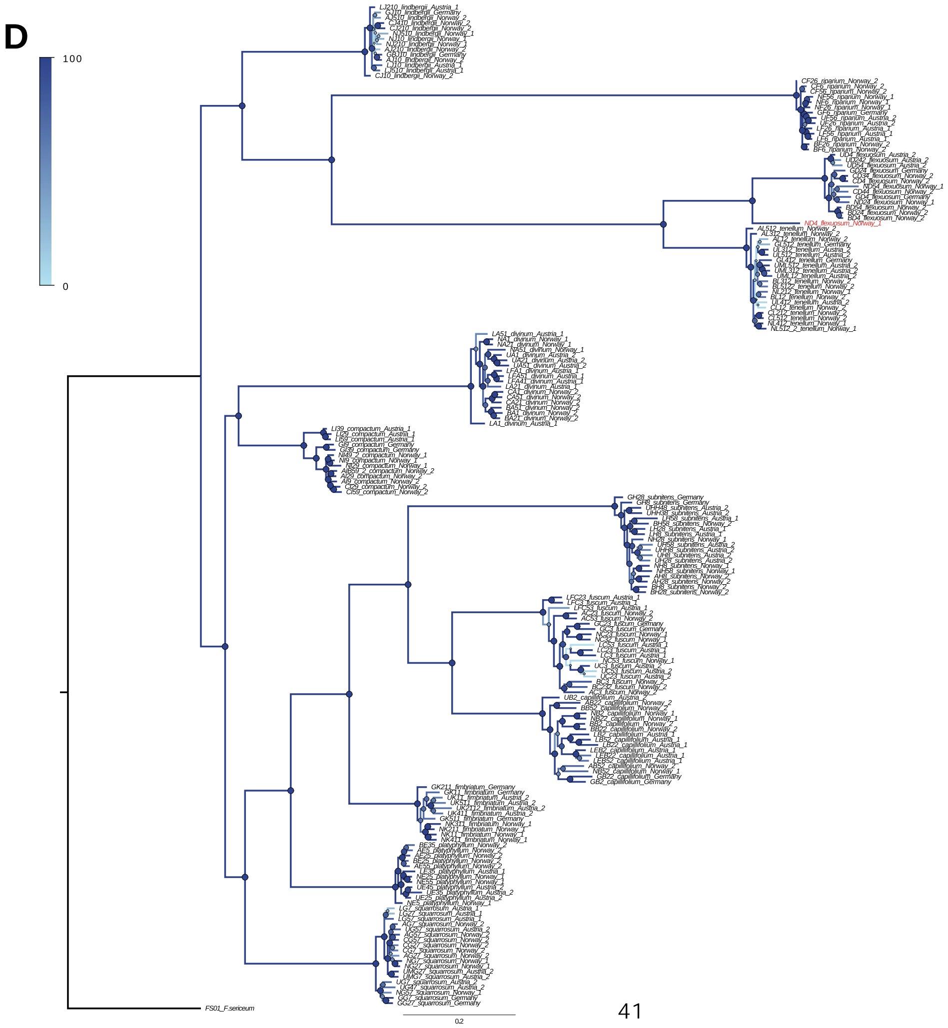

D
100
0
ND4_flexuosum_Norway_1
FS01_F.sericeum
0.2

Fig. S6. Coalescent-based and sliding-window analyses (A) Node recovery by the gene trees versus branch length in coalescent units. (B) The consensus tree inferred with sliding window analysis. Color of the nodes refers to the concordance factor as the percentage of sliding window trees recovering the respective node, color of tip branches refers to the species as shown on the right.

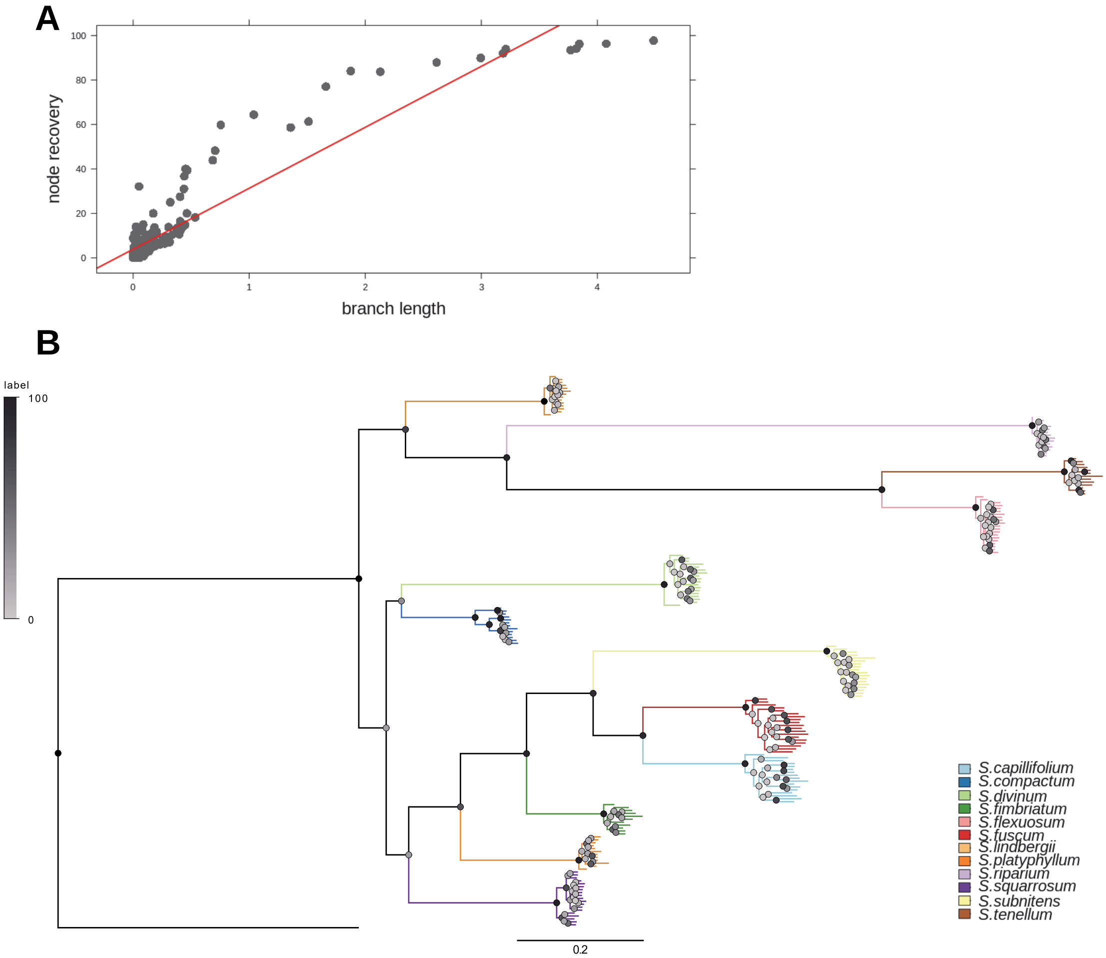


Fig. S7. *D*-statistic using *F. sericeum* as the outgroup in relation to other factors. (A) *D*-statistic, number of sites in all triplets, and number of triplets for a species pair. In all boxplots, the central line is the median, and lower and upper hinges represent the first and third quartiles. (B) The relationships between the number of sites under comparison and absolute *D*-statistic per triplet. (C) The relationships between the number of sites under comparison and average absolute *D*-statistic (calculated using triplets with significant *D* values only) per species pair. (D) The relationship between pairwise absolute average *D*-statistic (calculated using triplets with significant *D* values only) and pairwise F_{ST}. (E) Spearman's rank correlation between *D*-statistic values per triplet obtained with window size of 1-Mbp and 5-Mbp using *F. sericeum* as the outgroup. In all scatterplots, the numbers correspond to r_s followed by the probability value.

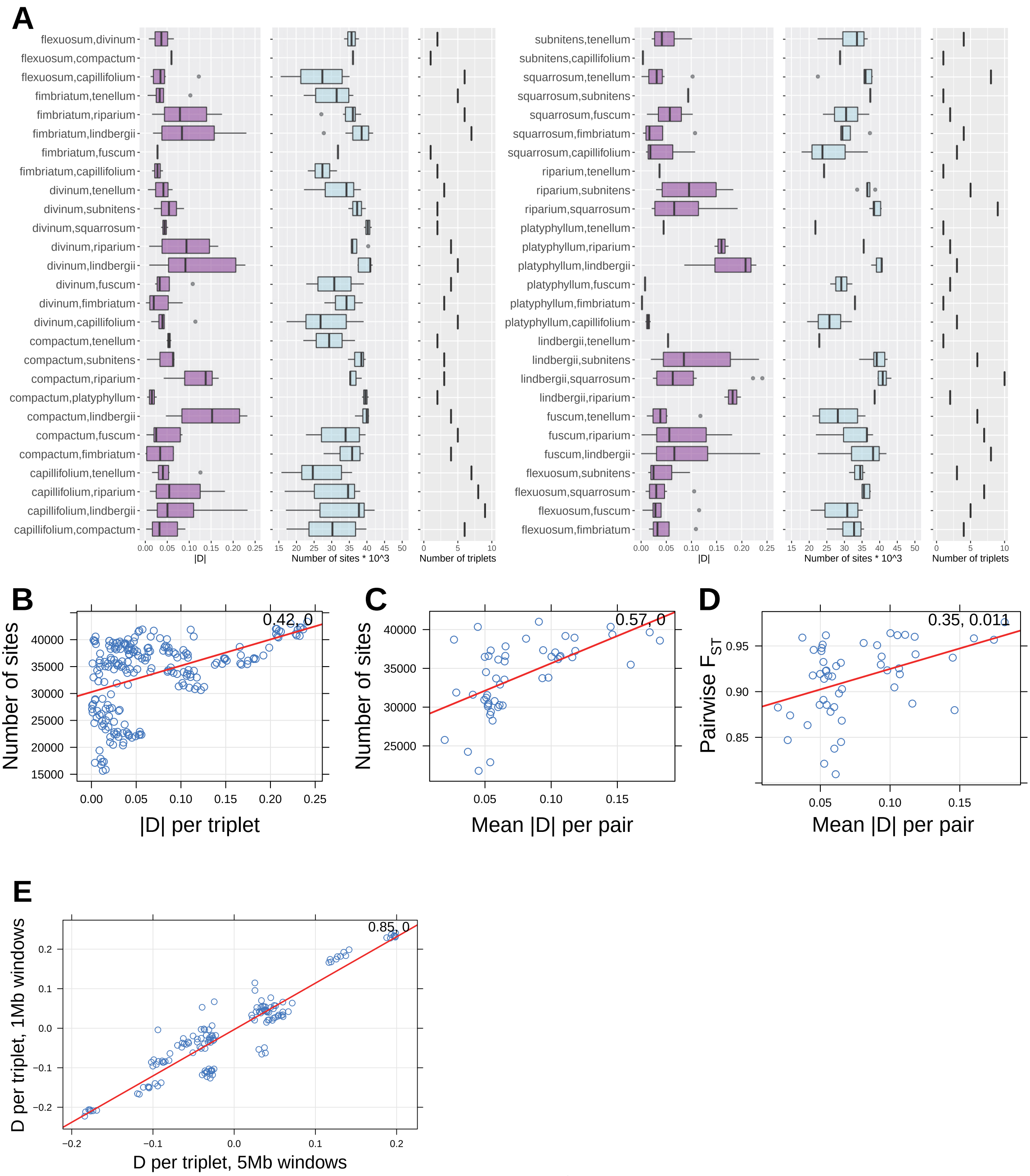


Fig. S8. Migration events reconstructed in TreeMix, the trees inferred with 0 to 5 migration events allowed (top to bottom) are shown on the left. The replicate with the highest likelihood is shown, the numbers correspond to variation explained by the model, standard error and the likelihood of the model. The scale bar on the left represent the migration weight. The residuals of the corresponding model are shown on the right, the scale on the right shows the standard error.

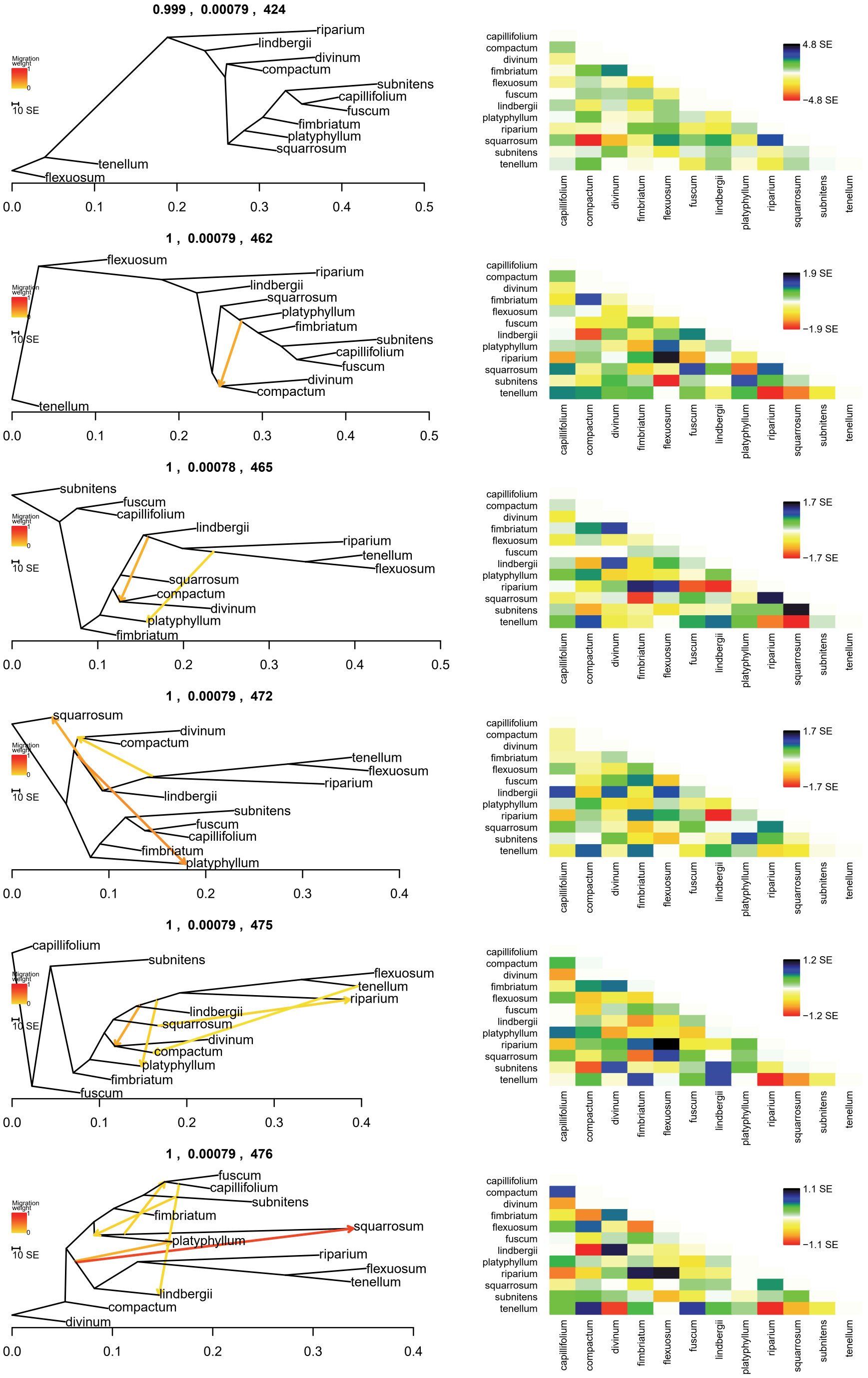


Fig. S9. QuIBL results for the triplets with significant evidence for introgression. (A) Relationships between internal branch length in coalescent units and total proportion of introgressed loci, blue symbols represent triplets with true topology, orange symbols represent triplets with discordant topology. (B) Distribution of average introgression probability for discordant topologies inferred with QuIBL in 2-kb sliding windows across the scaffolds longer than 1 Mb, gray colour corresponds to 20-kb gaps among the sliding windows or to sliding windows with missing data.

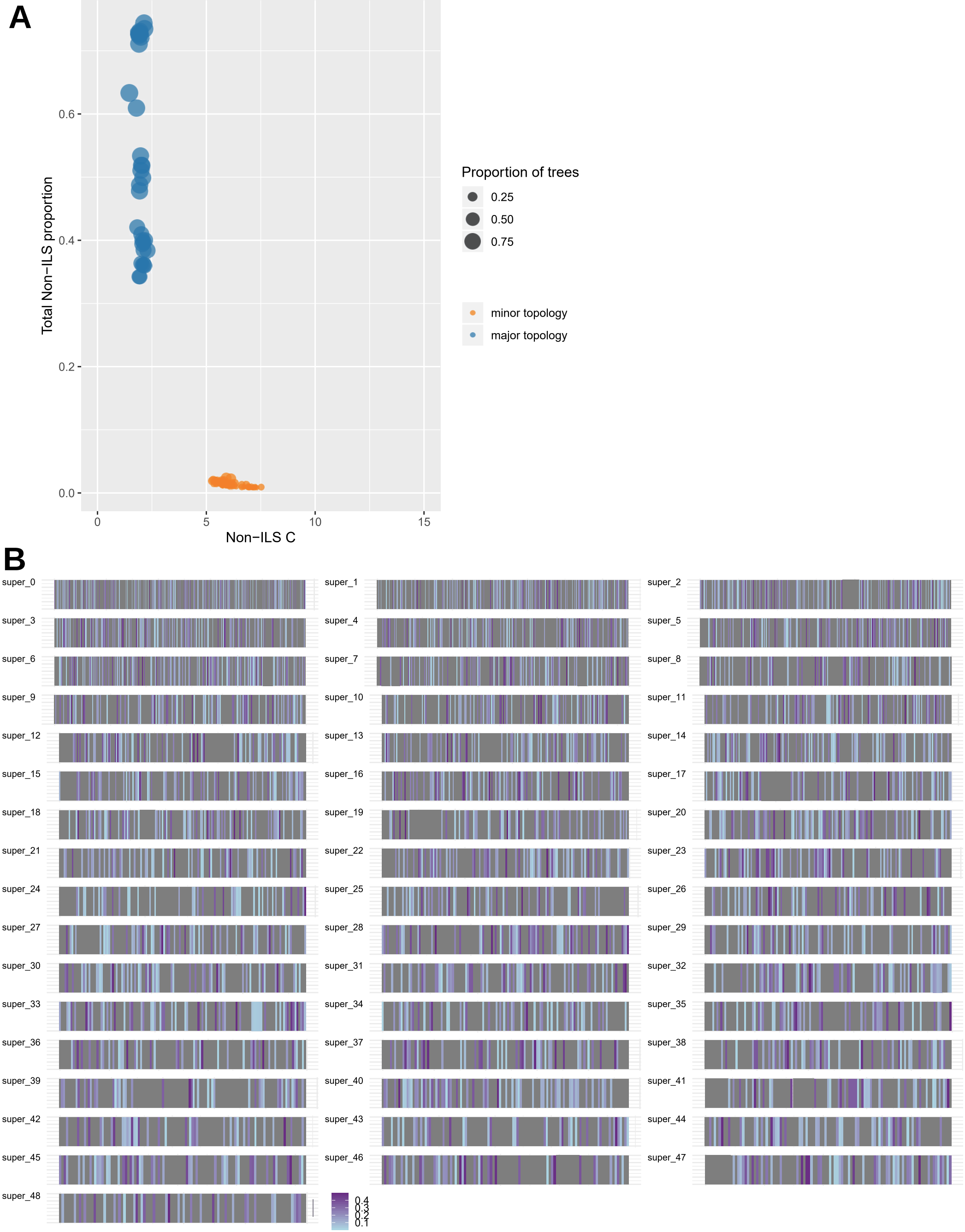


Fig. S10. Number of blocks of consecutive windows showing significant evidence for any introgression among all five-taxon phylogenies. In all boxplots, the central line is the median, and lower and upper hinges represent the first and third quartiles.

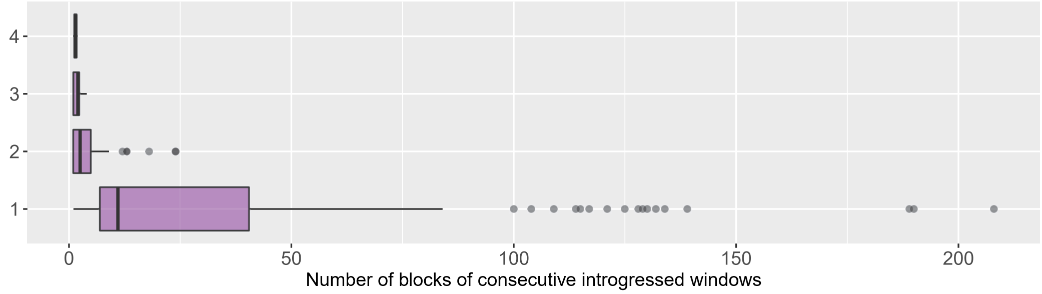


Fig. S11. Percentage of potentially heterozygous variants in all species.

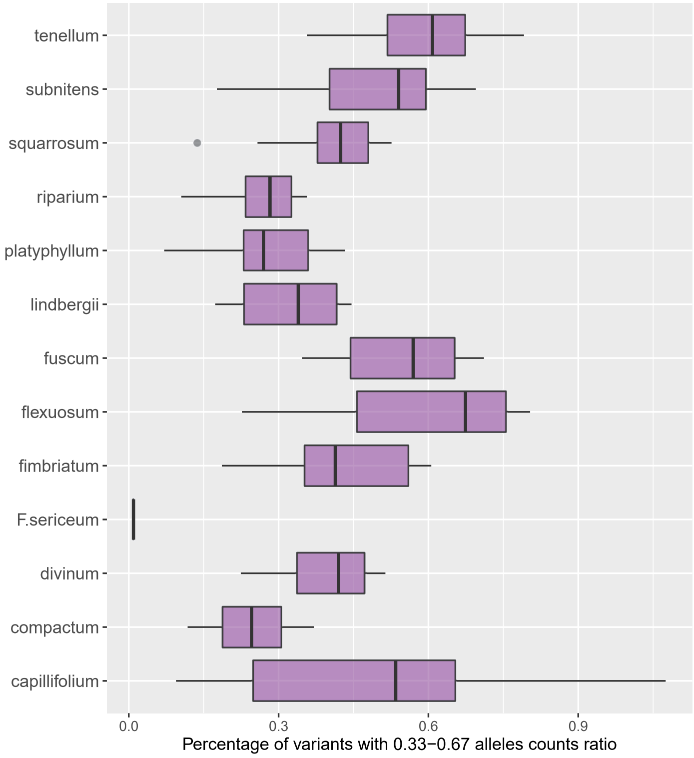


Table S1. Sequencing summary for all samples included in the study

Samples in italics and underlined belong to the first set of built libraries, samples in bold were used for QuIBL analysis, sampled marked with * were used for D_{FOIL} analysis

Columns 1-12:

1 Fraction of mapped reads, nuclear genome, 2 Fraction of uniquely mapped reads, nuclear genome, 3 Fraction of PCR duplicates, nuclear genome, 4 Coverage, nuclear genome, 5 Fraction of mapped reads, mitochondrial genome, 6 Fraction of uniquely mapped reads, mitochondrial genome, 7 Fraction of PCR duplicates, mitochondrial genome, 8 Coverage, mitochondrial genome, 9 Fraction of mapped reads, chloroplast genome, 10 Fraction of uniquely mapped reads, chloroplast genome, 11 Fraction of PCR duplicates, chloroplast genome, 12 Coverage, chloroplast genome

No	ID	Species	Subgenus	Trondheim Herbarium accession ID	Date	Population	Number of retained reads, nuclear genome	Number of nucleotides in retained reads, nuclear genome	1	2	3	4	5	6	7	8	9	10	11	12	Country	State	Locality	Ecology	Altitude, m	Coordinates
1	**BB22***	***Sphagnum capillifolium***	***Acutifolia***	111888	**08/09/17**	**Norway_2**	**60,862,104**	**8,383,151,942**	**0.59**	**0.54**	**0.09**	**9.72**	**0.01**	**0.01**	**0.15**	**421**	**0.02**	**0.02**	**0.10**	**1,119**	Norway	Sør-Trøndelag	Gjeddvatnet	Pine mire forest, hummock	158	63.38164°N 10.60083°E
2	BB2	*Sphagnum capillifolium*	*Acutifolia*	111887	08/09/17	Norway_2	62,162,736	9,244,531,875	0.53	0.45	0.15	9.54	0.01	0.01	0.24	520	0.02	0.02	0.18	1,176	Norway	Sør-Trøndelag	Gjeddvatnet	Pine mire forest, hummock	158	63.38164°N 10.60083°E
3	*NB22*	*Sphagnum capillifolium*	*Acutifolia*	111899	*10/25/17*	*Norway_1*	*70,680,196*	*10,646,672,446*	*0.43*	*0.39*	*0.11*	*9.08*	*0.00*	*0.00*	*0.21*	*220*	*0.01*	*0.01*	*0.13*	*704*	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Ombrotrophic bog with pine, transition to spruce forest, hummocks with Calluna sp.	102	64.26684°N 11.45651°E
4	UB2	*Sphagnum capillifolium*	*Acutifolia*	111707	06/04/17	Austria_2	107,612,440	14,466,330,665	0.32	0.26	0.19	8.24	0.01	0.00	0.21	415	0.01	0.00	0.18	489	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Poor fen hummock	752	47.76595°N 13.48423°E
5	LEB52	*Sphagnum capillifolium*	*Acutifolia*	111701	05/30/17	Austria_1	119,196,794	16,400,680,342	0.31	0.26	0.18	8.15	0.00	0.00	0.24	356	0.01	0.01	0.18	950	Austria	Salzburg	Distr. Lungau, Murau Mountains, Wirtsalmmoor	Hummock	1528	47.18762°N 13.86381°E
6	LEB2	*Sphagnum capillifolium*	*Acutifolia*	111697	05/30/17	Austria_1	84,499,031	11,657,053,659	0.38	0.35	0.08	7.71	0.01	0.01	0.14	423	0.02	0.02	0.09	1,203	Austria	Salzburg	Distr. Lungau, Murau Mountains, Wirtsalmmoor	Hummock	1528	47.18762°N 13.86381°E
7	LEB22	*Sphagnum capillifolium*	*Acutifolia*	111698	05/30/17	Austria_1	62,035,484	8,584,788,149	0.40	0.37	0.07	6.42	0.01	0.01	0.13	297	0.01	0.01	0.08	761	Austria	Salzburg	Distr. Lungau, Murau Mountains, Wirtsalmmoor	Hummock	1528	47.18762°N 13.86381°E
8	AB52	*Sphagnum capillifolium*	*Acutifolia*	111896	08/09/17	Norway_2	91,372,793	12,702,540,130	0.33	0.26	0.20	6.36	0.00	0.00	0.25	153	0.00	0.00	0.21	303	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Ombrotrophic bog with pine (Calluna-dominated)	354	63.31275°N 10.66944°E
9	NB2	*Sphagnum capillifolium*	*Acutifolia*	111898	10/25/17	Norway_1	42,589,626	6,371,502,031	0.49	0.42	0.15	6.03	0.01	0.01	0.23	212	0.01	0.01	0.17	498	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Ombrotrophic bog with pine, transition to spruce forest, hummocks with Calluna sp.	102	64.26684°N 11.45651°E
10	BB52	*Sphagnum capillifolium*	*Acutifolia*	111891	08/09/17	Norway_2	48,214,459	7,191,656,722	0.42	0.34	0.19	5.36	0.01	0.00	0.26	197	0.01	0.01	0.20	394	Norway	Sør-Trøndelag	Gjeddvatnet	Pine mire forest, hummock	158	63.38164°N 10.60083°E
11	LB2	*Sphagnum capillifolium*	*Acutifolia*	111702	05/31/17	Austria_1	47,057,474	6,762,906,161	0.41	0.35	0.14	5.28	0.01	0.01	0.21	258	0.02	0.02	0.16	714	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Among Pinus mugo in hummocks at mire margin	1697	47.08393°N 13.78174°E
12	LB52	*Sphagnum capillifolium*	*Acutifolia*	111706	05/31/17	Austria_1	82,765,470	12,220,213,716	0.26	0.17	0.35	4.80	0.01	0.00	0.42	263	0.01	0.01	0.37	598	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Among Pinus mugo in hummocks at mire margin	1697	47.08393°N 13.78174°E
13	GB2	*Sphagnum capillifolium*	*Acutifolia*	111840	11/03/17	Germany	40,904,976	6,020,011,281	0.31	0.26	0.16	3.60	0.00	0.00	0.21	112	0.01	0.01	0.17	268	Germany	Niedersachsen	Lower Saxony, Uelzen, Kallenbrock			52.856460°N 10.584730°E
14	NB52	*Sphagnum capillifolium*	*Acutifolia*	111902	10/25/17	Norway_1	32,416,618	4,877,314,908	0.32	0.28	0.14	3.08	0.00	0.00	0.20	105	0.01	0.01	0.16	177	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Ombrotrophic bog with pine, transition to spruce forest, hummocks with Calluna sp.	102	64.26684°N 11.45651°E
15	LB22	*Sphagnum capillifolium*	*Acutifolia*	111703	05/31/17	Austria_1	88,227,786	12,634,408,935	0.16	0.13	0.20	3.03	0.00	0.00	0.25	111	0.00	0.00	0.20	186	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Among Pinus mugo in hummocks at mire margin	1697	47.08393°N 13.78174°E
16	AB22	*Sphagnum capillifolium*	*Acutifolia*	111893	08/09/17	Norway_2	29,231,890	4,111,029,844	0.47	0.30	0.36	2.80	0.01	0.00	0.32	115	0.01	0.01	0.28	172	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Ombrotrophic bog with pine (Calluna-dominated)	354	63.31275°N 10.66944°E
17	GB22	*Sphagnum capillifolium*	*Acutifolia*	111841	11/03/17	Germany	14,604,158	2,150,522,439	0.45	0.39	0.14	1.92	0.00	0.00	0.17	47	0.01	0.01	0.14	85	Germany	Niedersachsen	Lower Saxony, Uelzen, Kallenbrock			52.856460°N 10.584730°E
18	**LI39***	***Sphagnum compactum***	***Rigida***	111710	**06/01/17**	**Austria_1**	**103,366,533**	**14,594,188,906**	**0.45**	**0.42**	**0.07**	**11.91**	**0.01**	**0.01**	**0.15**	**751**	**0.03**	**0.03**	**0.10**	**3,057**	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Grassed fen/meadow with Nardus stricta, Andromeda polifolia and Eriophorum vaginatum	1867	47.10812°N 13.88392°E

19	**AI9**	***Sphagnum compactum***	***Rigida***	111910	**08/09/17**	**Norway_2**	**36,405,206**	**5,434,879,303**	**0.74**	**0.67**	**0.10**	**8.02**	**0.02**	**0.01**	**0.19**	**512**	**0.05**	**0.04**	**0.13**	**1,511**	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Pure fen lawn	354	63.31293°N 10.66901°E
20	AI29	*Sphagnum compactum*	*Rigida*	111911	08/09/17	Norway_2	105,785,366	14,169,650,874	0.29	0.25	0.15	6.91	0.00	0.00	0.20	307	0.01	0.01	0.15	865	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Pure fen lawn	354	63.31293°N 10.66901°E
21	LI59	*Sphagnum compactum*	*Rigida*	111712	06/01/17	Austria_1	164,245,506	23,012,381,835	0.16	0.14	0.09	5.27	0.00	0.00	0.19	273	0.01	0.01	0.11	1,168	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Grassed fen/meadow with Nardus stricta, Andromeda polifolia and Eriophorum vaginatum	1867	47.10812°N 13.88392°E
22	NI9	*Sphagnum compactum*	*Rigida*	111916	10/25/17	Norway_1	269,534,230	39,053,630,598	0.11	0.06	0.41	5.27	0.00	0.00	0.46	259	0.00	0.00	0.39	751	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Ombrotrophic disturbed hollows, transition to carpets	99	64.26518°N 11.45628°E
23	AIB59_2	*Sphagnum compactum*	*Rigida*	111914	08/09/17	Norway_2	37,885,102	5,372,682,731	0.47	0.42	0.11	5.07	0.01	0.01	0.16	301	0.02	0.02	0.13	605	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Pure fen lawn	354	63.31293°N 10.66901°E
24	NI49_2	*Sphagnum compactum*	*Rigida*	111919	10/25/17	Norway_1	42,592,514	6,243,884,591	0.35	0.28	0.19	4.03	0.01	0.01	0.26	251	0.02	0.02	0.21	672	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Ombrotrophic disturbed hollows, transition to carpets	99	64.26518°N 11.45628°E
25	CI59	*Sphagnum compactum*	*Rigida*	111908	08/09/17	Norway_2	124,186,209	18,324,206,828	0.15	0.09	0.37	3.64	0.00	0.00	0.44	175	0.01	0.00	0.38	503	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Ombrotrophic carpet	177	63.36555°N 10.52418°E
26	LI29	*Sphagnum compactum*	*Rigida*	111709	06/01/17	Austria_1	106,045,325	15,625,267,679	0.12	0.10	0.17	3.59	0.00	0.00	0.27	241	0.01	0.01	0.18	979	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Grassed fen/meadow with Nardus stricta, Andromeda polifolia and Eriophorum vaginatum	1867	47.10812°N 13.88392°E
27	GI9	*Sphagnum compactum*	*Rigida*	111845	11/03/17	Germany	51,039,380	7,413,560,102	0.24	0.20	0.18	3.45	0.00	0.00	0.23	170	0.01	0.01	0.19	542	Germany	Niedersachsen	Lower Saxony, Bispingen, Benninghofer Heide			53.102470°N 9.925330°E
28	CI29	*Sphagnum compactum*	*Rigida*	111905	08/09/17	Norway_2	34,604,748	5,165,608,970	0.27	0.22	0.18	2.67	0.00	0.00	0.23	79	0.00	0.00	0.18	125	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Ombrotrophic carpet	177	63.36555°N 10.52418°E
29	GI39	*Sphagnum compactum*	*Rigida*	111847	11/03/17	Germany	19,555,078	2,772,931,702	0.42	0.37	0.12	2.25	0.01	0.00	0.17	73	0.01	0.01	0.12	207	Germany	Niedersachsen	Lower Saxony, Bispingen, Benninghofer Heide			53.102470°N 9.925330°E
30	*NI29*	*Sphagnum compactum*	*Rigida*	111917	*10/25/17*	*Norway_1*	*90,976,813*	*13,205,628,467*	*0.09*	*0.07*	*0.22*	*1.83*	*0.00*	*0.00*	*0.30*	*79*	*0.00*	*0.00*	*0.22*	*174*	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Ombrotrophic disturbed hollows, transition to carpets	99	64.26518°N 11.45628°E
31	***NA21****	***Sphagnum divinum***	***Sphagnum***	111929	***10/03/17***	***Norway_1***	***58,313,076***	***8,710,223,620***	***0.61***	***0.55***	***0.10***	***10.46***	***0.01***	***0.01***	***0.20***	***390***	***0.02***	***0.02***	***0.12***	***1,287***	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Low bog hummock		64.26684°N 11.45651°E
32	LFA41	*Sphagnum divinum*	*Sphagnum*	111723	06/01/17	Austria_1	158,627,028	21,892,608,433	0.28	0.21	0.23	10.32	0.01	0.00	0.29	574	0.01	0.01	0.24	1,555	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Low hummock in poor fen	1869	47.10778°N 13.88391°E
33	NA1	*Sphagnum divinum*	*Sphagnum*	111928	10/03/17	Norway_1	64,535,863	9,589,109,577	0.47	0.41	0.12	8.54	0.01	0.01	0.23	339	0.02	0.02	0.15	1,356	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Low bog hummock		64.26684°N 11.45651°E
34	LA51	*Sphagnum divinum*	*Sphagnum*	111719	05/31/17	Austria_1	154,489,040	21,285,303,879	0.23	0.22	0.08	8.06	0.00	0.00	0.15	522	0.01	0.01	0.10	1,337	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Among Pinus mugo in hummocks at mire margin	1697	47.08393°N 13.78174°E
35	LFA51	*Sphagnum divinum*	*Sphagnum*	111724	06/01/17	Austria_1	116,203,118	17,127,900,102	0.28	0.22	0.23	7.95	0.01	0.00	0.30	451	0.01	0.01	0.24	1,270	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Low hummock in poor fen	1869	47.10778°N 13.88391°E
36	CA51	*Sphagnum divinum*	*Sphagnum*	111937	06/04/18	Norway_2	62,544,938	9,093,925,295	0.41	0.38	0.09	7.34	0.01	0.01	0.16	354	0.02	0.01	0.10	898	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Margin, transition between ombrotrophic mire and forest	175	63.36565°N 10.52501°E
37	LA21	*Sphagnum divinum*	*Sphagnum*	111716	05/31/17	Austria_1	81,292,880	11,936,944,208	0.33	0.28	0.16	7.19	0.01	0.01	0.24	416	0.02	0.02	0.18	1,261	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Among Pinus mugo in hummocks at mire margin	1697	47.08393°N 13.78174°E
38	BA21	*Sphagnum divinum*	*Sphagnum*	111923	08/09/17	Norway_2	33,926,162	4,861,134,339	0.76	0.66	0.13	6.92	0.02	0.02	0.20	487	0.06	0.05	0.15	1,619	Norway	Sør-Trøndelag	Gjeddvatnet	Mire margin	153	63.38117°N 10.60006°E
39	LFA1	*Sphagnum divinum*	*Sphagnum*	111720	06/01/17	Austria_1	64,682,172	9,299,114,119	0.37	0.31	0.16	6.34	0.01	0.01	0.24	434	0.02	0.02	0.18	1,033	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Low hummock in poor fen	1869	47.10778°N 13.88391°E
40	BA51	*Sphagnum divinum*	*Sphagnum*	111926	08/09/17	Norway_2	77,173,148	10,778,292,872	0.37	0.26	0.28	6.22	0.01	0.00	0.36	266	0.02	0.02	0.31	1,160	Norway	Sør-Trøndelag	Gjeddvatnet	Mire margin	153	63.38117°N 10.60006°E
41	CA1	*Sphagnum divinum*	*Sphagnum*	111933	06/04/18	Norway_2	48,879,083	7,068,316,144	0.45	0.40	0.10	6.13	0.01	0.01	0.17	236	0.02	0.01	0.11	672	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Margin, transition between ombrotrophic mire and forest	175	63.36565°N 10.52501°E
42	CA21	*Sphagnum divinum*	*Sphagnum*	111934	06/04/18	Norway_2	56,700,030	8,357,905,701	0.33	0.28	0.13	5.10	0.00	0.00	0.20	183	0.01	0.01	0.14	503	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Margin, transition between ombrotrophic mire and forest	175	63.36565°N 10.52501°E
43	UA1	*Sphagnum divinum*	*Sphagnum*	111726	06/03/17	Austria_2	35,492,493	5,272,566,799	0.52	0.36	0.30	4.40	0.01	0.01	0.35	242	0.03	0.02	0.31	696	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor		428	48.05410°N 12.95769°E
44	UA21	*Sphagnum divinum*	*Sphagnum*	111727	06/03/17	Austria_2	53,565,280	7,633,528,014	0.32	0.26	0.16	4.24	0.00	0.00	0.22	141	0.01	0.01	0.18	348	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor		428	48.05410°N 12.95769°E
45	UA51	*Sphagnum divinum*	*Sphagnum*	111730	06/03/17	Austria_2	23,304,482	3,337,663,360	0.59	0.52	0.12	3.83	0.01	0.01	0.18	263	0.03	0.03	0.15	681	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor		428	48.05410°N 12.95769°E

46	BA1	*Sphagnum divinum*	*Sphagnum*	111922	08/09/17	Norway_2	20,059,546	3,000,795,576	0.60	0.50	0.17	3.45	0.02	0.01	0.24	228	0.03	0.03	0.18	575	Norway	Sør-Trøndelag	Gjeddvatnet	Mire margin	153	63.38117°N 10.60006°E
47	NA51	*Sphagnum divinum*	*Sphagnum*	111932	10/03/17	Norway_1	55,579,465	8,075,301,106	0.25	0.18	0.26	3.37	0.00	0.00	0.32	145	0.01	0.01	0.27	490	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Low bog hummock		64.26684°N 11.45651°E
48	LA1	*Sphagnum divinum*	*Sphagnum*	111715	05/31/17	Austria_1	24,757,611	3,630,607,832	0.39	0.34	0.15	2.77	0.01	0.01	0.21	242	0.03	0.02	0.17	603	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Among Pinus mugo in hummocks at mire margin	1697	47.08393°N 13.78174°E
49	***NK211****	***Sphagnum fimbriatum***	***Acutifolia***	111941	***10/03/17***	***Norway_1***	***65,928,684***	***9,687,960,278***	***0.60***	***0.51***	***0.15***	***10.78***	***0.01***	***0.01***	***0.23***	***336***	***0.02***	***0.02***	***0.16***	***1,229***	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
50	NK11	*Sphagnum fimbriatum*	*Acutifolia*	111940	10/03/17	Norway_1	120,274,630	16,147,507,383	0.32	0.30	0.05	9.80	0.01	0.01	0.09	457	0.01	0.01	0.06	1,035	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
51	NK411	*Sphagnum fimbriatum*	*Acutifolia*	111943	10/03/17	Norway_1	169,889,629	21,831,876,192	0.25	0.23	0.10	9.71	0.00	0.00	0.14	538	0.01	0.01	0.12	1,037	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
52	GK11	*Sphagnum fimbriatum*	*Acutifolia*	111850	11/02/17	Germany	74,130,375	10,069,417,111	0.38	0.37	0.04	7.20	0.01	0.01	0.09	341	0.02	0.02	0.05	1,361	Germany	Niedersachsen	Lower Saxony, Wedemark, Bissendorfer Moor			52.510970°N 9.677530°E
53	GK211	*Sphagnum fimbriatum*	*Acutifolia*	111851	11/02/17	Germany	47,177,600	6,636,440,293	0.48	0.44	0.10	6.38	0.01	0.01	0.17	264	0.03	0.02	0.11	1,056	Germany	Niedersachsen	Lower Saxony, Wedemark, Bissendorfer Moor			52.510970°N 9.677530°E
54	UK11	*Sphagnum fimbriatum*	*Acutifolia*	111739	06/04/17	Austria_2	53,894,387	7,335,800,155	0.40	0.34	0.13	5.49	0.01	0.01	0.18	227	0.01	0.01	0.14	513	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Poor fen margin, slightly disturbed	509	47.92954°N 13.17987°E
55	GK511	*Sphagnum fimbriatum*	*Acutifolia*	111854	11/02/17	Germany	61,724,900	8,988,227,360	0.36	0.25	0.29	5.37	0.01	0.00	0.33	256	0.01	0.01	0.29	538	Germany	Niedersachsen	Lower Saxony, Wedemark, Bissendorfer Moor			52.510970°N 9.677530°E
56	UK411	*Sphagnum fimbriatum*	*Acutifolia*	111742	06/04/17	Austria_2	30,173,653	4,486,154,257	0.45	0.41	0.10	4.14	0.01	0.01	0.19	244	0.03	0.02	0.14	722	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Poor fen margin, slightly disturbed	509	47.92954°N 13.17987°E
57	UK511	*Sphagnum fimbriatum*	*Acutifolia*	111743	06/04/17	Austria_2	54,359,222	8,044,056,703	0.28	0.22	0.22	3.96	0.01	0.01	0.29	331	0.02	0.02	0.24	889	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Poor fen margin, slightly disturbed	509	47.92954°N 13.17987°E
58	NK311	*Sphagnum fimbriatum*	*Acutifolia*	111942	10/03/17	Norway_1	25,163,167	3,756,427,162	0.48	0.42	0.11	3.60	0.01	0.01	0.17	129	0.01	0.01	0.13	285	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
59	UK2112	*Sphagnum fimbriatum*	*Acutifolia*	111740	06/04/17	Austria_2	43,183,466	6,271,706,860	0.23	0.18	0.21	2.40	0.00	0.00	0.26	74	0.01	0.00	0.24	177	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Poor fen margin, slightly disturbed	509	47.92954°N 13.17987°E
60	*ND4*	*Sphagnum flexuosum*	*Cuspidata*	111951	*10/03/17*	*Norway_1*	*69,023,606*	*10,125,123,323*	*0.62*	*0.57*	*0.09*	*13.70*	*0.01*	*0.01*	*0.17*	*426*	*0.02*	*0.02*	*0.11*	*1,178*	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
61	**BD54***	***Sphagnum flexuosum***	***Cuspidata***	111949	**08/09/17**	**Norway_2**	**77,877,775**	**10,354,872,883**	**0.53**	**0.50**	**0.06**	**12.06**	**0.01**	**0.01**	**0.09**	**541**	**0.01**	**0.01**	**0.07**	**842**	Norway	Sør-Trøndelag	Gjeddvatnet	Intermediate fen carpet	154	63.38119°N 10.59959°E
62	GD24	*Sphagnum flexuosum*	*Cuspidata*	111856	11/03/17	Germany	35,691,924	5,300,920,487	0.79	0.73	0.08	9.00	0.01	0.01	0.16	318	0.03	0.02	0.10	872	Germany	Niedersachsen	Lower Saxony, Döhle, Radenbachtal			53.177936°N 10.023846°E
63	CD4	*Sphagnum flexuosum*	*Cuspidata*	111957	06/04/18	Norway_2	39,149,660	5,808,139,221	0.58	0.51	0.11	6.97	0.01	0.01	0.18	217	0.02	0.01	0.13	530	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Poor-intermediate fen	174	63.36639°N 10.51944°E
64	CD34	*Sphagnum flexuosum*	*Cuspidata*	111959	06/04/18	Norway_2	50,095,180	7,360,501,517	0.43	0.39	0.09	6.72	0.01	0.00	0.15	231	0.01	0.01	0.11	462	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Poor-intermediate fen	174	63.36639°N 10.51944°E
65	BD4	*Sphagnum flexuosum*	*Cuspidata*	111945	08/09/17	Norway_2	26,335,874	3,797,072,700	0.81	0.72	0.12	6.51	0.01	0.01	0.20	261	0.03	0.03	0.13	737	Norway	Sør-Trøndelag	Gjeddvatnet	Intermediate fen carpet	154	63.38119°N 10.59959°E
66	CD44	*Sphagnum flexuosum*	*Cuspidata*	111960	06/04/18	Norway_2	59,599,622	8,910,607,491	0.40	0.30	0.23	6.47	0.00	0.00	0.29	181	0.01	0.01	0.25	409	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Poor-intermediate fen	174	63.36639°N 10.51944°E
67	BD24	*Sphagnum flexuosum*	*Cuspidata*	111946	08/09/17	Norway_2	25,111,618	3,757,932,159	0.71	0.64	0.10	5.73	0.02	0.01	0.19	324	0.03	0.03	0.12	685	Norway	Sør-Trøndelag	Gjeddvatnet	Intermediate fen carpet	154	63.38119°N 10.59959°E
68	ND24	*Sphagnum flexuosum*	*Cuspidata*	111952	10/03/17	Norway_1	24,305,554	3,445,339,213	0.75	0.72	0.04	5.71	0.01	0.01	0.09	185	0.02	0.02	0.05	497	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
69	UD4	*Sphagnum flexuosum*	*Cuspidata*	111745	06/04/17	Austria_2	29,517,238	4,317,025,451	0.66	0.53	0.19	5.62	0.02	0.01	0.24	391	0.04	0.03	0.21	932	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Swamp Alnus glutinosa forest	748	47.76602°N 13.48518°E
70	UD242	*Sphagnum flexuosum*	*Cuspidata*	111746	06/04/17	Austria_2	42,096,545	6,183,020,819	0.37	0.29	0.22	4.30	0.01	0.01	0.27	275	0.02	0.02	0.23	713	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Swamp Alnus glutinosa forest	748	47.76602°N 13.48518°E
71	GD4	*Sphagnum flexuosum*	*Cuspidata*	111855	11/03/17	Germany	15,909,530	2,377,180,426	0.74	0.62	0.16	3.58	0.01	0.01	0.22	120	0.02	0.02	0.17	260	Germany	Niedersachsen	Lower Saxony, Döhle, Radenbachtal			53.177936°N 10.023846°E
72	UD54	*Sphagnum flexuosum*	*Cuspidata*	111749	06/04/17	Austria_2	16,850,075	2,468,066,548	0.64	0.57	0.11	3.40	0.01	0.01	0.17	181	0.03	0.03	0.13	518	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Swamp Alnus glutinosa forest	748	47.76602°N 13.48518°E
73	ND54	*Sphagnum flexuosum*	*Cuspidata*	111955	10/03/17	Norway_1	15,313,808	2,295,862,929	0.51	0.46	0.11	2.52	0.01	0.01	0.16	79	0.01	0.01	0.12	167	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
74	**LFC23***	***Sphagnum fuscum***	***Acutifolia***	111757	**06/01/17**	**Austria_1**	**188,357,461**	**25,897,569,983**	**0.37**	**0.24**	**0.33**	**11.80**	**0.00**	**0.00**	**0.38**	**448**	**0.02**	**0.01**	**0.34**	**1,892**	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Hummocks in poor sloping fen	1874	47.10706°N 13.88425°E
75	AC53	*Sphagnum fuscum*	*Acutifolia*	111974	08/09/17	Norway_2	125,067,910	16,861,856,255	0.37	0.32	0.15	10.60	0.00	0.00	0.22	392	0.01	0.01	0.17	926	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Ombrotrophic bog with pine (Calluna-dominated)	354	63.31275°N 10.66944°E
76	BC232	*Sphagnum fuscum*	*Acutifolia*	111965	08/09/17	Norway_2	80,339,266	10,470,164,834	0.44	0.39	0.12	8.96	0.01	0.01	0.16	386	0.01	0.01	0.12	740	Norway	Sør-Trøndelag	Gjeddvatnet	Low hummock on ombrotrophic bog	157	63.38178°N 10.60146°E

77	LFC53	*Sphagnum fuscum*	*Acutifolia*	111760	06/01/17	Austria_1	97,400,942	13,749,719,116	0.36	0.28	0.22	8.46	0.01	0.00	0.31	416	0.03	0.02	0.24	1,908	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Hummocks in poor sloping fen	1874	47.10706°N 13.88425°E
78	LC23	*Sphagnum fuscum*	*Acutifolia*	111752	05/30/17	Austria_1	117,569,738	15,921,249,720	0.31	0.29	0.06	8.26	0.00	0.00	0.12	383	0.01	0.01	0.07	1,092	Austria	Salzburg	Distr. Lungau, Murau Mountains, Wirtsalmmoor	Hummocks	1529	47.18761°N 13.86390°E
79	NC32	*Sphagnum fuscum*	*Acutifolia*	111978	10/03/17	Norway_1	90,937,010	13,577,108,003	0.34	0.25	0.27	7.36	0.00	0.00	0.35	118	0.01	0.00	0.28	347	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Bog hummock		64.26684°N 11.45651°E
80	AC3	*Sphagnum fuscum*	*Acutifolia*	111970	08/09/17	Norway_2	48,566,818	6,760,460,600	0.55	0.48	0.12	7.04	0.01	0.01	0.19	285	0.02	0.02	0.12	895	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Ombrotrophic bog with pine (Calluna-dominated)	354	63.31275°N 10.66944°E
81	LFC3	*Sphagnum fuscum*	*Acutifolia*	111756	06/01/17	Austria_1	66,546,859	9,443,969,128	0.42	0.33	0.21	6.99	0.01	0.00	0.29	273	0.02	0.02	0.22	1,183	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Hummocks in poor sloping fen	1874	47.10706°N 13.88425°E
82	LC53	*Sphagnum fuscum*	*Acutifolia*	111755	05/30/17	Austria_1	85,978,350	12,248,224,235	0.33	0.23	0.30	6.20	0.01	0.00	0.37	345	0.02	0.01	0.31	1,205	Austria	Salzburg	Distr. Lungau, Murau Mountains, Wirtsalmmoor	Hummocks	1529	47.18761°N 13.86390°E
83	UC3	*Sphagnum fuscum*	*Acutifolia*	111762	06/04/17	Austria_2	47,602,040	7,146,001,932	0.47	0.38	0.19	6.20	0.01	0.01	0.28	251	0.02	0.01	0.21	616	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Poor fen hummock	752	47.76595°N 13.48423°E
84	*NC23*	*Sphagnum fuscum*	*Acutifolia*	*111977*	*10/03/17*	*Norway_1*	*55,131,900*	*8,261,748,900*	*0.39*	*0.34*	*0.15*	*6.08*	*0.00*	*0.00*	*0.22*	*107*	*0.01*	*0.00*	*0.16*	*275*	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Bog hummock		64.26684°N 11.45651°E
85	UC53	*Sphagnum fuscum*	*Acutifolia*	111766	06/04/17	Austria_2	62,953,413	8,701,316,600	0.36	0.31	0.13	5.88	0.01	0.01	0.17	263	0.01	0.01	0.14	709	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Poor fen hummock	752	47.76595°N 13.48423°E
86	AC23	*Sphagnum fuscum*	*Acutifolia*	111971	08/09/17	Norway_2	69,918,822	10,079,920,147	0.37	0.25	0.34	5.55	0.01	0.00	0.38	226	0.01	0.01	0.31	561	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Ombrotrophic bog with pine (Calluna-dominated)	354	63.31275°N 10.66944°E
87	UC23	*Sphagnum fuscum*	*Acutifolia*	111763	06/04/17	Austria_2	48,107,706	7,115,658,588	0.38	0.33	0.15	5.31	0.01	0.01	0.23	237	0.02	0.01	0.17	687	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Poor fen hummock	752	47.76595°N 13.48423°E
88	BC3	*Sphagnum fuscum*	*Acutifolia*	111964	08/09/17	Norway_2	88,903,601	10,686,511,794	0.24	0.19	0.22	4.47	0.00	0.00	0.24	126	0.00	0.00	0.19	142	Norway	Sør-Trøndelag	Gjeddvatnet	Low hummock on ombrotrophic bog	157	63.38178°N 10.60146°E
89	GC23	*Sphagnum fuscum*	*Acutifolia*	111861	11/02/17	Germany	26,830,958	3,994,730,221	0.55	0.46	0.15	4.25	0.01	0.01	0.23	151	0.02	0.02	0.17	440	Germany	Schleswig-Holstein	Bokel, Bullenkuhle			52.813197°N 10.516974°E
90	LC3	*Sphagnum fuscum*	*Acutifolia*	111751	05/30/17	Austria_1	51,488,949	7,265,538,716	0.30	0.25	0.15	3.89	0.01	0.00	0.22	197	0.01	0.01	0.18	519	Austria	Salzburg	Distr. Lungau, Murau Mountains, Wirtsalmmoor	Hummocks	1529	47.18761°N 13.86390°E
91	GC3	*Sphagnum fuscum*	*Acutifolia*	111860	11/02/17	Germany	43,772,030	6,525,022,516	0.30	0.23	0.22	3.46	0.00	0.00	0.28	104	0.01	0.01	0.23	296	Germany	Schleswig-Holstein	Bokel, Bullenkuhle			52.813197°N 10.516974°E
92	NC53	*Sphagnum fuscum*	*Acutifolia*	111980	10/03/17	Norway_1	21,072,562	3,145,408,422	0.54	0.44	0.19	3.12	0.01	0.01	0.25	130	0.02	0.02	0.21	389	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Bog hummock		64.26684°N 11.45651°E
93	***NJ210****	***Sphagnum lindbergii***	***Cuspidata***	111989	***10/03/17***	***Norway_1***	***55,896,288***	***8,406,335,894***	***0.56***	***0.50***	***0.12***	***9.52***	***0.01***	***0.01***	***0.21***	***453***	***0.02***	***0.02***	***0.16***	***1,027***	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
94	AJ10	*Sphagnum lindbergii*	*Cuspidata*	111982	08/09/17	Norway_2	47,442,770	7,062,214,385	0.70	0.61	0.13	9.42	0.01	0.01	0.23	470	0.04	0.03	0.17	1,620	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Intermediate fen carpet	354	63.31303°N 10.66961°E
95	LJ210	*Sphagnum lindbergii*	*Cuspidata*	111769	06/01/17	Austria_1	95,572,237	13,243,068,963	0.36	0.34	0.06	8.18	0.01	0.00	0.12	336	0.01	0.01	0.07	1,216	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Poor fen carpet with Eriophorum vaginatum, Carex rostrata and Eriophorum angustifolium	1865	47.10795°N 13.88510°E
96	GBJ10	*Sphagnum lindbergii*	*Cuspidata*	111866	11/03/17	Germany	62,861,145	9,008,581,554	0.46	0.37	0.20	7.97	0.01	0.01	0.26	352	0.01	0.01	0.22	744	Germany	Niedersachsen	Lower Saxony, Wedemark, Bissendorfer Moor			52.51°N 9.67°E
97	AJ510	*Sphagnum lindbergii*	*Cuspidata*	111986	08/09/17	Norway_2	57,470,132	8,120,368,835	0.51	0.47	0.08	7.93	0.01	0.01	0.15	338	0.02	0.02	0.09	982	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Intermediate fen carpet	354	63.31303°N 10.66961°E
98	GJ10	*Sphagnum lindbergii*	*Cuspidata*	111865	11/06/17	Germany	87,706,879	12,148,459,437	0.35	0.30	0.13	7.75	0.01	0.01	0.18	391	0.02	0.01	0.15	1,149	Germany	Niedersachsen	Lower Saxony, NP Harz, Brocken			51.80°N 10.60°E
99	AJ210	*Sphagnum lindbergii*	*Cuspidata*	111983	08/09/17	Norway_2	43,184,698	6,225,603,484	0.56	0.51	0.09	7.07	0.01	0.01	0.18	280	0.02	0.02	0.11	942	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Intermediate fen carpet	354	63.31303°N 10.66961°E
100	NJ10	*Sphagnum lindbergii*	*Cuspidata*	111988	10/03/17	Norway_1	28,734,210	4,099,801,959	0.74	0.70	0.05	5.99	0.01	0.01	0.10	289	0.03	0.03	0.07	745	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
101	LJ510	*Sphagnum lindbergii*	*Cuspidata*	111772	06/01/17	Austria_1	81,671,740	11,465,639,376	0.28	0.23	0.18	5.70	0.00	0.00	0.26	245	0.01	0.01	0.18	919	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Poor fen carpet with Eriophorum vaginatum, Carex rostrata and Eriophorum angustifolium	1865	47.10795°N 13.88510°E
102	CJ210	*Sphagnum lindbergii*	*Cuspidata*	111995	06/04/18	Norway_2	78,094,321	11,270,471,643	0.29	0.24	0.17	5.61	0.00	0.00	0.21	139	0.01	0.01	0.16	444	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Poor fen	175	63.36710°N 10.52150°E
103	CJ410	*Sphagnum lindbergii*	*Cuspidata*	111997	06/04/18	Norway_2	39,109,668	5,697,528,099	0.43	0.37	0.12	4.86	0.01	0.01	0.19	217	0.02	0.01	0.14	576	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Poor fen	175	63.36710°N 10.52150°E
104	CJ10	*Sphagnum lindbergii*	*Cuspidata*	111994	06/04/18	Norway_2	105,176,627	14,352,339,779	0.28	0.20	0.29	4.77	0.00	0.00	0.36	157	0.01	0.01	0.33	569	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Poor fen	175	63.36710°N 10.52150°E

105	LJ10	*Sphagnum lindbergii*	*Cuspidata*	111768	06/01/17	Austria_1	18,203,186	2,698,239,372	0.60	0.55	0.09	3.36	0.02	0.01	0.16	219	0.04	0.03	0.11	636	Austria	Salzburg	Distr. Lungau, Sauerfelder Berg, Salzriegelmoor	Poor fen carpet with Eriophorum vaginatum, Carex rostrata and Eriophorum angustifolium	1865	47.10795°N 13.88510°E
106	NJ510	*Sphagnum lindbergii*	*Cuspidata*	111992	10/03/17	Norway_1	16,790,053	2,507,057,594	0.60	0.54	0.10	3.09	0.01	0.01	0.17	192	0.03	0.03	0.12	448	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen carpet		64.26684°N 11.45651°E
107	***NE25****	***Sphagnum platyphyllum***	***Subsecunda***	112014	***10/25/17***	***Norway_1***	***68,938,400***	***10,069,233,728***	***0.53***	***0.48***	***0.11***	***10.31***	***0.01***	***0.01***	***0.20***	***303***	***0.02***	***0.02***	***0.12***	***1,121***	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Float zone of stream, fen-like habitat	97	64.26611°N 11.45409°E
108	BE25	*Sphagnum platyphyllum*	*Subsecunda*	112001	08/09/17	Norway_2	100,943,123	13,861,519,198	0.45	0.33	0.28	8.57	0.01	0.01	0.35	436	0.03	0.02	0.31	2,275	Norway	Sør-Trøndelag	Gjeddvatnet	Rich fen carpet	156	63.37966°N 10.60322°E
109	NE55	*Sphagnum platyphyllum*	*Subsecunda*	112017	10/25/17	Norway_1	57,973,500	8,559,971,680	0.48	0.43	0.09	8.47	0.01	0.01	0.19	555	0.03	0.02	0.12	1,460	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Float zone of stream, fen-like habitat	97	64.26611°N 11.45409°E
110	NE5	*Sphagnum platyphyllum*	*Subsecunda*	112013	10/25/17	Norway_1	40,965,232	5,854,776,100	0.65	0.58	0.11	7.58	0.01	0.01	0.17	212	0.01	0.01	0.13	324	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Float zone of stream, fen-like habitat	97	64.26611°N 11.45409°E
111	UE25	*Sphagnum platyphyllum*	*Subsecunda*	111777	06/03/17	Austria_2	49,588,234	7,221,845,875	0.60	0.42	0.31	6.77	0.02	0.01	0.36	625	0.05	0.03	0.32	1,618	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor	Intermediate-rich fen carpet	428	48.05470°N 12.96097°E
112	AE55	*Sphagnum platyphyllum*	*Subsecunda*	112011	08/09/17	Norway_2	51,201,908	7,509,696,733	0.42	0.35	0.17	5.76	0.01	0.01	0.27	357	0.03	0.03	0.19	1,377	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Intermediate fen carpet	352	63.31291°N 10.66944°E
113	UE45	*Sphagnum platyphyllum*	*Subsecunda*	111779	06/03/17	Austria_2	26,131,392	3,909,296,996	0.63	0.56	0.12	4.92	0.02	0.02	0.20	397	0.05	0.04	0.15	1,055	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor	Intermediate-rich fen carpet	428	48.05470°N 12.96097°E
114	AE25	*Sphagnum platyphyllum*	*Subsecunda*	112008	08/09/17	Norway_2	58,548,836	7,655,083,763	0.37	0.23	0.37	4.15	0.01	0.01	0.38	265	0.01	0.01	0.34	560	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Intermediate fen carpet	352	63.31291°N 10.66944°E
115	LE35	*Sphagnum platyphyllum*	*Subsecunda*	111775	05/30/17	Austria_1	40,763,341	6,012,199,518	0.32	0.27	0.17	3.61	0.01	0.01	0.28	289	0.04	0.03	0.21	1,250	Austria	Salzburg	Distr. Lungau, Murau Mountains, Wirtsalmmoor	Rich fen lawn	1530	47.18773°N 13.86452°E
116	AE5	*Sphagnum platyphyllum*	*Subsecunda*	112007	08/09/17	Norway_2	36,582,410	5,036,605,907	0.44	0.25	0.42	2.88	0.01	0.00	0.39	136	0.01	0.01	0.35	281	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Intermediate fen carpet	352	63.31291°N 10.66944°E
117	BE35	*Sphagnum platyphyllum*	*Subsecunda*	112002	08/09/17	Norway_2	86,425,700	10,995,210,493	0.22	0.13	0.40	2.86	0.01	0.00	0.43	198	0.01	0.01	0.37	538	Norway	Sør-Trøndelag	Gjeddvatnet	Rich fen carpet	156	63.37966°N 10.60322°E
118	UE35	*Sphagnum platyphyllum*	*Subsecunda*	111778	06/03/17	Austria_2	13,288,713	1,996,712,408	0.43	0.36	0.16	1.62	0.01	0.01	0.22	149	0.03	0.02	0.18	343	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor	Intermediate-rich fen carpet	428	48.05470°N 12.96097°E
119	**CF56**	***Sphagnum riparium***	***Cuspidata***	112023	**08/09/17**	**Norway_2**	**47,311,462**	**7,025,370,685**	**0.73**	**0.66**	**0.09**	**10.73**	**0.01**	**0.01**	**0.20**	**290**	**0.01**	**0.01**	**0.12**	**562**	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Low lawn\ intermediate high carpet	176	63.36523°N 10.52306°E
120	BF6	*Sphagnum riparium*	*Cuspidata*	112031	06/05/18	Norway_2	106,766,195	15,362,766,168	0.38	0.34	0.12	10.26	0.01	0.01	0.23	700	0.03	0.02	0.16	2,363	Norway	Sør-Trøndelag	Gjeddvatnet		120	63.37989°N 10.60096°E
121	NF26	*Sphagnum riparium*	*Cuspidata*	112026	10/25/17	Norway_1	47,985,082	6,925,637,552	0.65	0.61	0.06	9.06	0.01	0.01	0.15	353	0.03	0.03	0.08	1,253	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Stream brook margin, intermediate	97	64.26653°N 11.45473°E
122	CF26	*Sphagnum riparium*	*Cuspidata*	112020	08/09/17	Norway_2	38,552,660	5,297,122,325	0.73	0.69	0.05	8.24	0.01	0.01	0.13	294	0.02	0.02	0.08	806	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Low lawn\ intermediate high carpet	176	63.36523°N 10.52306°E
123	BF26	*Sphagnum riparium*	*Cuspidata*	112032	06/05/18	Norway_2	80,669,544	11,696,673,366	0.32	0.29	0.10	7.51	0.01	0.01	0.18	473	0.02	0.02	0.12	1,217	Norway	Sør-Trøndelag	Gjeddvatnet		120	63.37989°N 10.60096°E
124	LF26	*Sphagnum riparium*	*Cuspidata*	111785	05/31/17	Austria_1	46,499,008	6,564,309,410	0.55	0.53	0.04	7.23	0.01	0.01	0.10	299	0.02	0.02	0.05	875	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Poor fen	1695	47.08373°N 13.77972°E
125	NF6	*Sphagnum riparium*	*Cuspidata*	112025	10/25/17	Norway_1	36,585,690	5,377,210,581	0.64	0.60	0.06	7.18	0.01	0.01	0.15	270	0.02	0.02	0.08	725	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Stream brook margin, intermediate	97	64.26653°N 11.45473°E
126	CF6	*Sphagnum riparium*	*Cuspidata*	112019	08/09/17	Norway_2	28,489,760	4,133,827,748	0.79	0.73	0.07	6.83	0.01	0.01	0.17	275	0.03	0.03	0.09	888	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Low lawn\ intermediate high carpet	176	63.36523°N 10.52306°E
127	LF56	*Sphagnum riparium*	*Cuspidata*	111788	05/31/17	Austria_1	45,466,001	6,561,452,125	0.46	0.43	0.06	5.97	0.01	0.01	0.12	276	0.01	0.01	0.08	611	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Poor fen	1695	47.08373°N 13.77972°E
128	LF6	*Sphagnum riparium*	*Cuspidata*	111784	05/31/17	Austria_1	40,991,339	6,003,902,863	0.48	0.42	0.11	5.87	0.01	0.01	0.19	428	0.03	0.03	0.14	1,150	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Poor fen	1695	47.08373°N 13.77972°E
129	NF56	*Sphagnum riparium*	*Cuspidata*	112029	10/25/17	Norway_1	19,572,572	2,923,771,531	0.69	0.63	0.09	4.27	0.02	0.01	0.16	284	0.04	0.04	0.11	766	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Stream brook margin, intermediate	97	64.26653°N 11.45473°E
130	GF6	*Sphagnum riparium*	*Cuspidata*	111867	11/03/17	Germany	28,520,646	4,142,433,100	0.50	0.45	0.11	4.20	0.01	0.01	0.21	179	0.02	0.02	0.13	555	Germany	Niedersachsen	Lower Saxony, Masendorf, Brandgehge			53.027584°N 10.641374°E
131	UF26	*Sphagnum riparium*	*Cuspidata*	111789	10/01/17	Austria_2	19,820,387	2,929,401,731	0.67	0.59	0.12	4.00	0.01	0.01	0.21	192	0.04	0.04	0.14	785	Austria	Oberosterreich	Upper Austria, Waldzell	Swampy forest		48.09169°N 13.37251°E
132	UF56	*Sphagnum riparium*	*Cuspidata*	111792	10/01/17	Austria_2	15,086,382	2,208,673,383	0.70	0.64	0.09	3.28	0.01	0.01	0.17	149	0.04	0.04	0.10	568	Austria	Oberosterreich	Upper Austria, Waldzell	Swampy forest		48.09169°N 13.37251°E

133	**NG27***	***Sphagnum squarrosum***	***Acutifolia***	112049	**10/03/17**	**Norway_1**	**74,744,720**	**10,841,841,413**	**0.71**	**0.62**	**0.13**	**13.93**	**0.01**	**0.01**	**0.20**	**712**	**0.04**	**0.03**	**0.15**	**2,391**	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Swampy birch forest		64.26684°N 11.45651°E
134	AG7	*Sphagnum squarrosum*	*Acutifolia*	112042	08/09/17	Norway_2	41,421,384	6,166,314,103	0.73	0.67	0.08	8.98	0.01	0.01	0.17	482	0.03	0.03	0.11	1,236	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Spring influenced sloping fen, spruce forest	367	63.31231°N 10.66892°E
135	CG57	*Sphagnum squarrosum*	*Acutifolia*	112040	08/09/17	Norway_2	92,823,291	12,860,500,655	0.38	0.36	0.06	8.92	0.00	0.00	0.14	303	0.01	0.01	0.07	966	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Spruce swampy pine forest	175	63.36470°N 10.52398°E
136	AG57	*Sphagnum squarrosum*	*Acutifolia*	112046	08/09/17	Norway_2	52,093,824	7,547,981,440	0.60	0.54	0.09	8.71	0.01	0.01	0.17	268	0.02	0.01	0.11	734	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Spring influenced sloping fen, spruce forest	367	63.31231°N 10.66892°E
137	NG7	*Sphagnum squarrosum*	*Acutifolia*	112048	10/03/17	Norway_1	58,316,083	7,922,845,936	0.59	0.57	0.04	8.52	0.01	0.01	0.08	397	0.02	0.02	0.05	1,155	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Swampy birch forest		64.26684°N 11.45651°E
138	CG7	*Sphagnum squarrosum*	*Acutifolia*	112036	08/09/17	Norway_2	48,225,746	7,025,820,191	0.56	0.50	0.11	7.67	0.01	0.01	0.19	368	0.03	0.02	0.12	1,117	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Spruce swampy pine forest	175	63.36470°N 10.52398°E
139	CG27	*Sphagnum squarrosum*	*Acutifolia*	112037	08/09/17	Norway_2	35,955,896	5,367,577,179	0.57	0.48	0.15	5.68	0.01	0.01	0.22	264	0.02	0.01	0.15	531	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Spruce swampy pine forest	175	63.36470°N 10.52398°E
140	LG7	*Sphagnum squarrosum*	*Acutifolia*	111794	05/31/17	Austria_1	49,779,568	7,117,414,369	0.39	0.36	0.08	5.48	0.01	0.01	0.15	538	0.03	0.03	0.09	1,367	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Spring influenced fen by road	1718	47.08611°N 13.78039°E
141	UG7	*Sphagnum squarrosum*	*Acutifolia*	111799	06/04/17	Austria_2	43,247,618	6,289,543,844	0.47	0.39	0.17	5.47	0.01	0.01	0.23	307	0.02	0.02	0.19	735	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Intermediate fen lawn	507	47.92944°N 13.18033°E
142	AG27	*Sphagnum squarrosum*	*Acutifolia*	112043	08/09/17	Norway_2	25,275,292	3,558,928,860	0.71	0.66	0.07	5.05	0.01	0.01	0.13	260	0.03	0.02	0.08	602	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Spring influenced sloping fen, spruce forest	367	63.31231°N 10.66892°E
143	UMG7	*Sphagnum squarrosum*	*Acutifolia*	111805	06/04/17	Austria_2	32,959,640	4,904,689,493	0.54	0.45	0.17	4.97	0.01	0.01	0.25	345	0.03	0.02	0.19	769	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Swamp Alnus glutinosa forest	748	47.76602°N 13.48518°E
144	UMG27	*Sphagnum squarrosum*	*Acutifolia*	111806	06/04/17	Austria_2	32,325,254	4,746,804,047	0.52	0.45	0.13	4.94	0.01	0.01	0.21	366	0.03	0.03	0.15	849	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Swamp Alnus glutinosa forest	748	47.76602°N 13.48518°E
145	LG27	*Sphagnum squarrosum*	*Acutifolia*	111795	05/31/17	Austria_1	36,136,699	5,192,139,971	0.51	0.43	0.14	4.91	0.02	0.01	0.20	442	0.04	0.03	0.16	1,125	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Spring influenced fen by road	1718	47.08611°N 13.78039°E
146	GG27	*Sphagnum squarrosum*	*Acutifolia*	111873	11/03/17	Germany	28,606,380	4,252,148,158	0.55	0.46	0.16	4.47	0.01	0.01	0.23	248	0.02	0.02	0.18	534	Germany	Niedersachsen	Lower Saxony, Munster, Brambostel			52.941882°N 10.236250°E
147	LG57	*Sphagnum squarrosum*	*Acutifolia*	111796	05/31/17	Austria_1	54,710,037	8,150,055,326	0.30	0.24	0.19	4.45	0.01	0.01	0.28	498	0.03	0.02	0.22	1,391	Austria	Salzburg	Distr. Lungau, Schwarzenberg, Seemoos and surroundings	Spring influenced fen by road	1718	47.08611°N 13.78039°E
148	UG57	*Sphagnum squarrosum*	*Acutifolia*	111803	06/04/17	Austria_2	24,601,186	3,701,030,695	0.63	0.52	0.17	4.40	0.02	0.02	0.26	371	0.04	0.03	0.21	822	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Intermediate fen lawn	507	47.92944°N 13.18033°E
149	NG57	*Sphagnum squarrosum*	*Acutifolia*	112052	10/03/17	Norway_1	24,291,792	3,651,907,719	0.55	0.50	0.10	4.07	0.01	0.01	0.18	187	0.02	0.02	0.12	441	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Swampy birch forest		64.26684°N 11.45651°E
150	GG7	*Sphagnum squarrosum*	*Acutifolia*	111872	11/03/17	Germany	26,225,595	3,862,516,536	0.49	0.42	0.14	3.64	0.01	0.01	0.21	205	0.02	0.02	0.16	509	Germany	Niedersachsen	Lower Saxony, Munster, Brambostel			52.941882°N 10.236250°E
151	UG47	*Sphagnum squarrosum*	*Acutifolia*	111802	06/04/17	Austria_2	22,839,223	3,240,336,996	0.53	0.46	0.13	3.22	0.01	0.01	0.18	231	0.03	0.03	0.14	654	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Intermediate fen lawn	507	47.92944°N 13.18033°E
152	**NH28***	***Sphagnum subnitens***	***Acutifolia***	112067	**10/25/17**	**Norway_1**	**67,366,498**	**9,971,610,366**	**0.66**	**0.59**	**0.11**	**12.92**	**0.01**	**0.01**	**0.21**	**443**	**0.03**	**0.03**	**0.13**	**1,806**	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen lawn	102	64.26635°N 11.45917°E
153	LH8	*Sphagnum subnitens*	*Acutifolia*	111811	05/31/17	Austria_1	140,345,937	18,400,197,296	0.36	0.32	0.10	12.49	0.01	0.01	0.15	786	0.02	0.02	0.13	1,978	Austria	Salzburg	Distr. Lungau, Mur valley, Saumoos W St. Margarethen, eastern part		1066	47.08374°N 13.67892°E
154	BH28	*Sphagnum subnitens*	*Acutifolia*	112055	08/09/17	Norway_2	58,193,082	7,826,734,797	0.66	0.60	0.08	10.48	0.01	0.01	0.15	418	0.02	0.02	0.10	1,122	Norway	Sør-Trøndelag	Gjeddvatnet	Intermediate fen carpet	153	63.38116°N 10.59988°E
155	AH28	*Sphagnum subnitens*	*Acutifolia*	112061	08/09/17	Norway_2	75,479,194	10,603,734,152	0.45	0.37	0.16	8.53	0.01	0.00	0.23	291	0.01	0.01	0.16	800	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Intermediate fen lawn	354	63.31303°N 10.66961°E
156	GH8	*Sphagnum subnitens*	*Acutifolia*	111877	11/06/17	Germany	61,421,114	9,119,947,400	0.44	0.37	0.14	7.81	0.01	0.00	0.24	262	0.01	0.01	0.17	766	Germany	Mecklenburg-Vorpommern	Mecklenburg-Western Pomerania, Zarrentin am Schaalsee, Zarrentiner Moor			53.546389°N 10.930390°E
157	LH28	*Sphagnum subnitens*	*Acutifolia*	111812	05/31/17	Austria_1	42,226,412	5,880,976,685	0.62	0.60	0.04	7.25	0.01	0.01	0.10	362	0.04	0.04	0.05	1,413	Austria	Salzburg	Distr. Lungau, Mur valley, Saumoos W St. Margarethen, eastern part		1066	47.08374°N 13.67892°E
158	UH28	*Sphagnum subnitens*	*Acutifolia*	111823	10/01/17	Austria_2	49,962,292	7,118,370,986	0.48	0.43	0.10	6.82	0.01	0.01	0.19	238	0.02	0.02	0.12	828	Austria	Oberosterreich	Upper Austria, Waldzell	Silicate spring		48.09351°N 13.37443°E
159	BH8	*Sphagnum subnitens*	*Acutifolia*	112054	08/09/17	Norway_2	37,372,116	5,565,693,923	0.67	0.56	0.16	6.80	0.01	0.01	0.25	401	0.04	0.03	0.19	1,301	Norway	Sør-Trøndelag	Gjeddvatnet	Intermediate fen carpet	153	63.38116°N 10.59988°E
160	UH58	*Sphagnum subnitens*	*Acutifolia*	111826	10/01/17	Austria_2	64,747,959	8,632,521,042	0.44	0.36	0.18	6.74	0.01	0.00	0.20	212	0.01	0.01	0.18	636	Austria	Oberosterreich	Upper Austria, Waldzell	Silicate spring		48.09351°N 13.37443°E
161	AH8	*Sphagnum subnitens*	*Acutifolia*	112060	08/09/17	Norway_2	111,336,706	15,580,322,930	0.34	0.20	0.42	6.61	0.00	0.00	0.42	128	0.00	0.00	0.38	303	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Intermediate fen lawn	354	63.31303°N 10.66961°E

162	NH8	*Sphagnum subnitens*	*Acutifolia*	112066	10/25/17	Norway_1	43,520,569	6,363,605,682	0.51	0.43	0.14	6.12	0.01	0.01	0.21	224	0.02	0.02	0.16	675	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen lawn	102	64.26635°N 11.45917°E
163	UHH8	*Sphagnum subnitens*	*Acutifolia*	111816	06/03/17	Austria_2	83,082,018	11,676,443,454	0.25	0.22	0.12	5.32	0.00	0.00	0.18	279	0.01	0.01	0.13	534	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor	Mire swamp with Alnus and Frangula	428	48.05410°N 12.95769°E
164	UHH38	*Sphagnum subnitens*	*Acutifolia*	111818	06/03/17	Austria_2	81,901,948	11,524,373,062	0.27	0.21	0.21	5.27	0.00	0.00	0.27	255	0.01	0.01	0.21	780	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor	Mire swamp with Alnus and Frangula	428	48.05410°N 12.95769°E
165	GH28	*Sphagnum subnitens*	*Acutifolia*	111878	11/06/17	Germany	73,730,165	10,819,679,184	0.23	0.20	0.15	4.98	0.00	0.00	0.22	134	0.01	0.00	0.15	352	Germany	Mecklenburg-Vorpommern	Mecklenburg-Western Pomerania, Zarrentin am Schaalsee, Zarrentiner Moor			53.546389°N 10.930390°E
166	BH58	*Sphagnum subnitens*	*Acutifolia*	112058	08/09/17	Norway_2	161,567,495	21,381,337,167	0.18	0.11	0.38	4.67	0.00	0.00	0.45	223	0.00	0.00	0.42	317	Norway	Sør-Trøndelag	Gjeddvatnet	Intermediate fen carpet	153	63.38116°N 10.59988°E
167	UHH48	*Sphagnum subnitens*	*Acutifolia*	111819	06/03/17	Austria_2	58,859,377	8,560,569,856	0.29	0.25	0.16	4.60	0.01	0.01	0.23	303	0.01	0.01	0.18	714	Austria	Oberosterreich	Upper Austria, Ibmer moor, Eggelsberg, Ibmer moor	Mire swamp with Alnus and Frangula	428	48.05410°N 12.95769°E
168	UH8	*Sphagnum subnitens*	*Acutifolia*	111822	10/01/17	Austria_2	34,035,320	4,965,037,186	0.43	0.38	0.12	4.38	0.01	0.01	0.18	177	0.01	0.01	0.13	433	Austria	Oberosterreich	Upper Austria, Waldzell	Silicate spring		48.09351°N 13.37443°E
169	NH58	*Sphagnum subnitens*	*Acutifolia*	112070	10/25/17	Norway_1	26,036,745	3,838,961,198	0.53	0.48	0.09	4.25	0.01	0.01	0.16	180	0.02	0.02	0.10	443	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Intermediate fen lawn	102	64.26635°N 11.45917°E
170	LH58	*Sphagnum subnitens*	*Acutifolia*	111815	05/31/17	Austria_1	23,520,581	3,457,014,652	0.33	0.28	0.17	2.20	0.01	0.01	0.23	124	0.02	0.01	0.18	333	Austria	Salzburg	Distr. Lungau, Mur valley, Saumoos W St. Margarethen, eastern part		1066	47.08374°N 13.67892°E
171	**CL512***	***Sphagnum tenellum***	***Cuspidata***	112082	**08/09/17**	**Norway_2**	**306,057,128**	**39,545,260,759**	**0.26**	**0.23**	**0.12**	**14.36**	**0.00**	**0.00**	**0.18**	**597**	**0.01**	**0.00**	**0.14**	**1,270**	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Ombrotrophic carpet	177	63.36555°N 10.52418°E
172	AL312	*Sphagnum tenellum*	*Cuspidata*	112086	08/09/17	Norway_2	104,753,480	14,042,429,567	0.41	0.34	0.17	10.36	0.01	0.01	0.21	486	0.01	0.01	0.16	843	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Pure fen lawn	354	63.31293°N 10.66901°E
173	NL412	*Sphagnum tenellum*	*Cuspidata*	112093	10/03/17	Norway_1	186,665,810	25,033,755,064	0.27	0.24	0.12	10.10	0.00	0.00	0.18	524	0.01	0.01	0.13	1,322	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Bog lawn		64.26684°N 11.45651°E
174	CL212	*Sphagnum tenellum*	*Cuspidata*	112079	08/09/17	Norway_2	123,241,574	16,078,980,637	0.34	0.27	0.19	8.95	0.00	0.00	0.22	362	0.01	0.01	0.17	770	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Ombrotrophic carpet	177	63.36555°N 10.52418°E
175	BL12	*Sphagnum tenellum*	*Cuspidata*	112072	08/09/17	Norway_2	40,620,642	5,719,356,446	0.62	0.54	0.13	7.08	0.01	0.01	0.16	234	0.01	0.01	0.12	410	Norway	Sør-Trøndelag	Gjeddvatnet	Poor fen carpet	156	63.38147°N 10.60011°E
176	BL5122	*Sphagnum tenellum*	*Cuspidata*	112076	08/09/17	Norway_2	111,637,591	15,575,626,249	0.22	0.18	0.20	6.51	0.00	0.00	0.26	307	0.01	0.01	0.20	644	Norway	Sør-Trøndelag	Gjeddvatnet	Poor fen carpet	156	63.38147°N 10.60011°E
177	UL512	*Sphagnum tenellum*	*Cuspidata*	111832	06/04/17	Austria_2	36,420,122	5,450,983,208	0.54	0.43	0.22	5.50	0.01	0.01	0.28	319	0.03	0.02	0.24	751	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Ombrotrophic mire, low hummocks close to lawn	509	47.92902°N 13.17992°E
178	UML512	*Sphagnum tenellum*	*Cuspidata*	111838	06/04/17	Austria_2	82,262,242	11,586,301,230	0.33	0.25	0.25	5.40	0.00	0.00	0.30	204	0.01	0.01	0.26	590	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Poor fen lawn, grassed peaty soil	752	47.76622°N 13.48408°E
179	AL512	*Sphagnum tenellum*	*Cuspidata*	112088	08/09/17	Norway_2	199,389,269	26,354,319,640	0.18	0.14	0.25	5.35	0.00	0.00	0.35	262	0.01	0.00	0.30	873	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Pure fen lawn	354	63.31293°N 10.66901°E
180	*NL212*	*Sphagnum tenellum*	Cuspidata	112091	*10/03/17*	*Norway_1*	*77,303,515*	*10,991,453,641*	*0.29*	*0.22*	*0.23*	*5.17*	*0.00*	*0.00*	*0.28*	*170*	*0.01*	*0.01*	*0.22*	*418*	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Bog lawn		64.26684°N 11.45651°E
181	BL312	*Sphagnum tenellum*	*Cuspidata*	112074	08/09/17	Norway_2	107,661,644	14,946,501,268	0.24	0.16	0.33	4.88	0.01	0.00	0.36	305	0.01	0.01	0.32	696	Norway	Sør-Trøndelag	Gjeddvatnet	Poor fen carpet	156	63.38147°N 10.60011°E
182	UML312	*Sphagnum tenellum*	*Cuspidata*	111836	06/04/17	Austria_2	38,880,833	5,687,432,078	0.41	0.34	0.17	4.70	0.01	0.01	0.24	232	0.02	0.01	0.18	591	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Poor fen lawn, grassed peaty soil	752	47.76622°N 13.48408°E
183	CL12	*Sphagnum tenellum*	*Cuspidata*	112078	08/09/17	Norway_2	74,258,301	10,464,859,016	0.36	0.19	0.48	4.68	0.01	0.00	0.46	202	0.01	0.01	0.41	475	Norway	Sør-Trøndelag	Mire S of Greistad, NW of Digresmyra	Ombrotrophic carpet	177	63.36555°N 10.52418°E
184	GL512	*Sphagnum tenellum*	*Cuspidata*	111886	11/02/17	Germany	29,910,954	4,233,997,311	0.56	0.48	0.16	4.67	0.01	0.01	0.19	254	0.02	0.02	0.16	462	Germany	Niedersachsen	Lower Saxony, Bad Bodenteich, Schweimker Moor			52.782910°N 10.630540°E
185	UL412	*Sphagnum tenellum*	*Cuspidata*	111831	06/04/17	Austria_2	52,996,611	7,773,025,798	0.29	0.25	0.15	4.66	0.01	0.01	0.23	251	0.02	0.01	0.16	730	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Ombrotrophic mire, low hummocks close to lawn	509	47.92902°N 13.17992°E
186	AL12	*Sphagnum tenellum*	*Cuspidata*	112084	08/09/17	Norway_2	99,679,383	14,588,353,396	0.27	0.13	0.51	4.65	0.00	0.00	0.50	174	0.01	0.00	0.48	317	Norway	Sør-Trøndelag	Draksten, mire N of Svarttjønnåsen	Pure fen lawn	354	63.31293°N 10.66901°E
187	NL512_2	*Sphagnum tenellum*	*Cuspidata*	112094	10/03/17	Norway_1	46,770,131	6,735,272,463	0.35	0.30	0.14	4.57	0.01	0.00	0.19	178	0.01	0.01	0.16	429	Norway	Nord-Trøndelag	E of Langvatnet by Daltjønnbakken (Daltjønna)	Bog lawn		64.26684°N 11.45651°E
188	UML12	*Sphagnum tenellum*	*Cuspidata*	111834	06/04/17	Austria_2	47,018,665	6,707,398,296	0.42	0.30	0.28	4.55	0.01	0.00	0.31	189	0.01	0.01	0.28	453	Austria	Oberosterreich	Upper Austria, St. Wolfgang, Schwarzensee	Poor fen lawn, grassed peaty soil	752	47.76622°N 13.48408°E
189	UL312	*Sphagnum tenellum*	*Cuspidata*	111830	06/04/17	Austria_2	72,027,272	10,159,989,602	0.23	0.20	0.14	4.42	0.00	0.00	0.19	183	0.01	0.01	0.13	361	Austria	Salzburg	Flachgau, Wenger moor by Wallersee	Ombrotrophic mire, low hummocks close to lawn	509	47.92902°N 13.17992°E
190	GL412	*Sphagnum tenellum*	*Cuspidata*	111885	11/02/17	Germany	43,753,141	6,436,257,413	0.27	0.23	0.15	3.54	0.00	0.00	0.20	116	0.01	0.00	0.16	200	Germany	Niedersachsen	Lower Saxony, Bad Bodenteich, Schweimker Moor			52.782910°N 10.630540°E
191	FS01	*Flatbergium sericeum*		105364	01/2019		252,634,072	37,653,756,089	0.19	0.13	0.31	8.45	0.01	0.01	0.38	1,709	0.03	0.02	0.36	4,300	China	Taiwan	Yilan County, Mt. Taiping			24.499°N 121.532°E

Table S2. Sequencing summary statistics

Parameter	Mean	Median	SD	SE	Minimum	Maximum	Upper Quantile 75%	Lower Quartile 25%	Coefficient of Variation	Sample size
Number of retained reads	65,104,262	52,996,611	45,063,147	3,260,655	13,288,713	306,057,128	81,482,310	36,501,266	0.69	191
Fraction of reads mapped to the nuclear genome	0.44	0.43	0.16	0.01	0.09	0.81	0.55	0.32	0.36	191
Fraction of PCR duplicates	0.16	0.14	0.09	0.01	0.04	0.51	0.19	0.10	0.55	191
Fraction of reads uniquely mapped to the nuclear genome	0.38	0.36	0.16	0.01	0.06	0.73	0.48	0.25	0.41	191
Coverage, nuclear genome	6.25	5.73	2.56	0.19	1.62	14.36	7.94	4.40	0.41	191
Fraction of reads uniquely mapped to the mitochondrial genome	0.01	0.01	0.01	0.00	0.00	0.02	0.01	0.00	0.81	191
Coverage, mitochondrial genome	300	265	171	12	47	1,709	370	197	0.57	191
Fraction of reads uniquely mapped to the chloroplast genome	0.02	0.01	0.01	0.00	0.00	0.05	0.02	0.01	0.61	191
Coverage, chloroplast genome	830	725	529	38	85	4,300	1,118	500	0.64	191

Table S3. Number of genetic markers used in different analyses

Analysis	Software	Marker type	Number	Sampled across
PCA	ANGSD, R	nuclear biallelic sites, based on allele counts	16274743	whole nuclear genome
Ancestry assignment and admixture	ADMIXTURE	independent SNPs, nuclear	23560	63% of the nuclear reference genome length
F_{ST} calculation	ANGSD	nuclear biallelic sites based on GLs, pairwise	121±10M (SD)	whole nuclear genome
F_{ST} calculation	R	nuclear SNPs	455724	whole nuclear genome
Phylogenetic analysis	RaxML	nuclear SNPs	455724	whole nuclear genome
Phylogenetic analysis	RaxML	chloroplast SNPs	1953	whole chloroplast genome
Phylogenetic analysis	RaxML	mitochondrial SNPs	1032	whole mitochondrial genome
Admixture with TreeMix	TreeMix	independent SNPs, nuclear	23560	63% of the nuclear reference genome length
Admixture with *f*3 statistics	TreeMix	independent SNPs, nuclear	23560	63% of the nuclear reference genome length
Admixture with D-statistics, 1st test	ANGSD	nuclear biallelic sites based on Gls	35029±5895 (SD)	70.3% of the nuclear reference genome length
Admixture with D-statistics, 2nd test	ANGSD	nuclear biallelic sites based on Gls	193839±39386 (SD)	70.3% of the nuclear reference genome length

Table S4. Summary statistics for all gene trees

Parameter	Total	Mean	Median	SD	SE	Minimum	Maximum	Upper Quantile 75%	Lower Quartile 25%	Coefficient of Variation	Sample size
Total number of nucleotide sites	1,661,556	1,682	1,385	1,164	37.04	255	9,408	2,090	914	0.69	988
Number of distinct site patterns	1,541,639	1,560	1,290	1,071	34.09	252	8,780	1,920	869	0.69	988
Number of parsimony informative sites	117,724	119	97	90	2.86	11	758	148	62	0.76	988
Number of constant sites	1,494,764	1,513	1,251	1,045	33.23	221	8,470	1,887	830	0.69	988
AIC		8,471	7,026	5,583	177.63	1,594	45,296	10,466	4,884	0.66	988
cAIC		12,848	7,672	28,549	908.27	3,054	285,915	11,236	5,695	2.22	988
BIC		10,434	9,003	5,825	185.33	2,610	48,020	12,642	6,701	0.56	988
Mean node bootstrap support		56	57	10	0.31	25	78	63	50	0.18	988
Discordance score		13	14	3.79	0.12	2	20	16	10	0.29	988

Table S5. Summary statistics for all sliding-window trees

Parameter	Total	Mean	Median	SD	SE	Minimum	Maximum	Upper Quantile 75%	Lower Quartile 25%	Coefficient of Variation	Sample size
Number of distinct site patterns	140,874,417	79,455	80,976	8,502	201.91	3,531	91,901	83,785	77,467	0.11	1773
Number of parsimony informative sites	18,838,614	10,625	10,935	1,561	37.08	465	14,148	11,548	10,181	0.15	1773
Number of constant sites	150,113,976	84,667	85,404	6,786	161.17	3,513	95,316	86,169	84,672	0.08	1773
Mean node bootstrap support	NA	86.69	86.97	2.85	0.07	69	93	89	85	0.03	1773
Discordance score	NA	6.06	6.00	2.79	0.07	0	18	8	4	0.46	1773

Table S6. D-statistic test results with *Flatbergium sericeum* as an outgroup.

Only phylogenetically correct triplets are shown. Non-significant values are underlined

No	D, average D-statistic	JK.D, jackknife estimate of D	V.JK.D., variance of D	Z score	pvalue from the Z score	nABBA, number of ABBA patterns observed	nBABA, number of BABA patterns observed	nBlocks, number of blocks with observed data	P1	P2	P3	Outgroup	Species Pair
1	-0.04	-0.04	0.0000	-5.99	0.0000	10915	11711	339	capillifolium	subnitens	compactum	F.sericeum	capillifolium,compactum
2	0.03	0.03	0.0000	5.15	0.0000	13788	12971	338	fimbriatum	capillifolium	compactum	F.sericeum	capillifolium,compactum
3	0.09	0.09	0.0000	15.98	0.0000	20573	17294	340	squarrosum	capillifolium	compactum	F.sericeum	capillifolium,compactum
4	0.09	0.09	0.0000	17.20	0.0000	18470	15367	339	platyphyllum	capillifolium	compactum	F.sericeum	capillifolium,compactum
5	-0.01	-0.01	0.0000	-1.91	0.0566	8543	8753	338	capillifolium	fuscum	compactum	F.sericeum	capillifolium,compactum
6	0.00	0.00	0.0000	0.35	0.7235	20006	19910	339	divinum	compactum	capillifolium	F.sericeum	capillifolium,compactum
7	-0.23	-0.23	0.0000	-44.79	0.0000	16209	26060	337	lindbergii	flexuosum	capillifolium	F.sericeum	capillifolium,lindbergii
8	-0.21	-0.21	0.0000	-40.67	0.0000	16664	25318	339	lindbergii	tenellum	capillifolium	F.sericeum	capillifolium,lindbergii
9	-0.08	-0.08	0.0000	-14.75	0.0000	17823	21039	337	lindbergii	riparium	capillifolium	F.sericeum	capillifolium,lindbergii
10	-0.05	-0.05	0.0000	-8.57	0.0000	17945	19873	339	capillifolium	compactum	lindbergii	F.sericeum	capillifolium,lindbergii
11	-0.04	-0.04	0.0000	-6.37	0.0000	18909	20395	339	capillifolium	divinum	lindbergii	F.sericeum	capillifolium,lindbergii
12	0.11	0.11	0.0000	19.84	0.0000	18621	14919	339	platyphyllum	capillifolium	lindbergii	F.sericeum	capillifolium,lindbergii
13	-0.03	-0.03	0.0000	-4.46	0.0000	10888	11512	340	capillifolium	subnitens	lindbergii	F.sericeum	capillifolium,lindbergii
14	0.01	0.01	0.0000	1.01	0.3149	13472	13299	338	fimbriatum	capillifolium	lindbergii	F.sericeum	capillifolium,lindbergii
15	0.00	0.00	0.0000	-0.58	0.5620	8529	8595	338	capillifolium	fuscum	lindbergii	F.sericeum	capillifolium,lindbergii
16	-0.18	-0.18	0.0000	-34.98	0.0000	14958	21599	338	riparium	flexuosum	capillifolium	F.sericeum	capillifolium,riparium
17	-0.15	-0.15	0.0000	-27.24	0.0000	15554	20965	339	riparium	tenellum	capillifolium	F.sericeum	capillifolium,riparium
18	-0.06	-0.06	0.0000	-9.84	0.0000	17195	19467	338	capillifolium	compactum	riparium	F.sericeum	capillifolium,riparium
19	-0.05	-0.05	0.0000	-8.00	0.0000	18171	20005	339	capillifolium	divinum	riparium	F.sericeum	capillifolium,riparium
20	0.12	0.12	0.0000	21.88	0.0000	18424	14543	340	platyphyllum	capillifolium	riparium	F.sericeum	capillifolium,riparium
21	-0.03	-0.03	0.0000	-4.84	0.0000	10646	11309	340	capillifolium	subnitens	riparium	F.sericeum	capillifolium,riparium
22	0.01	0.01	0.0000	1.73	0.0832	13267	12975	339	fimbriatum	capillifolium	riparium	F.sericeum	capillifolium,riparium
23	-0.01	-0.01	0.0000	-1.68	0.0923	8292	8475	338	capillifolium	fuscum	riparium	F.sericeum	capillifolium,riparium
24	-0.05	-0.05	0.0000	-8.26	0.0000	16374	18140	338	capillifolium	compactum	tenellum	F.sericeum	capillifolium,tenellum
25	-0.04	-0.04	0.0000	-6.68	0.0000	17209	18665	338	capillifolium	divinum	tenellum	F.sericeum	capillifolium,tenellum
26	-0.04	-0.04	0.0000	-5.32	0.0000	10073	10820	338	capillifolium	subnitens	tenellum	F.sericeum	capillifolium,tenellum
27	0.06	0.06	0.0000	8.79	0.0000	11794	10547	338	flexuosum	tenellum	capillifolium	F.sericeum	capillifolium,tenellum
28	0.13	0.13	0.0000	22.46	0.0000	17573	13642	338	platyphyllum	capillifolium	tenellum	F.sericeum	capillifolium,tenellum
29	0.03	0.03	0.0000	4.05	0.0001	12683	12061	338	fimbriatum	capillifolium	tenellum	F.sericeum	capillifolium,tenellum
30	-0.02	-0.02	0.0001	-2.25	0.0244	7802	8054	338	capillifolium	fuscum	tenellum	F.sericeum	capillifolium,tenellum
31	0.06	0.06	0.0000	11.27	0.0000	20086	17674	339	squarrosum	fimbriatum	compactum	F.sericeum	compactum,fimbriatum
32	0.07	0.07	0.0000	11.56	0.0000	18134	15893	339	platyphyllum	fimbriatum	compactum	F.sericeum	compactum,fimbriatum
33	0.00	0.00	0.0001	0.70	0.4847	19691	19497	338	divinum	compactum	fimbriatum	F.sericeum	compactum,fimbriatum
34	0.00	0.00	0.0000	-0.15	0.8805	13890	13914	339	fimbriatum	subnitens	compactum	F.sericeum	compactum,fimbriatum
35	0.08	0.08	0.0000	14.86	0.0000	20495	17452	335	squarrosum	fuscum	compactum	F.sericeum	compactum,fuscum
36	0.09	0.09	0.0000	15.43	0.0000	18467	15571	337	platyphyllum	fuscum	compactum	F.sericeum	compactum,fuscum
37	-0.03	-0.03	0.0000	-4.54	0.0000	11113	11692	338	fuscum	subnitens	compactum	F.sericeum	compactum,fuscum
38	0.02	0.02	0.0000	3.48	0.0005	13879	13323	338	fimbriatum	fuscum	compactum	F.sericeum	compactum,fuscum
39	0.00	0.00	0.0000	0.47	0.6378	19913	19787	337	divinum	compactum	fuscum	F.sericeum	compactum,fuscum
40	-0.23	-0.23	0.0000	-47.30	0.0000	15613	25081	339	lindbergii	flexuosum	compactum	F.sericeum	compactum,lindbergii
41	-0.21	-0.21	0.0000	-44.07	0.0000	15982	24422	339	lindbergii	tenellum	compactum	F.sericeum	compactum,lindbergii
42	-0.10	-0.10	0.0000	-19.05	0.0000	16582	20103	338	lindbergii	riparium	compactum	F.sericeum	compactum,lindbergii
43	0.05	0.05	0.0000	7.74	0.0000	20775	18894	340	platyphyllum	compactum	lindbergii	F.sericeum	compactum,lindbergii
44	0.03	0.03	0.0000	3.85	0.0001	19866	18837	338	divinum	compactum	platyphyllum	F.sericeum	compactum,platyphyllum
45	0.00	0.00	0.0000	0.83	0.4046	20379	20193	339	squarrosum	platyphyllum	compactum	F.sericeum	compactum,platyphyllum
46	-0.17	-0.17	0.0000	-34.75	0.0000	14716	20640	338	riparium	flexuosum	compactum	F.sericeum	compactum,riparium
47	-0.14	-0.14	0.0000	-28.19	0.0000	15230	20102	338	riparium	tenellum	compactum	F.sericeum	compactum,riparium
48	0.04	0.04	0.0000	7.08	0.0000	20128	18488	338	platyphyllum	compactum	riparium	F.sericeum	compactum,riparium
49	0.06	0.06	0.0000	11.70	0.0000	20481	18029	340	squarrosum	subnitens	compactum	F.sericeum	compactum,subnitens
50	0.07	0.07	0.0000	11.68	0.0000	18516	16189	339	platyphyllum	subnitens	compactum	F.sericeum	compactum,subnitens
51	0.00	0.00	0.0000	0.61	0.5424	19951	19788	338	divinum	compactum	subnitens	F.sericeum	compactum,subnitens
52	0.05	0.05	0.0000	7.77	0.0000	11569	10483	339	flexuosum	tenellum	compactum	F.sericeum	compactum,tenellum
53	0.06	0.06	0.0000	9.53	0.0000	19447	17256	337	platyphyllum	compactum	tenellum	F.sericeum	compactum,tenellum
54	-0.04	-0.04	0.0000	-6.31	0.0000	10950	11850	340	capillifolium	subnitens	divinum	F.sericeum	divinum,capillifolium
55	0.03	0.03	0.0000	5.13	0.0000	13898	13047	340	fimbriatum	capillifolium	divinum	F.sericeum	divinum,capillifolium
56	0.04	0.04	0.0000	7.62	0.0000	20427	18721	340	squarrosum	capillifolium	divinum	F.sericeum	divinum,capillifolium
57	0.11	0.11	0.0000	20.08	0.0000	19070	15152	340	platyphyllum	capillifolium	divinum	F.sericeum	divinum,capillifolium
58	-0.01	-0.01	0.0000	-2.06	0.0393	8544	8785	340	capillifolium	fuscum	divinum	F.sericeum	divinum,capillifolium
59	0.09	0.09	0.0000	14.58	0.0000	18615	15680	339	platyphyllum	fimbriatum	divinum	F.sericeum	divinum,fimbriatum
60	0.02	0.02	0.0000	3.45	0.0006	19840	19070	339	squarrosum	fimbriatum	divinum	F.sericeum	divinum,fimbriatum
61	0.00	0.00	0.0000	-0.32	0.7515	13982	14036	339	fimbriatum	subnitens	divinum	F.sericeum	divinum,fimbriatum
62	0.04	0.04	0.0000	6.84	0.0000	20355	18885	334	squarrosum	fuscum	divinum	F.sericeum	divinum,fuscum
63	0.11	0.11	0.0000	19.39	0.0000	19042	15316	336	platyphyllum	fuscum	divinum	F.sericeum	divinum,fuscum
64	-0.03	-0.03	0.0000	-5.00	0.0000	11105	11774	338	fuscum	subnitens	divinum	F.sericeum	divinum,fuscum
65	0.02	0.02	0.0000	3.79	0.0002	13963	13339	339	fimbriatum	fuscum	divinum	F.sericeum	divinum,fuscum
66	-0.23	-0.23	0.0000	-48.24	0.0000	15856	25229	339	lindbergii	flexuosum	divinum	F.sericeum	divinum,lindbergii
67	-0.21	-0.21	0.0000	-43.73	0.0000	16283	24748	339	lindbergii	tenellum	divinum	F.sericeum	divinum,lindbergii
68	-0.09	-0.09	0.0000	-17.47	0.0000	17088	20543	338	lindbergii	riparium	divinum	F.sericeum	divinum,lindbergii
69	0.05	0.05	0.0000	9.41	0.0000	21957	19728	339	platyphyllum	divinum	lindbergii	F.sericeum	divinum,lindbergii
70	0.01	0.01	0.0000	1.65	0.0991	18894	18531	339	compactum	divinum	lindbergii	F.sericeum	divinum,lindbergii
71	-0.17	-0.17	0.0000	-34.50	0.0000	14827	20747	339	riparium	flexuosum	divinum	F.sericeum	divinum,riparium
72	-0.14	-0.14	0.0000	-26.81	0.0000	15361	20355	339	riparium	tenellum	divinum	F.sericeum	divinum,riparium
73	0.05	0.05	0.0000	9.05	0.0000	21204	19242	339	platyphyllum	divinum	riparium	F.sericeum	divinum,riparium
74	0.01	0.01	0.0000	1.60	0.1089	18231	17893	338	compactum	divinum	riparium	F.sericeum	divinum,riparium
75	-0.05	-0.05	0.0000	-9.26	0.0000	19636	21812	338	squarrosum	platyphyllum	divinum	F.sericeum	divinum,squarrosum
76	-0.04	-0.04	0.0000	-5.80	0.0000	18901	20340	338	divinum	compactum	squarrosum	F.sericeum	divinum,squarrosum
77	0.09	0.09	0.0000	15.48	0.0000	18958	15869	339	platyphyllum	subnitens	divinum	F.sericeum	divinum,subnitens
78	0.02	0.02	0.0000	3.64	0.0003	20291	19494	339	squarrosum	subnitens	divinum	F.sericeum	divinum,subnitens
79	0.04	0.04	0.0000	6.67	0.0000	11588	10660	338	flexuosum	tenellum	divinum	F.sericeum	divinum,tenellum
80	0.06	0.06	0.0000	10.87	0.0000	20402	17995	339	platyphyllum	divinum	tenellum	F.sericeum	divinum,tenellum
81	0.01	0.01	0.0000	1.10	0.2723	17252	17031	338	compactum	divinum	tenellum	F.sericeum	divinum,tenellum
82	0.04	0.04	0.0000	6.28	0.0000	16446	15156	339	subnitens	capillifolium	fimbriatum	F.sericeum	fimbriatum,capillifolium
83	0.02	0.02	0.0001	2.22	0.0267	11851	11483	335	fuscum	capillifolium	fimbriatum	F.sericeum	fimbriatum,capillifolium

84	0.03	0.03	0.0000	4.25	0.0000	16391	15488	337	subnitens	fuscum	fimbriatum	F.sericeum	fimbriatum,fuscum
85	-0.23	-0.23	0.0000	-45.75	0.0000	16103	25746	339	lindbergii	flexuosum	fimbriatum	F.sericeum	fimbriatum,lindbergii
86	-0.21	-0.21	0.0000	-43.38	0.0000	16352	25135	338	lindbergii	tenellum	fimbriatum	F.sericeum	fimbriatum,lindbergii
87	-0.08	-0.08	0.0000	-15.28	0.0000	17674	20914	336	lindbergii	riparium	fimbriatum	F.sericeum	fimbriatum,lindbergii
88	-0.04	-0.04	0.0000	-7.22	0.0000	18221	19934	340	fimbriatum	compactum	lindbergii	F.sericeum	fimbriatum,lindbergii
89	-0.03	-0.03	0.0000	-5.27	0.0000	19192	20452	339	fimbriatum	divinum	lindbergii	F.sericeum	fimbriatum,lindbergii
90	0.10	0.10	0.0000	18.21	0.0000	18748	15244	339	platyphyllum	fimbriatum	lindbergii	F.sericeum	fimbriatum,lindbergii
91	-0.02	-0.02	0.0000	-2.97	0.0029	13679	14185	340	fimbriatum	subnitens	lindbergii	F.sericeum	fimbriatum,lindbergii
92	-0.17	-0.17	0.0000	-31.60	0.0000	14889	21203	339	riparium	flexuosum	fimbriatum	F.sericeum	fimbriatum,riparium
93	-0.15	-0.15	0.0000	-27.47	0.0000	15324	20781	338	riparium	tenellum	fimbriatum	F.sericeum	fimbriatum,riparium
94	-0.05	-0.05	0.0000	-8.35	0.0000	17534	19475	337	fimbriatum	compactum	riparium	F.sericeum	fimbriatum,riparium
95	-0.04	-0.04	0.0000	-6.95	0.0000	18425	20020	338	fimbriatum	divinum	riparium	F.sericeum	fimbriatum,riparium
96	0.11	0.11	0.0000	19.01	0.0000	18416	14877	338	platyphyllum	fimbriatum	riparium	F.sericeum	fimbriatum,riparium
97	-0.02	-0.02	0.0000	-2.59	0.0095	13367	13802	338	fimbriatum	subnitens	riparium	F.sericeum	fimbriatum,riparium
98	-0.03	-0.03	0.0000	-5.42	0.0000	16891	18059	339	fimbriatum	compactum	tenellum	F.sericeum	fimbriatum,tenellum
99	0.04	0.04	0.0000	6.60	0.0000	11549	10617	339	flexuosum	tenellum	fimbriatum	F.sericeum	fimbriatum,tenellum
100	0.10	0.10	0.0000	17.50	0.0000	17374	14129	338	platyphyllum	fimbriatum	tenellum	F.sericeum	fimbriatum,tenellum
101	-0.03	-0.03	0.0000	-4.25	0.0000	17655	18576	339	fimbriatum	divinum	tenellum	F.sericeum	fimbriatum,tenellum
102	-0.01	-0.01	0.0000	-0.92	0.3573	12702	12850	338	fimbriatum	subnitens	tenellum	F.sericeum	fimbriatum,tenellum
103	-0.05	-0.05	0.0000	-7.55	0.0000	16136	17740	338	capillifolium	compactum	flexuosum	F.sericeum	flexuosum,capillifolium
104	-0.04	-0.04	0.0000	-5.37	0.0000	9824	10542	338	capillifolium	subnitens	flexuosum	F.sericeum	flexuosum,capillifolium
105	-0.03	-0.03	0.0000	-5.88	0.0000	16967	18192	338	capillifolium	divinum	flexuosum	F.sericeum	flexuosum,capillifolium
106	0.12	0.12	0.0000	21.91	0.0000	17189	13443	339	platyphyllum	capillifolium	flexuosum	F.sericeum	flexuosum,capillifolium
107	0.01	0.01	0.0000	2.24	0.0249	12303	11968	339	fimbriatum	capillifolium	flexuosum	F.sericeum	flexuosum,capillifolium
108	-0.01	-0.01	0.0000	-1.93	0.0541	7719	7918	337	capillifolium	fuscum	flexuosum	F.sericeum	flexuosum,capillifolium
109	0.06	0.06	0.0000	9.92	0.0000	19150	16980	340	platyphyllum	compactum	flexuosum	F.sericeum	flexuosum,compactum
110	0.07	0.07	0.0000	11.81	0.0000	20158	17678	339	platyphyllum	divinum	flexuosum	F.sericeum	flexuosum,divinum
111	0.01	0.01	0.0000	1.42	0.1549	16946	16658	338	compactum	divinum	flexuosum	F.sericeum	flexuosum,divinum
112	-0.04	-0.04	0.0000	-6.05	0.0000	16550	17869	340	fimbriatum	compactum	flexuosum	F.sericeum	flexuosum,fimbriatum
113	0.11	0.11	0.0000	19.42	0.0000	17237	13839	339	platyphyllum	fimbriatum	flexuosum	F.sericeum	flexuosum,fimbriatum
114	-0.03	-0.03	0.0000	-4.63	0.0000	17303	18288	339	fimbriatum	divinum	flexuosum	F.sericeum	flexuosum,fimbriatum
115	-0.02	-0.02	0.0000	-2.52	0.0118	12310	12714	339	fimbriatum	subnitens	flexuosum	F.sericeum	flexuosum,fimbriatum
116	-0.04	-0.04	0.0000	-6.15	0.0000	16230	17587	335	fuscum	compactum	flexuosum	F.sericeum	flexuosum,fuscum
117	0.12	0.12	0.0000	20.18	0.0000	17192	13630	339	platyphyllum	fuscum	flexuosum	F.sericeum	flexuosum,fuscum
118	-0.03	-0.03	0.0000	-4.77	0.0000	17101	18121	338	fuscum	divinum	flexuosum	F.sericeum	flexuosum,fuscum
119	-0.02	-0.02	0.0000	-3.95	0.0001	9987	10482	339	fuscum	subnitens	flexuosum	F.sericeum	flexuosum,fuscum
120	0.00	0.00	0.0000	0.54	0.5923	12295	12215	339	fimbriatum	fuscum	flexuosum	F.sericeum	flexuosum,fuscum
121	-0.11	-0.11	0.0000	-18.38	0.0000	16765	20733	339	squarrosum	platyphyllum	flexuosum	F.sericeum	flexuosum,squarrosum
122	-0.05	-0.05	0.0000	-8.24	0.0000	17565	19493	339	squarrosum	compactum	flexuosum	F.sericeum	flexuosum,squarrosum
123	-0.04	-0.04	0.0000	-7.36	0.0000	17885	19453	338	squarrosum	divinum	flexuosum	F.sericeum	flexuosum,squarrosum
124	-0.03	-0.03	0.0000	-4.85	0.0000	17224	18310	338	squarrosum	subnitens	flexuosum	F.sericeum	flexuosum,squarrosum
125	-0.02	-0.02	0.0000	-3.15	0.0017	17153	17814	339	squarrosum	fimbriatum	flexuosum	F.sericeum	flexuosum,squarrosum
126	-0.02	-0.02	0.0000	-2.54	0.0110	17251	17793	337	squarrosum	fuscum	flexuosum	F.sericeum	flexuosum,squarrosum
127	-0.01	-0.01	0.0000	-1.56	0.1180	17312	17643	337	squarrosum	capillifolium	flexuosum	F.sericeum	flexuosum,squarrosum
128	0.10	0.10	0.0000	16.94	0.0000	17191	14135	339	platyphyllum	subnitens	flexuosum	F.sericeum	flexuosum,subnitens
129	-0.03	-0.03	0.0000	-3.83	0.0001	16812	17680	337	subnitens	compactum	flexuosum	F.sericeum	flexuosum,subnitens
130	-0.01	-0.01	0.0000	-2.43	0.0149	17675	18200	339	subnitens	divinum	flexuosum	F.sericeum	flexuosum,subnitens
131	-0.24	-0.24	0.0000	-44.55	0.0000	15998	25919	334	lindbergii	flexuosum	fuscum	F.sericeum	fuscum,lindbergii
132	-0.21	-0.21	0.0000	-40.05	0.0000	16457	25186	340	lindbergii	tenellum	fuscum	F.sericeum	fuscum,lindbergii
133	-0.09	-0.09	0.0000	-15.52	0.0000	17607	20927	337	lindbergii	riparium	fuscum	F.sericeum	fuscum,lindbergii
134	-0.05	-0.05	0.0000	-7.95	0.0000	17977	19743	338	fuscum	compactum	lindbergii	F.sericeum	fuscum,lindbergii
135	-0.03	-0.03	0.0000	-5.76	0.0000	18993	20293	334	fuscum	divinum	lindbergii	F.sericeum	fuscum,lindbergii
136	0.11	0.11	0.0000	19.62	0.0000	18634	15034	338	platyphyllum	fuscum	lindbergii	F.sericeum	fuscum,lindbergii
137	-0.03	-0.03	0.0000	-4.26	0.0000	10940	11513	339	fuscum	subnitens	lindbergii	F.sericeum	fuscum,lindbergii
138	0.00	0.00	0.0000	0.11	0.9122	13569	13550	338	fimbriatum	fuscum	lindbergii	F.sericeum	fuscum,lindbergii
139	-0.18	-0.18	0.0000	-34.15	0.0000	14906	21500	337	riparium	flexuosum	fuscum	F.sericeum	fuscum,riparium
140	-0.15	-0.15	0.0000	-27.72	0.0000	15488	20901	338	riparium	tenellum	fuscum	F.sericeum	fuscum,riparium
141	-0.06	-0.06	0.0000	-8.96	0.0000	17211	19273	335	fuscum	compactum	riparium	F.sericeum	fuscum,riparium
142	-0.04	-0.04	0.0000	-7.11	0.0000	18263	19868	334	fuscum	divinum	riparium	F.sericeum	fuscum,riparium
143	0.11	0.11	0.0000	21.21	0.0000	18363	14703	338	platyphyllum	fuscum	riparium	F.sericeum	fuscum,riparium
144	-0.02	-0.02	0.0000	-3.45	0.0006	10731	11192	338	fuscum	subnitens	riparium	F.sericeum	fuscum,riparium
145	0.00	0.00	0.0000	0.21	0.8310	13257	13222	337	fimbriatum	fuscum	riparium	F.sericeum	fuscum,riparium
146	-0.04	-0.04	0.0000	-6.90	0.0000	16528	18013	337	fuscum	compactum	tenellum	F.sericeum	fuscum,tenellum
147	-0.03	-0.03	0.0000	-5.55	0.0000	17366	18603	338	fuscum	divinum	tenellum	F.sericeum	fuscum,tenellum
148	0.05	0.05	0.0000	8.31	0.0000	11740	10555	340	flexuosum	tenellum	fuscum	F.sericeum	fuscum,tenellum
149	0.12	0.12	0.0000	20.85	0.0000	17516	13813	339	platyphyllum	fuscum	tenellum	F.sericeum	fuscum,tenellum
150	-0.02	-0.02	0.0000	-3.23	0.0012	10250	10686	339	fuscum	subnitens	tenellum	F.sericeum	fuscum,tenellum
151	0.01	0.01	0.0000	1.88	0.0601	12624	12329	339	fimbriatum	fuscum	tenellum	F.sericeum	fuscum,tenellum
152	0.17	0.17	0.0000	33.15	0.0000	22527	16124	338	tenellum	riparium	lindbergii	F.sericeum	lindbergii,riparium
153	0.20	0.20	0.0000	41.52	0.0000	23079	15430	338	flexuosum	riparium	lindbergii	F.sericeum	lindbergii,riparium
154	-0.24	-0.24	0.0000	-47.45	0.0000	16441	26888	339	lindbergii	flexuosum	squarrosum	F.sericeum	lindbergii,squarrosum
155	-0.22	-0.22	0.0000	-45.06	0.0000	16699	26259	338	lindbergii	tenellum	squarrosum	F.sericeum	lindbergii,squarrosum
156	-0.11	-0.11	0.0000	-19.39	0.0000	18604	23245	340	squarrosum	platyphyllum	lindbergii	F.sericeum	lindbergii,squarrosum
157	-0.08	-0.08	0.0000	-15.26	0.0000	18354	21736	338	lindbergii	riparium	squarrosum	F.sericeum	lindbergii,squarrosum
158	-0.07	-0.07	0.0000	-11.57	0.0000	19382	22283	340	squarrosum	compactum	lindbergii	F.sericeum	lindbergii,squarrosum
159	-0.06	-0.06	0.0000	-9.53	0.0000	19750	22139	340	squarrosum	divinum	lindbergii	F.sericeum	lindbergii,squarrosum
160	-0.04	-0.04	0.0000	-6.93	0.0000	19219	20854	340	squarrosum	subnitens	lindbergii	F.sericeum	lindbergii,squarrosum
161	-0.03	-0.03	0.0000	-4.92	0.0000	19138	20251	340	squarrosum	fuscum	lindbergii	F.sericeum	lindbergii,squarrosum
162	-0.03	-0.03	0.0000	-4.72	0.0000	19152	20280	340	squarrosum	fimbriatum	lindbergii	F.sericeum	lindbergii,squarrosum
163	-0.02	-0.02	0.0000	-4.17	0.0000	19250	20193	340	squarrosum	capillifolium	lindbergii	F.sericeum	lindbergii,squarrosum
164	-0.23	-0.23	0.0000	-45.36	0.0000	16172	26079	340	lindbergii	flexuosum	subnitens	F.sericeum	lindbergii,subnitens
165	-0.21	-0.21	0.0000	-40.90	0.0000	16657	25354	339	lindbergii	tenellum	subnitens	F.sericeum	lindbergii,subnitens
166	-0.08	-0.08	0.0000	-14.44	0.0000	17717	20864	339	lindbergii	riparium	subnitens	F.sericeum	lindbergii,subnitens
167	-0.03	-0.03	0.0000	-5.48	0.0000	18513	19756	339	subnitens	compactum	lindbergii	F.sericeum	lindbergii,subnitens
168	0.09	0.09	0.0000	16.05	0.0000	18613	15560	340	platyphyllum	subnitens	lindbergii	F.sericeum	lindbergii,subnitens
169	-0.02	-0.02	0.0000	-3.49	0.0005	19489	20282	339	subnitens	divinum	lindbergii	F.sericeum	lindbergii,subnitens
170	-0.05	-0.05	0.0000	-8.70	0.0000	10827	12063	339	tenellum	flexuosum	lindbergii	F.sericeum	lindbergii,tenellum
171	0.02	0.02	0.0000	3.16	0.0016	13137	12632	339	subnitens	capillifolium	platyphyllum	F.sericeum	platyphyllum,capillifolium
172	-0.01	-0.01	0.0000	-2.25	0.0245	15836	16297	339	capillifolium	fimbriatum	platyphyllum	F.sericeum	platyphyllum,capillifolium
173	0.01	0.01	0.0000	1.34	0.1807	9801	9625	338	fuscum	capillifolium	platyphyllum	F.sericeum	platyphyllum,capillifolium

174	0.00	0.00	0.0000	0.37	0.7127	16537	16462	339	subnitens	fimbriatum	platyphyllum	F.sericeum	platyphyllum,fimbriatum
175	0.01	0.01	0.0000	1.51	0.1319	13114	12879	338	subnitens	fuscum	platyphyllum	F.sericeum	platyphyllum,fuscum
176	-0.01	-0.01	0.0000	-1.20	0.2287	16005	16256	338	fuscum	fimbriatum	platyphyllum	F.sericeum	platyphyllum,fuscum
177	-0.23	-0.23	0.0000	-44.48	0.0000	15720	25073	338	lindbergii	flexuosum	platyphyllum	F.sericeum	platyphyllum,lindbergii
178	-0.21	-0.21	0.0000	-40.22	0.0000	16069	24499	338	lindbergii	tenellum	platyphyllum	F.sericeum	platyphyllum,lindbergii
179	-0.09	-0.09	0.0000	-16.30	0.0000	17173	20415	338	lindbergii	riparium	platyphyllum	F.sericeum	platyphyllum,lindbergii
180	-0.17	-0.17	0.0000	-31.52	0.0000	14640	20810	338	riparium	flexuosum	platyphyllum	F.sericeum	platyphyllum,riparium
181	-0.15	-0.15	0.0000	-26.30	0.0000	15155	20344	338	riparium	tenellum	platyphyllum	F.sericeum	platyphyllum,riparium
182	0.05	0.05	0.0000	7.12	0.0000	11387	10402	339	flexuosum	tenellum	platyphyllum	F.sericeum	platyphyllum,tenellum
183	-0.19	-0.19	0.0000	-38.75	0.0000	14970	22089	337	riparium	flexuosum	squarrosum	F.sericeum	riparium,squarrosum
184	-0.17	-0.17	0.0000	-31.62	0.0000	15453	21647	337	riparium	tenellum	squarrosum	F.sericeum	riparium,squarrosum
185	-0.11	-0.11	0.0000	-20.22	0.0000	17970	22608	339	squarrosum	platyphyllum	riparium	F.sericeum	riparium,squarrosum
186	-0.08	-0.08	0.0000	-12.52	0.0000	18595	21680	337	squarrosum	compactum	riparium	F.sericeum	riparium,squarrosum
187	-0.07	-0.07	0.0000	-11.59	0.0000	18937	21622	339	squarrosum	divinum	riparium	F.sericeum	riparium,squarrosum
188	-0.04	-0.04	0.0000	-6.58	0.0000	18744	20234	339	squarrosum	subnitens	riparium	F.sericeum	riparium,squarrosum
189	-0.03	-0.03	0.0000	-4.72	0.0000	18560	19621	338	squarrosum	fimbriatum	riparium	F.sericeum	riparium,squarrosum
190	-0.03	-0.03	0.0000	-4.45	0.0000	18711	19704	337	squarrosum	fuscum	riparium	F.sericeum	riparium,squarrosum
191	-0.02	-0.02	0.0000	-3.62	0.0003	18735	19556	339	squarrosum	capillifolium	riparium	F.sericeum	riparium,squarrosum
192	-0.18	-0.18	0.0000	-36.32	0.0000	14869	21549	338	riparium	flexuosum	subnitens	F.sericeum	riparium,subnitens
193	-0.15	-0.15	0.0000	-29.31	0.0000	15519	20973	338	riparium	tenellum	subnitens	F.sericeum	riparium,subnitens
194	-0.04	-0.04	0.0000	-6.75	0.0000	17822	19397	338	subnitens	compactum	riparium	F.sericeum	riparium,subnitens
195	-0.03	-0.03	0.0000	-5.24	0.0000	18782	19955	339	subnitens	divinum	riparium	F.sericeum	riparium,subnitens
196	0.10	0.10	0.0000	17.54	0.0000	18423	15205	338	platyphyllum	subnitens	riparium	F.sericeum	riparium,subnitens
197	-0.04	-0.04	0.0000	-5.93	0.0000	11669	12569	335	tenellum	flexuosum	riparium	F.sericeum	riparium,tenellum
198	-0.11	-0.11	0.0000	-18.07	0.0000	16354	20305	339	capillifolium	platyphyllum	squarrosum	F.sericeum	squarrosum,capillifolium
199	0.02	0.02	0.0000	3.19	0.0014	12116	11666	339	subnitens	capillifolium	squarrosum	F.sericeum	squarrosum,capillifolium
200	0.01	0.01	0.0000	1.55	0.1218	9028	8846	338	fuscum	capillifolium	squarrosum	F.sericeum	squarrosum,capillifolium
201	-0.11	-0.11	0.0000	-18.13	0.0000	16618	20625	339	fimbriatum	platyphyllum	squarrosum	F.sericeum	squarrosum,fimbriatum
202	0.02	0.02	0.0000	3.55	0.0004	15250	14599	338	subnitens	fimbriatum	squarrosum	F.sericeum	squarrosum,fimbriatum
203	0.01	0.01	0.0000	2.09	0.0367	14685	14329	337	fuscum	fimbriatum	squarrosum	F.sericeum	squarrosum,fimbriatum
204	0.00	0.00	0.0000	0.69	0.4881	14524	14403	338	capillifolium	fimbriatum	squarrosum	F.sericeum	squarrosum,fimbriatum
205	-0.10	-0.10	0.0000	-17.37	0.0000	16618	20437	339	fuscum	platyphyllum	squarrosum	F.sericeum	squarrosum,fuscum
206	0.01	0.01	0.0000	1.98	0.0476	12104	11816	337	subnitens	fuscum	squarrosum	F.sericeum	squarrosum,fuscum
207	-0.09	-0.09	0.0000	-15.14	0.0000	16916	20425	339	subnitens	platyphyllum	squarrosum	F.sericeum	squarrosum,subnitens
208	-0.10	-0.10	0.0000	-17.51	0.0000	17083	20993	338	squarrosum	platyphyllum	tenellum	F.sericeum	squarrosum,tenellum
209	-0.05	-0.05	0.0000	-7.72	0.0000	17946	19721	338	squarrosum	compactum	tenellum	F.sericeum	squarrosum,tenellum
210	-0.04	-0.04	0.0000	-7.14	0.0000	18240	19790	338	squarrosum	divinum	tenellum	F.sericeum	squarrosum,tenellum
211	0.04	0.04	0.0000	6.18	0.0000	11710	10783	338	flexuosum	tenellum	squarrosum	F.sericeum	squarrosum,tenellum
212	-0.02	-0.02	0.0000	-3.66	0.0003	17743	18545	338	squarrosum	subnitens	tenellum	F.sericeum	squarrosum,tenellum
213	-0.02	-0.02	0.0000	-3.07	0.0021	17460	18107	338	squarrosum	fimbriatum	tenellum	F.sericeum	squarrosum,tenellum
214	-0.01	-0.01	0.0000	-1.51	0.1318	17684	18004	338	squarrosum	fuscum	tenellum	F.sericeum	squarrosum,tenellum
215	0.00	0.00	0.0000	-0.23	0.8216	17768	17815	337	squarrosum	capillifolium	tenellum	F.sericeum	squarrosum,tenellum
216	0.00	0.00	0.0001	-0.56	0.5778	14330	14448	340	capillifolium	fuscum	subnitens	F.sericeum	subnitens,capillifolium
217	0.054	0.054	0.0000	8.15	0.0000	11,819	10,602	338	flexuosum	tenellum	subnitens	F.sericeum	subnitens,tenellum
218	0.102	0.102	0.0000	17.45	0.0000	17,593	14,348	338	platyphyllum	subnitens	tenellum	F.sericeum	subnitens,tenellum
219	-0.029	-0.029	0.0000	-4.69	0.0000	17,084	18,114	338	subnitens	compactum	tenellum	F.sericeum	subnitens,tenellum
220	-0.022	-0.022	0.0000	-3.51	0.0004	17,919	18,707	339	subnitens	divinum	tenellum	F.sericeum	subnitens,tenellum

Table S7. Average pairwise absolute D-statistic *Flatbergium sericeum* as an outgroup)

Pair	D	Average number of ABBA and BABA patterns observed	Number of triplets
capillifolium,compactum	0.061	30,310	4
capillifolium,lindbergii	0.107	36,573	7
capillifolium,riparium	0.098	33,790	6
capillifolium,tenellum	0.056	28,250	6
compactum,fimbriatum	0.065	35,967	2
compactum,fuscum	0.053	30,500	4
compactum,lindbergii	0.146	39,374	4
compactum,platyphyllum	0.027	38,790	1
compactum,riparium	0.116	36,460	3
compactum,subnitens	0.065	36,547	2
compactum,tenellum	0.054	29,386	2
divinum,capillifolium	0.057	30,811	4
divinum,fimbriatum	0.053	36,667	2
divinum,fuscum	0.049	30,945	4
divinum,lindbergii	0.145	40,366	4
divinum,riparium	0.118	37,265	3
divinum,squarrosum	0.045	40,416	2
divinum,subnitens	0.054	37,249	2
divinum,tenellum	0.052	30,324	2
fimbriatum,capillifolium	0.041	31,720	1
fimbriatum,fuscum	0.028	31,980	1
fimbriatum,lindbergii	0.118	38,981	6
fimbriatum,riparium	0.105	36,228	5
fimbriatum,tenellum	0.051	31,235	4
flexuosum,capillifolium	0.060	29,993	4
flexuosum,compactum	0.060	36,178	1
flexuosum,divinum	0.066	37,872	1
flexuosum,fimbriatum	0.058	33,736	3
flexuosum,fuscum	0.052	30,101	4
flexuosum,squarrosum	0.050	36,500	5
flexuosum,subnitens	0.061	32,906	2
fuscum,lindbergii	0.106	36,475	7
fuscum,riparium	0.093	33,753	6
fuscum,tenellum	0.054	29,021	5
lindbergii,riparium	0.182	38,579	2
lindbergii,squarrosum	0.091	41,040	10
lindbergii,subnitens	0.111	39,180	6
lindbergii,tenellum	0.054	22,916	1
platyphyllum,capillifolium	0.020	25,769	1
platyphyllum,lindbergii	0.174	39,637	3
platyphyllum,riparium	0.160	35,477	2
platyphyllum,tenellum	0.045	21,764	1
riparium,squarrosum	0.081	38,855	9
riparium,subnitens	0.100	36,514	5
riparium,tenellum	0.037	24,261	1
squarrosum,capillifolium	0.063	32,318	2
squarrosum,fimbriatum	0.065	33,535	2
squarrosum,fuscum	0.103	36,980	1
squarrosum,subnitens	0.094	37,407	1
squarrosum,tenellum	0.051	34,619	5
subnitens,tenellum	0.052	31,547	4
51 significant out of 63 tested			175

Table S8.The *f*3 statistics inferred with TreeMix
Only phylogenetically correct tripets are shown

Triplet	F3 statistics	SE	Z-score
((compactum;fimbriatum),flexuosum)	0.044	0.001	34
((fimbriatum;compactum),flexuosum)	0.090	0.002	50
((divinum;compactum),fimbriatum)	0.108	0.002	54
((compactum;fimbriatum),riparium)	0.046	0.001	34
((fimbriatum;compactum),riparium)	0.088	0.002	48
((compactum;fimbriatum),tenellum)	0.044	0.001	33
((fimbriatum;compactum),tenellum)	0.090	0.002	49
((compactum;fimbriatum),lindbergii)	0.047	0.001	34
((fimbriatum;compactum),lindbergii)	0.087	0.002	48
((compactum;subnitens),flexuosum)	0.044	0.001	33
((subnitens;compactum),flexuosum)	0.190	0.003	75
((divinum;compactum),subnitens)	0.107	0.002	54
((compactum;subnitens),riparium)	0.046	0.001	33
((subnitens;compactum),riparium)	0.188	0.003	74
((compactum;subnitens),tenellum)	0.044	0.001	33
((subnitens;compactum),tenellum)	0.189	0.003	75
((compactum;subnitens),lindbergii)	0.048	0.001	34
((subnitens;compactum),lindbergii)	0.186	0.003	74
((capillifolium;compactum),flexuosum)	0.142	0.002	64
((compactum;capillifolium),flexuosum)	0.045	0.001	34
((divinum;compactum),capillifolium)	0.108	0.002	54
((capillifolium;compactum),riparium)	0.141	0.002	63
((compactum;capillifolium),riparium)	0.045	0.001	33
((capillifolium;compactum),tenellum)	0.142	0.002	63
((compactum;capillifolium),tenellum)	0.045	0.001	33
((capillifolium;compactum),lindbergii)	0.138	0.002	62
((compactum;capillifolium),lindbergii)	0.048	0.001	35
((divinum;compactum),flexuosum)	0.109	0.002	55
((squarrosum;compactum),flexuosum)	0.067	0.002	43
((fuscum;compactum),flexuosum)	0.151	0.002	66
((platyphyllum;compactum),flexuosum)	0.076	0.002	45
((compactum;divinum),riparium)	0.044	0.001	33
((compactum;divinum),squarrosum)	0.045	0.001	34
((divinum;compactum),squarrosum)	0.107	0.002	54
((compactum;divinum),tenellum)	0.043	0.001	33
((divinum;compactum),tenellum)	0.109	0.002	54
((compactum;divinum),lindbergii)	0.047	0.001	34
((divinum;compactum),lindbergii)	0.106	0.002	53
((compactum;divinum),fuscum)	0.045	0.001	34
((divinum;compactum),fuscum)	0.108	0.002	54
((compactum;divinum),platyphyllum)	0.043	0.001	33
((divinum;compactum),platyphyllum)	0.109	0.002	54
((squarrosum;compactum),riparium)	0.066	0.002	42
((fuscum;compactum),riparium)	0.150	0.002	66
((platyphyllum;compactum),riparium)	0.076	0.002	45
((compactum;squarrosum),tenellum)	0.050	0.001	35
((squarrosum;compactum),tenellum)	0.069	0.002	43
((compactum;squarrosum),lindbergii)	0.055	0.001	37
((squarrosum;compactum),lindbergii)	0.065	0.002	41
((fuscum;compactum),tenellum)	0.150	0.002	66
((platyphyllum;compactum),tenellum)	0.077	0.002	45
((fuscum;compactum),lindbergii)	0.147	0.002	65
((platyphyllum;compactum),lindbergii)	0.074	0.002	44
((fimbriatum;subnitens),flexuosum)	0.042	0.001	33
((subnitens;fimbriatum),flexuosum)	0.142	0.002	63
((fimbriatum;subnitens),divinum)	0.043	0.001	33
((subnitens;fimbriatum),divinum)	0.141	0.002	62
((fimbriatum;subnitens),riparium)	0.042	0.001	32
((subnitens;fimbriatum),riparium)	0.142	0.002	62
((fimbriatum;subnitens),squarrosum)	0.044	0.001	33
((subnitens;fimbriatum),squarrosum)	0.139	0.002	62
((fimbriatum;subnitens),tenellum)	0.042	0.001	32
((subnitens;fimbriatum),tenellum)	0.141	0.002	62
((fimbriatum;subnitens),lindbergii)	0.043	0.001	33
((fimbriatum;subnitens),platyphyllum)	0.044	0.001	33
((subnitens;fimbriatum),platyphyllum)	0.140	0.002	62
((capillifolium;fimbriatum),flexuosum)	0.094	0.002	50
((fimbriatum;capillifolium),flexuosum)	0.043	0.001	34
((capillifolium;fimbriatum),divinum)	0.095	0.002	50
((fimbriatum;capillifolium),divinum)	0.042	0.001	33
((capillifolium;fimbriatum),riparium)	0.096	0.002	50
((fimbriatum;capillifolium),riparium)	0.041	0.001	32
((capillifolium;fimbriatum),squarrosum)	0.093	0.002	50
((fimbriatum;capillifolium),squarrosum)	0.045	0.001	34
((capillifolium;fimbriatum),tenellum)	0.094	0.002	50

((fimbriatum;capillifolium),tenellum)	0.043	0.001	33
((capillifolium;fimbriatum),lindbergii)	0.094	0.002	50
((fimbriatum;capillifolium),lindbergii)	0.044	0.001	33
((capillifolium;fimbriatum),platyphyllum)	0.094	0.002	50
((fimbriatum;capillifolium),platyphyllum)	0.044	0.001	34
((divinum;fimbriatum),flexuosum)	0.108	0.002	54
((fimbriatum;flexuosum),riparium)	0.163	0.002	69
((flexuosum;fimbriatum),riparium)	0.231	0.003	85
((squarrosum;fimbriatum),flexuosum)	0.059	0.001	39
((fuscum;fimbriatum),flexuosum)	0.103	0.002	53
((platyphyllum;fimbriatum),flexuosum)	0.052	0.001	37
((divinum;fimbriatum),riparium)	0.110	0.002	54
((fimbriatum;divinum),riparium)	0.088	0.002	48
((squarrosum;fimbriatum),divinum)	0.066	0.002	41
((divinum;fimbriatum),tenellum)	0.109	0.002	54
((fimbriatum;divinum),tenellum)	0.089	0.002	48
((divinum;fimbriatum),lindbergii)	0.108	0.002	53
((fimbriatum;divinum),lindbergii)	0.089	0.002	48
((fuscum;fimbriatum),divinum)	0.103	0.002	53
((platyphyllum;fimbriatum),divinum)	0.056	0.001	38
((squarrosum;fimbriatum),riparium)	0.060	0.002	39
((fuscum;fimbriatum),riparium)	0.105	0.002	53
((platyphyllum;fimbriatum),riparium)	0.054	0.001	37
((fimbriatum;squarrosum),tenellum)	0.088	0.002	48
((squarrosum;fimbriatum),tenellum)	0.061	0.002	39
((fimbriatum;squarrosum),lindbergii)	0.090	0.002	48
((squarrosum;fimbriatum),lindbergii)	0.059	0.002	39
((fuscum;fimbriatum),squarrosum)	0.101	0.002	52
((platyphyllum;fimbriatum),squarrosum)	0.054	0.001	37
((fuscum;fimbriatum),tenellum)	0.103	0.002	52
((platyphyllum;fimbriatum),tenellum)	0.053	0.001	36
((platyphyllum;fimbriatum),lindbergii)	0.053	0.001	37
((fimbriatum;fuscum),platyphyllum)	0.043	0.001	33
((fuscum;fimbriatum),platyphyllum)	0.103	0.002	52
((capillifolium;subnitens),flexuosum)	0.066	0.002	41
((subnitens;capillifolium),flexuosum)	0.115	0.002	56
((capillifolium;subnitens),divinum)	0.068	0.002	42
((subnitens;capillifolium),divinum)	0.113	0.002	55
((capillifolium;subnitens),riparium)	0.068	0.002	41
((subnitens;capillifolium),riparium)	0.113	0.002	55
((capillifolium;subnitens),squarrosum)	0.067	0.002	41
((subnitens;capillifolium),squarrosum)	0.114	0.002	56
((capillifolium;subnitens),tenellum)	0.066	0.002	41
((subnitens;capillifolium),tenellum)	0.114	0.002	56
((capillifolium;subnitens),lindbergii)	0.067	0.002	41
((subnitens;capillifolium),lindbergii)	0.114	0.002	56
((capillifolium;subnitens),platyphyllum)	0.067	0.002	41
((subnitens;capillifolium),platyphyllum)	0.114	0.002	56
((divinum;subnitens),flexuosum)	0.107	0.002	54
((squarrosum;subnitens),flexuosum)	0.056	0.001	39
((fuscum;subnitens),flexuosum)	0.075	0.002	44
((platyphyllum;subnitens),flexuosum)	0.050	0.001	36
((divinum;subnitens),riparium)	0.109	0.002	54
((subnitens;divinum),riparium)	0.187	0.003	74
((squarrosum;subnitens),divinum)	0.065	0.002	41
((divinum;subnitens),tenellum)	0.108	0.002	53
((subnitens;divinum),tenellum)	0.187	0.003	74
((divinum;subnitens),lindbergii)	0.108	0.002	53
((subnitens;divinum),lindbergii)	0.187	0.003	74
((fuscum;subnitens),divinum)	0.077	0.002	44
((platyphyllum;subnitens),divinum)	0.055	0.001	37
((squarrosum;subnitens),riparium)	0.058	0.002	38
((platyphyllum;subnitens),riparium)	0.052	0.001	36
((squarrosum;subnitens),tenellum)	0.059	0.002	39
((subnitens;squarrosum),tenellum)	0.186	0.003	73
((squarrosum;subnitens),lindbergii)	0.058	0.002	38
((subnitens;squarrosum),lindbergii)	0.186	0.003	73
((fuscum;subnitens),squarrosum)	0.075	0.002	44
((platyphyllum;subnitens),squarrosum)	0.055	0.001	37
((fuscum;subnitens),tenellum)	0.075	0.002	44
((subnitens;tenellum),fuscum)	0.115	0.002	56
((platyphyllum;subnitens),tenellum)	0.051	0.001	36
((fuscum;subnitens),lindbergii)	0.076	0.002	44
((platyphyllum;subnitens),lindbergii)	0.053	0.001	36
((fuscum;subnitens),platyphyllum)	0.077	0.002	44
((subnitens;fuscum),platyphyllum)	0.113	0.002	55
((divinum;capillifolium),flexuosum)	0.109	0.002	55
((squarrosum;capillifolium),flexuosum)	0.057	0.001	39
((fuscum;capillifolium),flexuosum)	0.056	0.001	38

((platyphyllum;capillifolium),flexuosum)	0.051	0.001	37
((capillifolium;divinum),riparium)	0.142	0.002	63
((divinum;capillifolium),riparium)	0.109	0.002	54
((squarrosum;capillifolium),divinum)	0.064	0.002	41
((capillifolium;divinum),tenellum)	0.141	0.002	63
((divinum;capillifolium),tenellum)	0.110	0.002	54
((capillifolium;divinum),lindbergii)	0.141	0.002	63
((divinum;capillifolium),lindbergii)	0.109	0.002	54
((fuscum;capillifolium),divinum)	0.055	0.001	38
((platyphyllum;capillifolium),divinum)	0.054	0.001	37
((squarrosum;capillifolium),riparium)	0.056	0.001	38
((fuscum;capillifolium),riparium)	0.055	0.001	38
((platyphyllum;capillifolium),riparium)	0.051	0.001	36
((capillifolium;squarrosum),tenellum)	0.138	0.002	62
((squarrosum;capillifolium),tenellum)	0.059	0.002	39
((capillifolium;squarrosum),lindbergii)	0.139	0.002	62
((squarrosum;capillifolium),lindbergii)	0.058	0.002	39
((fuscum;capillifolium),squarrosum)	0.055	0.001	38
((platyphyllum;capillifolium),squarrosum)	0.055	0.001	38
((fuscum;capillifolium),tenellum)	0.055	0.001	38
((platyphyllum;capillifolium),tenellum)	0.052	0.001	37
((fuscum;capillifolium),lindbergii)	0.055	0.001	38
((platyphyllum;capillifolium),lindbergii)	0.053	0.001	37
((capillifolium;fuscum),platyphyllum)	0.046	0.001	34
((fuscum;capillifolium),platyphyllum)	0.056	0.001	38
((riparium;flexuosum),divinum)	0.187	0.003	74
((tenellum;flexuosum),divinum)	0.066	0.002	43
((lindbergii;flexuosum),divinum)	0.063	0.002	41
((flexuosum;riparium),squarrosum)	0.230	0.003	84
((riparium;flexuosum),squarrosum)	0.186	0.003	74
((tenellum;flexuosum),riparium)	0.069	0.002	44
((flexuosum;riparium),lindbergii)	0.227	0.003	84
((riparium;flexuosum),lindbergii)	0.188	0.003	74
((flexuosum;riparium),fuscum)	0.229	0.003	84
((riparium;flexuosum),fuscum)	0.186	0.003	74
((flexuosum;riparium),platyphyllum)	0.229	0.003	84
((riparium;flexuosum),platyphyllum)	0.187	0.003	74
((tenellum;flexuosum),squarrosum)	0.068	0.002	44
((lindbergii;flexuosum),squarrosum)	0.064	0.002	41
((flexuosum;tenellum),lindbergii)	0.082	0.002	46
((tenellum;flexuosum),lindbergii)	0.066	0.002	43
((flexuosum;tenellum),fuscum)	0.084	0.002	46
((tenellum;flexuosum),fuscum)	0.065	0.002	43
((flexuosum;tenellum),platyphyllum)	0.082	0.002	46
((tenellum;flexuosum),platyphyllum)	0.067	0.002	43
((flexuosum;lindbergii),fuscum)	0.277	0.003	96
((flexuosum;lindbergii),platyphyllum)	0.275	0.003	96
((lindbergii;flexuosum),platyphyllum)	0.065	0.002	42
((squarrosum;divinum),riparium)	0.065	0.002	41
((fuscum;divinum),riparium)	0.150	0.002	65
((platyphyllum;divinum),riparium)	0.077	0.002	44
((divinum;squarrosum),tenellum)	0.114	0.002	55
((squarrosum;divinum),tenellum)	0.067	0.002	41
((divinum;squarrosum),lindbergii)	0.115	0.002	55
((squarrosum;divinum),lindbergii)	0.066	0.002	41
((platyphyllum;divinum),tenellum)	0.076	0.002	44
((platyphyllum;divinum),lindbergii)	0.078	0.002	45
((tenellum;riparium),squarrosum)	0.217	0.003	81
((lindbergii;riparium),squarrosum)	0.066	0.002	41
((riparium;squarrosum),lindbergii)	0.235	0.003	85
((riparium;tenellum),lindbergii)	0.190	0.003	74
((tenellum;riparium),lindbergii)	0.214	0.003	80
((riparium;tenellum),fuscum)	0.190	0.003	74
((tenellum;riparium),fuscum)	0.214	0.003	80
((riparium;tenellum),platyphyllum)	0.189	0.003	74
((tenellum;riparium),platyphyllum)	0.215	0.003	80
((lindbergii;riparium),fuscum)	0.064	0.002	41
((riparium;lindbergii),fuscum)	0.237	0.003	85
((lindbergii;riparium),platyphyllum)	0.066	0.002	41
((riparium;lindbergii),platyphyllum)	0.235	0.003	85
((fuscum;squarrosum),tenellum)	0.146	0.002	64
((platyphyllum;squarrosum),tenellum)	0.075	0.002	44
((fuscum;squarrosum),lindbergii)	0.147	0.002	64
((platyphyllum;squarrosum),lindbergii)	0.077	0.002	44
((lindbergii;tenellum),fuscum)	0.064	0.002	41
((tenellum;lindbergii),fuscum)	0.260	0.003	91
((lindbergii;tenellum),platyphyllum)	0.065	0.002	41
((tenellum;lindbergii),platyphyllum)	0.260	0.003	91

Table S9. The QuIBL analysis results

The samples used in this analysis are listed in Table S1.
Discordant topologies with significant non-ILS component are shown in bold; triplets, for which the outgroup supported by the most trees is not phylogenetically correct, are underlined

C1, C2: The time (in coalescent units) since two sister species became isolated from the third species for a triplet topology under the ILS-only and the ILS+introgression distribution model, respectively;
mixprop1, mixprop2: The inferred mixing proroptions for the ILS+introgression and the ILS-only distribution model, respectively;
lambda2Dist, lambda1Dist: The scaling factor to convert the input branch length unit into coalescent units for the ILS+introgression and the ILS-only distribution model, respectively;

BIC1Dist, BIC2Dist: The Bayesian Information Criterion scores for the ILS-only and ILS+introgression model, respectively;

Count: The total number of trees supporting a triplet topology;
BICdiff: *Δ*BIC
totalIntroProp: Proportion of trees arising via introgression;
isSig: Is the ILS+introgression model supported over the ILS-only model;
IsMostCommon: Is the topology supported by the most trees phylogenetically correct.

See the original publication (Edelman et al. 2019) for detailed information

No	The triplet analyzed	outgroup	C1	C2	mixprop1	mixprop2	lambda2Dist	lambda1Dist	BIC2Dist	BIC1Dist	Count	true_outgroup	BICdiff	totalIntroProp	isSig	IsMostCommon	Pair
1	capillifolium_divinum_fuscum	capillifolium	0	4.09	0.83	0.17	0.00	0.00	-2,733	-2,751	286	divinum	18	0.02	FALSE	TRUE	divinum_fuscum
2	capillifolium_divinum_fuscum	divinum	0	2.03	0.36	0.64	0.00	0.01	-22,229	-21,870	2608	divinum	-359	0.52	TRUE	TRUE	capillifolium_fuscum
3	capillifolium_divinum_fuscum	fuscum	0	3.59	0.79	0.21	0.00	0.00	-2,915	-2,942	301	divinum	27	0.02	FALSE	TRUE	capillifolium_divinum
4	capillifolium_divinum_subnitens	capillifolium	0	4.12	0.85	0.15	0.00	0.00	-3,922	-3,941	401	divinum	19	0.02	FALSE	TRUE	divinum_subnitens
5	capillifolium_divinum_subnitens	divinum	0	2.07	0.46	0.54	0.00	0.00	-20,832	-20,729	2377	divinum	-103	0.40	TRUE	TRUE	capillifolium_subnitens
6	capillifolium_divinum_subnitens	subnitens	0	3.98	0.87	0.13	0.00	0.00	-4,071	-4,097	417	divinum	26	0.02	FALSE	TRUE	capillifolium_divinum
7	capillifolium_divinum_fimbriatum	capillifolium	0	3.84	0.86	0.14	0.00	0.00	-5,508	-5,547	569	divinum	39	0.02	FALSE	TRUE	divinum_fimbriatum
8	capillifolium_divinum_fimbriatum	divinum	0	2.05	0.61	0.39	0.00	0.00	-19,152	-19,261	2094	divinum	108	0.26	FALSE	TRUE	capillifolium_fimbriatum
9	capillifolium_divinum_fimbriatum	fimbriatum	0	5.43	0.92	0.08	0.00	0.00	-5,147	-5,138	532	divinum	-9	0.01	FALSE	TRUE	capillifolium_divinum
10	capillifolium_divinum_compactum	capillifolium	0	3.32	0.84	0.16	0.00	0.00	-12,972	-13,088	1362	capillifolium	116	0.07	FALSE	TRUE	divinum_compactum
11	capillifolium_divinum_compactum	divinum	0	4.85	0.90	0.10	0.00	0.00	-9,257	-9,265	919	capillifolium	8	0.03	FALSE	TRUE	capillifolium_compactum
12	capillifolium_divinum_compactum	compactum	0	4.79	0.90	0.10	0.00	0.00	-9,066	-9,075	914	capillifolium	9	0.03	FALSE	TRUE	capillifolium_divinum
13	capillifolium_divinum_flexuosum	capillifolium	0	3.17	0.81	0.19	0.00	0.00	-12,008	-12,126	1271	flexuosum	118	0.08	FALSE	FALSE	divinum_flexuosum
14	capillifolium_divinum_flexuosum	divinum	0	4.60	0.90	0.10	0.00	0.00	-6,747	-6,768	693	flexuosum	21	0.02	FALSE	TRUE	capillifolium_flexuosum
15	capillifolium_divinum_flexuosum	flexuosum	0	4.03	0.84	0.16	0.00	0.00	-11,335	-11,383	1231	flexuosum	48	0.06	FALSE	FALSE	capillifolium_divinum
16	capillifolium_divinum_tenellum	capillifolium	0	3.19	0.80	0.20	0.00	0.00	-12,035	-12,149	1276	tenellum	113	0.08	FALSE	FALSE	divinum_tenellum
17	capillifolium_divinum_tenellum	divinum	0	4.68	0.90	0.10	0.00	0.00	-6,771	-6,786	694	tenellum	16	0.02	FALSE	TRUE	capillifolium_tenellum
18	capillifolium_divinum_tenellum	tenellum	0	3.79	0.84	0.16	0.00	0.00	-11,301	-11,372	1225	tenellum	71	0.06	FALSE	FALSE	capillifolium_divinum
19	capillifolium_divinum_lindbergii	capillifolium	0	3.40	0.82	0.18	0.00	0.00	-12,649	-12,759	1329	lindbergii	110	0.07	FALSE	FALSE	divinum_lindbergii
20	capillifolium_divinum_lindbergii	divinum	0	4.22	0.90	0.10	0.00	0.00	-8,287	-8,328	839	lindbergii	41	0.03	FALSE	TRUE	capillifolium_lindbergii
21	capillifolium_divinum_lindbergii	lindbergii	0	4.13	0.89	0.11	0.00	0.00	-10,179	-10,235	1027	lindbergii	56	0.04	FALSE	FALSE	capillifolium_divinum
22	capillifolium_divinum_riparium	capillifolium	0	2.98	0.79	0.21	0.00	0.00	-12,041	-12,163	1271	riparium	122	0.08	FALSE	FALSE	divinum_riparium
23	capillifolium_divinum_riparium	divinum	0	4.59	0.90	0.10	0.00	0.00	-7,508	-7,527	764	riparium	18	0.02	FALSE	TRUE	capillifolium_riparium
24	capillifolium_divinum_riparium	riparium	0	3.57	0.85	0.15	0.00	0.00	-11,158	-11,243	1160	riparium	85	0.05	FALSE	FALSE	capillifolium_divinum
25	capillifolium_divinum_squarrosum	capillifolium	0	3.82	0.85	0.15	0.00	0.00	-11,741	-11,811	1220	divinum	70	0.06	FALSE	FALSE	divinum_squarrosum
26	capillifolium_divinum_squarrosum	divinum	0	3.72	0.88	0.12	0.00	0.00	-10,782	-10,859	1096	divinum	77	0.04	FALSE	FALSE	capillifolium_squarrosum
27	capillifolium_divinum_squarrosum	squarrosum	0	3.86	0.89	0.11	0.00	0.00	-8,755	-8,820	879	divinum	65	0.03	FALSE	TRUE	capillifolium_divinum
28	capillifolium_divinum_platyphyllum	capillifolium	0	4.08	0.84	0.16	0.00	0.00	-6,863	-6,896	697	divinum	32	0.04	FALSE	TRUE	divinum_platyphyllum
29	capillifolium_divinum_platyphyllum	divinum	0	2.64	0.77	0.23	0.00	0.00	-12,836	-12,975	1360	divinum	139	0.10	FALSE	TRUE	capillifolium_platyphyllum
30	capillifolium_divinum_platyphyllum	platyphyllum	0	3.65	0.72	0.28	0.00	0.01	-9,565	-9,610	1138	divinum	45	0.10	FALSE	TRUE	capillifolium_divinum
31	capillifolium_fuscum_subnitens	capillifolium	0	3.93	0.88	0.12	0.00	0.00	-7,084	-7,130	722	subnitens	46	0.03	FALSE	TRUE	fuscum_subnitens
32	capillifolium_fuscum_subnitens	fuscum	0	4.39	0.86	0.14	0.00	0.00	-7,291	-7,309	724	subnitens	18	0.03	FALSE	TRUE	capillifolium_subnitens
33	capillifolium_fuscum_subnitens	subnitens	0	2.57	0.76	0.24	0.00	0.00	-16,602	-16,773	1749	subnitens	170	0.13	FALSE	TRUE	capillifolium_fuscum
34	capillifolium_fuscum_fimbriatum	capillifolium	0	3.56	0.81	0.19	0.00	0.00	-4,583	-4,620	471	fimbriatum	37	0.03	FALSE	TRUE	fuscum_fimbriatum
35	capillifolium_fuscum_fimbriatum	fuscum	0	4.50	0.88	0.12	0.00	0.00	-4,823	-4,839	493	fimbriatum	16	0.02	FALSE	TRUE	capillifolium_fimbriatum
36	capillifolium_fuscum_fimbriatum	fimbriatum	0	1.85	0.56	0.44	0.00	0.00	-20,192	-20,234	2231	fimbriatum	43	0.31	FALSE	TRUE	capillifolium_fuscum
37	capillifolium_fuscum_compactum	capillifolium	0	4.81	0.86	0.14	0.00	0.00	-2,743	-2,748	285	compactum	5	0.01	FALSE	TRUE	fuscum_compactum
38	capillifolium_fuscum_compactum	fuscum	0	4.32	0.79	0.21	0.00	0.00	-2,811	-2,821	286	compactum	10	0.02	FALSE	TRUE	capillifolium_compactum
39	capillifolium_fuscum_compactum	compactum	0	1.99	0.35	0.65	0.00	0.01	-22,396	-22,006	2624	compactum	-391	0.53	TRUE	TRUE	capillifolium_fuscum
40	capillifolium_fuscum_flexuosum	capillifolium	0	3.97	0.81	0.19	0.00	0.00	-2,398	-2,417	252	flexuosum	19	0.02	FALSE	TRUE	fuscum_flexuosum
41	capillifolium_fuscum_flexuosum	fuscum	0	3.52	0.81	0.19	0.00	0.00	-2,704	-2,732	278	flexuosum	29	0.02	FALSE	TRUE	capillifolium_flexuosum
42	capillifolium_fuscum_flexuosum	flexuosum	0	1.94	0.43	0.57	0.00	0.01	-21,838	-21,637	2665	flexuosum	-201	0.48	TRUE	TRUE	capillifolium_fuscum
43	capillifolium_fuscum_tenellum	capillifolium	0	4.50	0.85	0.15	0.00	0.00	-2,387	-2,398	251	tenellum	11	0.01	FALSE	TRUE	fuscum_tenellum
44	capillifolium_fuscum_tenellum	fuscum	0	3.69	0.79	0.21	0.00	0.00	-2,786	-2,812	286	tenellum	26	0.02	FALSE	TRUE	capillifolium_tenellum
45	capillifolium_fuscum_tenellum	tenellum	0	1.94	0.41	0.59	0.00	0.01	-21,819	-21,589	2658	tenellum	-230	0.49	TRUE	TRUE	capillifolium_fuscum
46	capillifolium_fuscum_lindbergii	capillifolium	0	3.74	0.85	0.15	0.00	0.00	-2,720	-2,744	282	lindbergii	23	0.01	FALSE	TRUE	fuscum_lindbergii
47	capillifolium_fuscum_lindbergii	fuscum	0	3.71	0.80	0.20	0.00	0.00	-2,932	-2,957	299	lindbergii	24	0.02	FALSE	TRUE	capillifolium_lindbergii
48	capillifolium_fuscum_lindbergii	lindbergii	0	2.05	0.37	0.63	0.00	0.01	-22,156	-21,797	2614	lindbergii	-359	0.52	TRUE	TRUE	capillifolium_fuscum
49	capillifolium_fuscum_riparium	capillifolium	0	3.92	0.82	0.18	0.00	0.00	-2,496	-2,515	262	riparium	19	0.01	FALSE	TRUE	fuscum_riparium
50	capillifolium_fuscum_riparium	fuscum	0	3.66	0.83	0.17	0.00	0.00	-2,848	-2,874	289	riparium	27	0.02	FALSE	TRUE	capillifolium_riparium
51	capillifolium_fuscum_riparium	riparium	0	2.00	0.38	0.62	0.00	0.01	-22,136	-21,819	2644	riparium	-317	0.51	TRUE	TRUE	capillifolium_fuscum
52	capillifolium_fuscum_squarrosum	capillifolium	0	4.28	0.83	0.17	0.00	0.00	-2,764	-2,778	293	squarrosum	14	0.02	FALSE	TRUE	fuscum_squarrosum
53	capillifolium_fuscum_squarrosum	fuscum	0	4.11	0.82	0.18	0.00	0.00	-3,119	-3,136	311	squarrosum	17	0.02	FALSE	TRUE	capillifolium_squarrosum
54	capillifolium_fuscum_squarrosum	squarrosum	0	2.08	0.38	0.62	0.00	0.01	-22,287	-21,987	2591	squarrosum	-300	0.50	TRUE	TRUE	capillifolium_fuscum
55	capillifolium_fuscum_platyphyllum	capillifolium	0	4.26	0.86	0.14	0.00	0.00	-2,717	-2,733	285	platyphyllum	16	0.01	FALSE	TRUE	fuscum_platyphyllum
56	capillifolium_fuscum_platyphyllum	fuscum	0	4.14	0.86	0.14	0.00	0.00	-3,088	-3,111	311	platyphyllum	23	0.01	FALSE	TRUE	capillifolium_platyphyllum
57	capillifolium_fuscum_platyphyllum	platyphyllum	0	2.15	0.64	0.36	0.00	0.01	-20,978	-21,159	2599	platyphyllum	181	0.30	FALSE	TRUE	capillifolium_fuscum
58	capillifolium_subnitens_fimbriatum	capillifolium	0	3.60	0.84	0.16	0.00	0.00	-7,157	-7,219	730	fimbriatum	61	0.04	FALSE	TRUE	subnitens_fimbriatum
59	capillifolium_subnitens_fimbriatum	subnitens	0	4.10	0.89	0.11	0.00	0.00	-7,159	-7,201	726	fimbriatum	41	0.02	FALSE	TRUE	capillifolium_fimbriatum
60	capillifolium_subnitens_fimbriatum	fimbriatum	0	2.48	0.71	0.29	0.00	0.00	-16,239	-16,400	1739	fimbriatum	161	0.16	FALSE	TRUE	capillifolium_subnitens
61	capillifolium_subnitens_compactum	capillifolium	0	4.30	0.86	0.14	0.00	0.00	-4,154	-4,172	423	compactum	18	0.02	FALSE	TRUE	subnitens_compactum
62	capillifolium_subnitens_compactum	subnitens	0	4.34	0.85	0.15	0.00	0.00	-3,925	-3,940	399	compactum	15	0.02	FALSE	TRUE	capillifolium_compactum
63	capillifolium_subnitens_compactum	compactum	0	1.83	0.43	0.57	0.00	0.00	-20,806	-20,650	2373	compactum	-156	0.42	TRUE	TRUE	capillifolium_subnitens
64	capillifolium_subnitens_flexuosum	capillifolium	0	4.16	0.85	0.15	0.00	0.00	-3,864	-3,886	396	flexuosum	22	0.02	FALSE	TRUE	subnitens_flexuosum
65	capillifolium_subnitens_flexuosum	subnitens	0	3.89	0.87	0.13	0.00	0.00	-3,444	-3,472	359	flexuosum	27	0.01	FALSE	TRUE	capillifolium_flexuosum
66	capillifolium_subnitens_flexuosum	flexuosum	0	2.08	0.55	0.45	0.00	0.01	-20,401	-20,443	2440	flexuosum	42	0.34	FALSE	TRUE	capillifolium_subnitens
67	capillifolium_subnitens_tenellum	capillifolium	0	4.14	0.85	0.15	0.00	0.00	-3,820	-3,839	394	tenellum	19	0.02	FALSE	TRUE	subnitens_tenellum
68	capillifolium_subnitens_tenellum	subnitens	0	3.95	0.87	0.13	0.00	0.00	-3,466	-3,491	361	tenellum	26	0.02	FALSE	TRUE	capillifolium_tenellum
69	capillifolium_subnitens_tenellum	tenellum	0	2.11	0.55	0.45	0.00	0.01	-20,437	-20,475	2440	tenellum	38	0.35	FALSE	TRUE	capillifolium_subnitens
70	capillifolium_subnitens_lindbergii	capillifolium	0	4.14	0.86	0.14	0.00	0.00	-3,878	-3,897	399	lindbergii	19	0.02	FALSE	TRUE	subnitens_lindbergii
71	capillifolium_subnitens_lindbergii	subnitens	0	3.98	0.87	0.13	0.00	0.00	-4,079	-4,107	416	lindbergii	28	0.02	FALSE	TRUE	capillifolium_lindbergii
72	capillifolium_subnitens_lindbergii	lindbergii	0	2.13	0.47	0.53	0.00	0.00	-20,686	-20,592	2380	lindbergii	-93	0.40	TRUE	TRUE	capillifolium_subnitens
73	capillifolium_subnitens_riparium	capillifolium	0	4.12	0.85	0.15	0.00	0.00	-3,896	-3,915	402	riparium	19	0.02	FALSE	TRUE	subnitens_riparium
74	capillifolium_subnitens_riparium	subnitens	0	3.78	0.86	0.14	0.00	0.00	-3,715	-3,748	382	riparium	32	0.02	FALSE	TRUE	capillifolium_riparium
75	capillifolium_subnitens_riparium	riparium	0	2.13	0.49	0.51	0.00	0.01	-20,652	-20,591	2411	riparium	-60	0.38	TRUE	TRUE	capillifolium_subnitens
76	capillifolium_subnitens_squarrosum	capillifolium	0	4.55	0.87	0.13	0.00	0.00	-4,379	-4,390	446	squarrosum	11	0.02	FALSE	TRUE	subnitens_squarrosum
77	capillifolium_subnitens_squarrosum	subnitens	0	4.51	0.85	0.15	0.00	0.00	-4,153	-4,163	417	squarrosum	10	0.02	FALSE	TRUE	capillifolium_squarrosum
78	capillifolium_subnitens_squarrosum	squarrosum	0	2.16	0.51	0.49	0.00	0.00	-20,621	-20,588	2332	squarrosum	-32	0.36	TRUE	TRUE	capillifolium_subnitens
79	capillifolium_subnitens_platyphyllum	capillifolium	0	4.12	0.86	0.14	0.00	0.00	-4,414	-4,437	452	platyphyllum	23	0.02	FALSE	TRUE	subnitens_platyphyllum
80	capillifolium_subnitens_platyphyllum	subnitens	0	3.89	0.89	0.11	0.00	0.00	-4,304	-4,336	440	platyphyllum	32	0.02	FALSE	TRUE	capillifolium_platyphyllum
81	capillifolium_subnitens_platyphyllum	platyphyllum	0	2.92	0.77	0.23	0.00	0.01	-18,991	-19,201	2303	platyphyllum	210	0.17	FALSE	TRUE	capillifolium_subnitens
82	capillifolium_fimbriatum_compactum	capillifolium	0	3.84	0.85	0.15	0.00	0.00	-5,596	-5,633	577	compactum	37	0.03	FALSE	TRUE	fimbriatum_compactum
83	capillifolium_fimbriatum_compactum	fimbriatum	0	4.38	0.88	0.12	0.00	0.00	-4,998	-5,024	518	compactum	26	0.02	FALSE	TRUE	capillifolium_compactum
84	capillifolium_fimbriatum_compactum	compactum	0	1.95	0.57	0.43	0.00	0.00	-19,200	-19,280	2100	compactum	80	0.28	FALSE	TRUE	capillifolium_fimbriatum
85	capillifolium_fimbriatum_flexuosum	capillifolium	0	3.87	0.83	0.17	0.00	0.00	-5,247	-5,281	547	flexuosum	34	0.03	FALSE	TRUE	fimbriatum_flexuosum
86	**capillifolium_fimbriatum_flexuosum**	**fimbriatum**	**0**	**6.18**	**0.93**	**0.07**	**0.00**	**0.00**	**-4,448**	**-4,423**	**461**	**flexuosum**	**-25**	**0.01**	**TRUE**	**TRUE**	**capillifolium_flexuosum**
87	capillifolium_fimbriatum_flexuosum	flexuosum	0	2.36	0.69	0.31	0.00	0.00	-18,960	-19,148	2187	flexuosum	188	0.21	FALSE	TRUE	capillifolium_fimbriatum
88	capillifolium_fimbriatum_tenellum	capillifolium	0	3.87	0.83	0.17	0.00	0.00	-5,237	-5,271	545	tenellum	34	0.03	FALSE	TRUE	fimbriatum_tenellum
89	capillifolium_fimbriatum_tenellum	fimbriatum	0	4.88	0.90	0.10	0.00	0.00	-4,425	-4,432	463	tenellum	7	0.02	FALSE	TRUE	capillifolium_tenellum
90	capillifolium_fimbriatum_tenellum	tenellum	0	2.30	0.68	0.32	0.00	0.00	-19,006	-19,179	2187	tenellum	173	0.22	FALSE	TRUE	capillifolium_fimbriatum
91	capillifolium_fimbriatum_lindbergii	capillifolium	0	3.92	0.85	0.15	0.00	0.00	-5,487	-5,522	564	lindbergii	35	0.03	FALSE	TRUE	fimbriatum_lindbergii
92	capillifolium_fimbriatum_lindbergii	fimbriatum	0	4.73	0.89	0.11	0.00	0.00	-5,105	-5,119	525	lindbergii	14	0.02	FALSE	TRUE	capillifolium_lindbergii
93	capillifolium_fimbriatum_lindbergii	lindbergii	0	2.09	0.58	0.42	0.00	0.00	-19,153	-19,213	2106	lindbergii	60	0.28	FALSE	TRUE	capillifolium_fimbriatum

94	capillifolium_fimbriatum_riparium	capillifolium	0	4.17	0.86	0.14	0.00	0.00	-5,352	-5,378	553	riparium	26	0.02	FALSE	TRUE	fimbriatum_riparium
95	**capillifolium_fimbriatum_riparium**	**fimbriatum**	**0**	**5.80**	**0.92**	**0.08**	**0.00**	**0.00**	**-4,940**	**-4,927**	**506**	**riparium**	**-13**	**0.01**	**TRUE**	**TRUE**	**capillifolium_riparium**
96	capillifolium_fimbriatum_riparium	riparium	0	2.26	0.61	0.39	0.00	0.00	-19,018	-19,127	2136	riparium	109	0.26	FALSE	TRUE	capillifolium_fimbriatum
97	capillifolium_fimbriatum_squarrosum	capillifolium	0	4.20	0.87	0.13	0.00	0.00	-5,989	-6,017	614	squarrosum	28	0.02	FALSE	TRUE	fimbriatum_squarrosum
98	capillifolium_fimbriatum_squarrosum	fimbriatum	0	4.28	0.89	0.11	0.00	0.00	-5,719	-5,745	582	squarrosum	27	0.02	FALSE	TRUE	capillifolium_squarrosum
99	capillifolium_fimbriatum_squarrosum	squarrosum	0	2.10	0.65	0.35	0.00	0.00	-18,473	-18,596	1999	squarrosum	123	0.22	FALSE	TRUE	capillifolium_fimbriatum
100	capillifolium_fimbriatum_platyphyllum	capillifolium	0	3.95	0.86	0.14	0.00	0.00	-6,135	-6,170	625	platyphyllum	35	0.03	FALSE	TRUE	fimbriatum_platyphyllum
101	capillifolium_fimbriatum_platyphyllum	fimbriatum	0	4.96	0.90	0.10	0.00	0.00	-6,297	-6,299	632	platyphyllum	2	0.02	FALSE	TRUE	capillifolium_platyphyllum
102	capillifolium_fimbriatum_platyphyllum	platyphyllum	0	3.86	0.84	0.16	0.00	0.00	-16,567	-16,667	1938	platyphyllum	100	0.10	FALSE	TRUE	capillifolium_fimbriatum
103	capillifolium_compactum_flexuosum	capillifolium	0	3.47	0.83	0.17	0.00	0.00	-11,142	-11,234	1175	flexuosum	92	0.06	FALSE	TRUE	compactum_flexuosum
104	capillifolium_compactum_flexuosum	compactum	0	4.59	0.90	0.10	0.00	0.00	-7,313	-7,337	757	flexuosum	24	0.02	FALSE	TRUE	capillifolium_flexuosum
105	capillifolium_compactum_flexuosum	flexuosum	0	4.00	0.85	0.15	0.00	0.00	-11,639	-11,689	1263	flexuosum	51	0.06	FALSE	TRUE	capillifolium_compactum
106	capillifolium_compactum_tenellum	capillifolium	0	3.35	0.82	0.18	0.00	0.00	-11,247	-11,349	1187	tenellum	102	0.07	FALSE	TRUE	compactum_tenellum
107	capillifolium_compactum_tenellum	compactum	0	5.06	0.91	0.09	0.00	0.00	-7,231	-7,237	746	tenellum	6	0.02	FALSE	TRUE	capillifolium_tenellum
108	capillifolium_compactum_tenellum	tenellum	0	3.73	0.84	0.16	0.00	0.00	-11,673	-11,754	1262	tenellum	81	0.06	FALSE	TRUE	capillifolium_compactum
109	capillifolium_compactum_lindbergii	capillifolium	0	3.62	0.84	0.16	0.00	0.00	-11,887	-11,976	1245	lindbergii	89	0.06	FALSE	FALSE	compactum_lindbergii
110	capillifolium_compactum_lindbergii	compactum	0	4.18	0.88	0.12	0.00	0.00	-8,634	-8,682	880	lindbergii	48	0.03	FALSE	TRUE	capillifolium_lindbergii
111	capillifolium_compactum_lindbergii	lindbergii	0	2.75	0.83	0.17	0.00	0.00	-10,632	-10,740	1070	lindbergii	108	0.06	FALSE	FALSE	capillifolium_compactum
112	capillifolium_compactum_riparium	capillifolium	0	3.40	0.83	0.17	0.00	0.00	-11,349	-11,450	1192	riparium	101	0.06	FALSE	TRUE	compactum_riparium
113	capillifolium_compactum_riparium	compactum	0	4.45	0.90	0.10	0.00	0.00	-7,815	-7,840	806	riparium	25	0.02	FALSE	TRUE	capillifolium_riparium
114	capillifolium_compactum_riparium	riparium	0	3.34	0.83	0.17	0.00	0.00	-11,506	-11,614	1197	riparium	108	0.06	FALSE	TRUE	capillifolium_compactum
115	capillifolium_compactum_squarrosum	capillifolium	0	3.88	0.83	0.17	0.00	0.00	-11,265	-11,325	1164	compactum	60	0.06	FALSE	FALSE	compactum_squarrosum
116	capillifolium_compactum_squarrosum	compactum	0	3.63	0.87	0.13	0.00	0.00	-10,760	-10,847	1111	compactum	87	0.05	FALSE	FALSE	capillifolium_squarrosum
117	capillifolium_compactum_squarrosum	squarrosum	0	4.99	0.91	0.09	0.00	0.00	-9,229	-9,236	920	compactum	7	0.03	FALSE	TRUE	capillifolium_compactum
118	capillifolium_compactum_platyphyllum	capillifolium	0	3.85	0.82	0.18	0.00	0.00	-6,661	-6,700	684	compactum	39	0.04	FALSE	TRUE	compactum_platyphyllum
119	capillifolium_compactum_platyphyllum	compactum	0	2.17	0.71	0.29	0.00	0.00	-12,896	-13,010	1364	compactum	114	0.12	FALSE	TRUE	capillifolium_platyphyllum
120	capillifolium_compactum_platyphyllum	platyphyllum	0	3.81	0.72	0.28	0.00	0.01	-9,730	-9,758	1147	compactum	29	0.10	FALSE	TRUE	capillifolium_compactum
121	capillifolium_flexuosum_tenellum	capillifolium	0	1.94	0.19	0.81	0.00	0.01	-23,046	-22,007	2864	capillifolium	-1040	0.73	TRUE	TRUE	flexuosum_tenellum
122	capillifolium_flexuosum_tenellum	flexuosum	0	3.12	0.83	0.17	0.00	0.00	-1,602	-1,628	178	capillifolium	25	0.01	FALSE	TRUE	capillifolium_tenellum
123	capillifolium_flexuosum_tenellum	tenellum	0	4.98	0.80	0.20	0.00	0.00	-1,397	-1,398	153	capillifolium	0	0.01	FALSE	TRUE	capillifolium_flexuosum
124	capillifolium_flexuosum_lindbergii	capillifolium	0	2.57	0.70	0.30	0.00	0.00	-15,259	-15,404	1668	capillifolium	145	0.15	FALSE	TRUE	flexuosum_lindbergii
125	capillifolium_flexuosum_lindbergii	flexuosum	0	4.12	0.83	0.17	0.00	0.00	-9,086	-9,122	981	capillifolium	36	0.05	FALSE	TRUE	capillifolium_lindbergii
126	**capillifolium_flexuosum_lindbergii**	**lindbergii**	**0**	**6.84**	**0.92**	**0.08**	**0.00**	**0.00**	**-5,505**	**-5,448**	**546**	**capillifolium**	**-58**	**0.01**	**TRUE**	**TRUE**	**capillifolium_flexuosum**
127	capillifolium_flexuosum_riparium	capillifolium	0	2.07	0.53	0.47	0.00	0.00	-19,317	-19,322	2198	capillifolium	5	0.32	FALSE	TRUE	flexuosum_riparium
128	capillifolium_flexuosum_riparium	flexuosum	0	4.03	0.80	0.20	0.00	0.00	-5,697	-5,723	621	capillifolium	26	0.04	FALSE	TRUE	capillifolium_riparium
129	**capillifolium_flexuosum_riparium**	**riparium**	**0**	**7.26**	**0.92**	**0.08**	**0.00**	**0.00**	**-3,705**	**-3,652**	**376**	**capillifolium**	**-52**	**0.01**	**TRUE**	**TRUE**	**capillifolium_flexuosum**
130	capillifolium_flexuosum_squarrosum	capillifolium	0	3.42	0.81	0.19	0.00	0.00	-11,771	-11,870	1249	flexuosum	99	0.07	FALSE	TRUE	flexuosum_squarrosum
131	capillifolium_flexuosum_squarrosum	flexuosum	0	3.41	0.81	0.19	0.00	0.00	-12,000	-12,099	1312	flexuosum	99	0.08	FALSE	TRUE	capillifolium_squarrosum
132	capillifolium_flexuosum_squarrosum	squarrosum	0	5.03	0.91	0.09	0.00	0.00	-6,332	-6,333	634	flexuosum	1	0.02	FALSE	TRUE	capillifolium_flexuosum
133	capillifolium_flexuosum_platyphyllum	capillifolium	0	3.73	0.85	0.15	0.00	0.00	-6,059	-6,106	634	flexuosum	47	0.03	FALSE	TRUE	flexuosum_platyphyllum
134	capillifolium_flexuosum_platyphyllum	flexuosum	0	3.09	0.79	0.21	0.00	0.00	-13,543	-13,676	1527	flexuosum	133	0.10	FALSE	TRUE	capillifolium_platyphyllum
135	capillifolium_flexuosum_platyphyllum	platyphyllum	0	3.52	0.69	0.31	0.00	0.01	-8,623	-8,665	1034	flexuosum	42	0.10	FALSE	TRUE	capillifolium_flexuosum
136	capillifolium_tenellum_lindbergii	capillifolium	0	2.57	0.71	0.29	0.00	0.00	-15,300	-15,448	1674	capillifolium	148	0.15	FALSE	TRUE	tenellum_lindbergii
137	capillifolium_tenellum_lindbergii	tenellum	0	3.80	0.85	0.15	0.00	0.00	-9,053	-9,115	974	capillifolium	63	0.05	FALSE	TRUE	capillifolium_lindbergii
138	**capillifolium_tenellum_lindbergii**	**lindbergii**	**0**	**6.08**	**0.91**	**0.09**	**0.00**	**0.00**	**-5,520**	**-5,487**	**547**	**capillifolium**	**-33**	**0.01**	**TRUE**	**TRUE**	**capillifolium_tenellum**
139	capillifolium_tenellum_riparium	capillifolium	0	2.04	0.53	0.47	0.00	0.00	-19,335	-19,337	2205	capillifolium	2	0.33	FALSE	TRUE	tenellum_riparium
140	capillifolium_tenellum_riparium	tenellum	0	3.36	0.83	0.17	0.00	0.00	-5,527	-5,583	603	capillifolium	56	0.03	FALSE	TRUE	capillifolium_riparium
141	**capillifolium_tenellum_riparium**	**riparium**	**0**	**6.73**	**0.92**	**0.08**	**0.00**	**0.00**	**-3,834**	**-3,797**	**387**	**capillifolium**	**-37**	**0.01**	**TRUE**	**TRUE**	**capillifolium_tenellum**
142	capillifolium_tenellum_squarrosum	capillifolium	0	3.59	0.82	0.18	0.00	0.00	-11,752	-11,846	1250	tenellum	94	0.07	FALSE	TRUE	tenellum_squarrosum
143	capillifolium_tenellum_squarrosum	tenellum	0	3.22	0.80	0.20	0.00	0.00	-12,074	-12,187	1313	tenellum	113	0.08	FALSE	TRUE	capillifolium_squarrosum
144	capillifolium_tenellum_squarrosum	squarrosum	0	4.80	0.90	0.10	0.00	0.00	-6,338	-6,346	632	tenellum	7	0.02	FALSE	TRUE	capillifolium_tenellum
145	capillifolium_tenellum_platyphyllum	capillifolium	0	3.84	0.84	0.16	0.00	0.00	-6,097	-6,139	634	tenellum	42	0.03	FALSE	TRUE	tenellum_platyphyllum
146	capillifolium_tenellum_platyphyllum	tenellum	0	2.91	0.78	0.22	0.00	0.00	-13,537	-13,678	1523	tenellum	142	0.11	FALSE	TRUE	capillifolium_platyphyllum
147	capillifolium_tenellum_platyphyllum	platyphyllum	0	3.62	0.69	0.31	0.00	0.01	-8,678	-8,708	1038	tenellum	30	0.10	FALSE	TRUE	capillifolium_tenellum
148	capillifolium_lindbergii_riparium	capillifolium	0	2.93	0.75	0.25	0.00	0.00	-15,944	-16,102	1727	capillifolium	158	0.13	FALSE	TRUE	lindbergii_riparium
149	**capillifolium_lindbergii_riparium**	**lindbergii**	**0**	**5.75**	**0.93**	**0.07**	**0.00**	**0.00**	**-6,024**	**-6,012**	**600**	**capillifolium**	**-12**	**0.01**	**TRUE**	**TRUE**	**capillifolium_riparium**
150	capillifolium_lindbergii_riparium	riparium	0	3.14	0.84	0.16	0.00	0.00	-8,444	-8,523	868	capillifolium	79	0.04	FALSE	TRUE	capillifolium_lindbergii
151	capillifolium_lindbergii_squarrosum	capillifolium	0	3.24	0.81	0.19	0.00	0.00	-12,068	-12,181	1273	lindbergii	112	0.08	FALSE	FALSE	lindbergii_squarrosum
152	capillifolium_lindbergii_squarrosum	lindbergii	0	3.28	0.82	0.18	0.00	0.00	-11,180	-11,289	1141	lindbergii	109	0.07	FALSE	FALSE	capillifolium_squarrosum
153	capillifolium_lindbergii_squarrosum	squarrosum	0	4.97	0.89	0.11	0.00	0.00	-7,875	-7,882	781	lindbergii	7	0.03	FALSE	TRUE	capillifolium_lindbergii
154	capillifolium_lindbergii_platyphyllum	capillifolium	0	3.83	0.83	0.17	0.00	0.00	-6,358	-6,398	653	lindbergii	40	0.03	FALSE	TRUE	lindbergii_platyphyllum
155	capillifolium_lindbergii_platyphyllum	lindbergii	0	2.34	0.70	0.30	0.00	0.00	-13,260	-13,374	1413	lindbergii	114	0.13	FALSE	TRUE	capillifolium_platyphyllum
156	capillifolium_lindbergii_platyphyllum	platyphyllum	0	3.77	0.71	0.29	0.00	0.01	-9,525	-9,552	1129	lindbergii	26	0.10	FALSE	TRUE	capillifolium_lindbergii
157	capillifolium_riparium_squarrosum	capillifolium	0	3.86	0.84	0.16	0.00	0.00	-12,059	-12,132	1271	riparium	72	0.07	FALSE	FALSE	riparium_squarrosum
158	capillifolium_riparium_squarrosum	riparium	0	3.35	0.80	0.20	0.00	0.00	-11,880	-11,979	1240	riparium	99	0.08	FALSE	FALSE	capillifolium_squarrosum
159	capillifolium_riparium_squarrosum	squarrosum	0	4.93	0.90	0.10	0.00	0.00	-6,891	-6,898	684	riparium	7	0.02	FALSE	TRUE	capillifolium_riparium
160	capillifolium_riparium_platyphyllum	capillifolium	0	3.89	0.81	0.19	0.00	0.00	-6,285	-6,323	649	riparium	39	0.04	FALSE	TRUE	riparium_platyphyllum
161	capillifolium_riparium_platyphyllum	riparium	0	2.45	0.70	0.30	0.00	0.00	-13,477	-13,601	1466	riparium	124	0.14	FALSE	TRUE	capillifolium_platyphyllum
162	capillifolium_riparium_platyphyllum	platyphyllum	0	3.67	0.69	0.31	0.00	0.01	-9,102	-9,131	1080	riparium	29	0.10	FALSE	TRUE	capillifolium_riparium
163	capillifolium_squarrosum_platyphyllum	capillifolium	0	4.29	0.86	0.14	0.00	0.00	-6,849	-6,870	699	squarrosum	21	0.03	FALSE	TRUE	squarrosum_platyphyllum
164	capillifolium_squarrosum_platyphyllum	squarrosum	0	2.24	0.73	0.27	0.00	0.00	-12,243	-12,357	1272	squarrosum	114	0.11	FALSE	TRUE	capillifolium_platyphyllum
165	capillifolium_squarrosum_platyphyllum	platyphyllum	0	3.91	0.74	0.26	0.00	0.01	-10,452	-10,476	1224	squarrosum	25	0.10	FALSE	TRUE	capillifolium_squarrosum
166	divinum_fuscum_subnitens	divinum	0	2.02	0.46	0.54	0.00	0.00	-21,253	-21,141	2419	divinum	-112	0.41	TRUE	TRUE	fuscum_subnitens
167	divinum_fuscum_subnitens	fuscum	0	4.59	0.84	0.16	0.00	0.00	-3,901	-3,913	392	divinum	12	0.02	FALSE	TRUE	divinum_subnitens
168	divinum_fuscum_subnitens	subnitens	0	3.61	0.85	0.15	0.00	0.00	-3,729	-3,766	384	divinum	37	0.02	FALSE	TRUE	divinum_fuscum
169	divinum_fuscum_fimbriatum	divinum	0	2.10	0.58	0.42	0.00	0.00	-18,950	-19,024	2067	divinum	74	0.27	FALSE	TRUE	fuscum_fimbriatum
170	divinum_fuscum_fimbriatum	fuscum	0	4.38	0.87	0.13	0.00	0.00	-5,948	-5,975	601	divinum	28	0.02	FALSE	TRUE	divinum_fimbriatum
171	**divinum_fuscum_fimbriatum**	**fimbriatum**	**0**	**5.36**	**0.91**	**0.09**	**0.00**	**0.00**	**-5,119**	**-5,109**	**527**	**divinum**	**-10**	**0.01**	**TRUE**	**TRUE**	**divinum_fuscum**
172	divinum_fuscum_compactum	divinum	0	4.56	0.89	0.11	0.00	0.00	-9,259	-9,288	924	fuscum	28	0.03	FALSE	TRUE	fuscum_compactum
173	divinum_fuscum_compactum	fuscum	0	3.35	0.84	0.16	0.00	0.00	-13,008	-13,126	1363	fuscum	118	0.07	FALSE	TRUE	divinum_compactum
174	divinum_fuscum_compactum	compactum	0	4.74	0.90	0.10	0.00	0.00	-9,003	-9,016	908	fuscum	13	0.03	FALSE	TRUE	divinum_fuscum
175	divinum_fuscum_flexuosum	divinum	0	4.75	0.90	0.10	0.00	0.00	-6,789	-6,803	691	flexuosum	14	0.02	FALSE	TRUE	fuscum_flexuosum
176	divinum_fuscum_flexuosum	fuscum	0	3.26	0.80	0.20	0.00	0.00	-12,185	-12,303	1281	flexuosum	118	0.08	FALSE	FALSE	divinum_flexuosum
177	divinum_fuscum_flexuosum	flexuosum	0	3.97	0.84	0.16	0.00	0.00	-11,277	-11,333	1223	flexuosum	56	0.06	FALSE	FALSE	divinum_fuscum
178	divinum_fuscum_tenellum	divinum	0	4.85	0.90	0.10	0.00	0.00	-6,749	-6,759	687	tenellum	10	0.02	FALSE	TRUE	fuscum_tenellum
179	divinum_fuscum_tenellum	fuscum	0	3.45	0.82	0.18	0.00	0.00	-12,331	-12,432	1296	tenellum	101	0.07	FALSE	FALSE	divinum_tenellum
180	divinum_fuscum_tenellum	tenellum	0	3.68	0.85	0.15	0.00	0.00	-11,179	-11,259	1212	tenellum	80	0.06	FALSE	FALSE	divinum_fuscum
181	divinum_fuscum_lindbergii	divinum	0	5.26	0.92	0.08	0.00	0.00	-8,190	-8,183	826	lindbergii	-7	0.02	FALSE	TRUE	fuscum_lindbergii
182	divinum_fuscum_lindbergii	fuscum	0	3.36	0.81	0.19	0.00	0.00	-12,709	-12,825	1333	lindbergii	116	0.08	FALSE	FALSE	divinum_lindbergii
183	divinum_fuscum_lindbergii	lindbergii	0	3.69	0.87	0.13	0.00	0.00	-10,274	-10,348	1036	lindbergii	74	0.04	FALSE	FALSE	divinum_fuscum
184	divinum_fuscum_riparium	divinum	0	4.88	0.91	0.09	0.00	0.00	-7,427	-7,436	755	riparium	9	0.02	FALSE	TRUE	fuscum_riparium
185	divinum_fuscum_riparium	fuscum	0	2.97	0.77	0.23	0.00	0.00	-12,254	-12,377	1285	riparium	123	0.09	FALSE	FALSE	divinum_riparium
186	divinum_fuscum_riparium	riparium	0	3.50	0.84	0.16	0.00	0.00	-11,134	-11,224	1155	riparium	90	0.06	FALSE	FALSE	divinum_fuscum
187	divinum_fuscum_squarrosum	divinum	0	3.55	0.87	0.13	0.00	0.00	-10,922	-11,012	1117	divinum	91	0.05	FALSE	FALSE	fuscum_squarrosum
188	divinum_fuscum_squarrosum	fuscum	0	3.75	0.84	0.16	0.00	0.00	-11,679	-11,756	1211	divinum	77	0.06	FALSE	FALSE	divinum_squarrosum
189	divinum_fuscum_squarrosum	squarrosum	0	4.50	0.90	0.10	0.00	0.00	-8,683	-8,717	867	divinum	34	0.03	FALSE	TRUE	divinum_fuscum
190	divinum_fuscum_platyphyllum	divinum	0	2.64	0.77	0.23	0.00	0.00	-12,947	-13,086	1371	divinum	139	0.10	FALSE	TRUE	fuscum_platyphyllum
191	divinum_fuscum_platyphyllum	fuscum	0	4.44	0.86	0.14	0.00	0.00	-6,835	-6,856	689	divinum	21	0.03	FALSE	TRUE	divinum_platyphyllum
192	divinum_fuscum_platyphyllum	platyphyllum	0	3.65	0.73	0.27	0.00	0.01	-9,550	-9,597	1135	divinum	47	0.10	FALSE	TRUE	divinum_fuscum
193	divinum_subnitens_fimbriatum	divinum	0	2.18	0.60	0.40	0.00	0.00	-18,884	-18,981	2068	divinum	97	0.26	FALSE	TRUE	subnitens_fimbriatum
194	divinum_subnitens_fimbriatum	subnitens	0	4.29	0.88	0.12	0.00	0.00	-5,848	-5,876	593	divinum	27	0.02	FALSE	TRUE	divinum_fimbriatum
195	divinum_subnitens_fimbriatum	fimbriatum	0	5.04	0.90	0.10	0.00	0.00	-5,240	-5,236	534	divinum	-4	0.02	FALSE	TRUE	divinum_subnitens
196	divinum_subnitens_compactum	divinum	0	4.83	0.91	0.09	0.00	0.00	-9,519	-9,530	944	subnitens	10	0.03	FALSE	TRUE	subnitens_compactum
197	divinum_subnitens_compactum	subnitens	0	3.25	0.84	0.16	0.00	0.00	-12,948	-13,071	1359	subnitens	123	0.07	FALSE	TRUE	divinum_compactum
198	divinum_subnitens_compactum	compactum	0	4.31	0.88	0.12	0.00	0.00	-8,834	-8,868	892	subnitens	34	0.03	FALSE	TRUE	divinum_subnitens
199	divinum_subnitens_flexuosum	divinum	0	4.55	0.90	0.10	0.00	0.00	-7,116	-7,138	724	flexuosum	22	0.02	FALSE	TRUE	subnitens_flexuosum
200	divinum_subnitens_flexuosum	subnitens	0	2.93	0.78	0.22	0.00	0.00	-11,740	-11,858	1246	flexuosum	118	0.08	FALSE	FALSE	divinum_flexuosum
201	divinum_subnitens_flexuosum	flexuosum	0	3.89	0.83	0.17	0.00	0.00	-11,299	-11,359	1225	flexuosum	60	0.07	FALSE	FALSE	divinum_subnitens
202	divinum_subnitens_tenellum	divinum	0	4.71	0.90	0.10	0.00	0.00	-7,102	-7,119	723	tenellum	17	0.02	FALSE	TRUE	subnitens_tenellum
203	divinum_subnitens_tenellum	subnitens	0	2.95	0.78	0.22	0.00	0.00	-11,839	-11,957	1257	tenellum	117	0.09	FALSE	FALSE	divinum_tenellum
204	divinum_subnitens_tenellum	tenellum	0	3.67	0.83	0.17	0.00	0.00	-11,229	-11,309	1215	tenellum	81	0.07	FALSE	FALSE	divinum_subnitens
205	divinum_subnitens_lindbergii	divinum	0	4.61	0.90	0.10	0.00	0.00	-8,363	-8,392	844	lindbergii	30	0.03	FALSE	TRUE	subnitens_lindbergii
206	divinum_subnitens_lindbergii	subnitens	0	3.24	0.79	0.21	0.00	0.00	-12,639	-12,747	1327	lindbergii	109	0.09	FALSE	FALSE	divinum_lindbergii
207	divinum_subnitens_lindbergii	lindbergii	0	3.74	0.87	0.13	0.00	0.00	-10,176	-10,249	1024	lindbergii	73	0.04	FALSE	FALSE	divinum_subnitens
208	divinum_subnitens_riparium	divinum	0	4.51	0.89	0.11	0.00	0.00	-7,563	-7,592	772	riparium	29	0.03	FALSE	TRUE	subnitens_riparium
209	divinum_subnitens_riparium	subnitens	0	2.84	0.75	0.25	0.00	0.00	-11,978	-12,095	1262	riparium	117	0.10	FALSE	FALSE	divinum_riparium
210	divinum_subnitens_riparium	riparium	0	3.69	0.84	0.16	0.00	0.00	-11,249	-11,326	1161	riparium	77	0.06	FALSE	FALSE	divinum_subnitens

211	divinum_subnitens_squarrosum	divinum	0	3.54	0.87	0.13	0.00	0.00	-11,154	-11,250	1139	divinum	96	0.05	FALSE	FALSE	subnitens_squarrosum
212	divinum_subnitens_squarrosum	subnitens	0	3.70	0.84	0.16	0.00	0.00	-11,413	-11,493	1193	divinum	80	0.06	FALSE	FALSE	divinum_squarrosum
213	divinum_subnitens_squarrosum	squarrosum	0	3.92	0.89	0.11	0.00	0.00	-8,601	-8,660	863	divinum	60	0.03	FALSE	TRUE	divinum_subnitens
214	divinum_subnitens_platyphyllum	divinum	0	2.48	0.75	0.25	0.00	0.00	-12,966	-13,104	1373	divinum	137	0.11	FALSE	TRUE	subnitens_platyphyllum
215	divinum_subnitens_platyphyllum	subnitens	0	4.56	0.89	0.11	0.00	0.00	-6,686	-6,699	679	divinum	12	0.02	FALSE	TRUE	divinum_platyphyllum
216	divinum_subnitens_platyphyllum	platyphyllum	0	3.68	0.73	0.27	0.00	0.01	-9,642	-9,687	1143	divinum	45	0.10	FALSE	TRUE	divinum_subnitens
217	divinum_fimbriatum_compactum	divinum	0	4.92	0.91	0.09	0.00	0.00	-9,231	-9,248	921	fimbriatum	17	0.03	FALSE	TRUE	fimbriatum_compactum
218	divinum_fimbriatum_compactum	fimbriatum	0	2.62	0.83	0.17	0.00	0.00	-12,687	-12,820	1335	fimbriatum	133	0.07	FALSE	TRUE	divinum_compactum
219	divinum_fimbriatum_compactum	compactum	0	4.30	0.89	0.11	0.00	0.00	-9,360	-9,401	939	fimbriatum	41	0.03	FALSE	TRUE	divinum_fimbriatum
220	divinum_fimbriatum_flexuosum	divinum	0	4.48	0.89	0.11	0.00	0.00	-7,101	-7,126	727	flexuosum	25	0.03	FALSE	TRUE	fimbriatum_flexuosum
221	divinum_fimbriatum_flexuosum	fimbriatum	0	2.71	0.80	0.20	0.00	0.00	-11,832	-11,958	1248	flexuosum	126	0.08	FALSE	FALSE	divinum_flexuosum
222	divinum_fimbriatum_flexuosum	flexuosum	0	4.04	0.85	0.15	0.00	0.00	-11,276	-11,325	1220	flexuosum	49	0.06	FALSE	FALSE	divinum_fimbriatum
223	divinum_fimbriatum_tenellum	divinum	0	4.62	0.90	0.10	0.00	0.00	-7,025	-7,044	719	tenellum	19	0.02	FALSE	TRUE	fimbriatum_tenellum
224	divinum_fimbriatum_tenellum	fimbriatum	0	2.75	0.80	0.20	0.00	0.00	-11,916	-12,041	1260	tenellum	125	0.08	FALSE	FALSE	divinum_tenellum
225	divinum_fimbriatum_tenellum	tenellum	0	3.91	0.84	0.16	0.00	0.00	-11,257	-11,319	1216	tenellum	62	0.06	FALSE	FALSE	divinum_fimbriatum
226	divinum_fimbriatum_lindbergii	divinum	0	4.51	0.90	0.10	0.00	0.00	-8,427	-8,456	851	lindbergii	29	0.03	FALSE	TRUE	fimbriatum_lindbergii
227	divinum_fimbriatum_lindbergii	fimbriatum	0	3.34	0.84	0.16	0.00	0.00	-12,533	-12,647	1316	lindbergii	114	0.07	FALSE	FALSE	divinum_lindbergii
228	divinum_fimbriatum_lindbergii	lindbergii	0	3.65	0.87	0.13	0.00	0.00	-10,191	-10,266	1028	lindbergii	75	0.04	FALSE	FALSE	divinum_fimbriatum
229	divinum_fimbriatum_riparium	divinum	0	3.94	0.88	0.12	0.00	0.00	-7,805	-7,856	795	riparium	51	0.03	FALSE	TRUE	fimbriatum_riparium
230	divinum_fimbriatum_riparium	fimbriatum	0	2.67	0.78	0.22	0.00	0.00	-11,911	-12,037	1255	riparium	126	0.09	FALSE	FALSE	divinum_riparium
231	divinum_fimbriatum_riparium	riparium	0	3.56	0.84	0.16	0.00	0.00	-11,025	-11,107	1145	riparium	82	0.06	FALSE	FALSE	divinum_fimbriatum
232	divinum_fimbriatum_squarrosum	divinum	0	3.67	0.87	0.13	0.00	0.00	-10,928	-11,012	1116	divinum	84	0.05	FALSE	FALSE	fimbriatum_squarrosum
233	divinum_fimbriatum_squarrosum	fimbriatum	0	3.59	0.86	0.14	0.00	0.00	-11,642	-11,740	1212	divinum	98	0.05	FALSE	FALSE	divinum_squarrosum
234	divinum_fimbriatum_squarrosum	squarrosum	0	4.06	0.89	0.11	0.00	0.00	-8,622	-8,674	867	divinum	52	0.03	FALSE	TRUE	divinum_fimbriatum
235	divinum_fimbriatum_platyphyllum	divinum	0	2.51	0.75	0.25	0.00	0.00	-12,958	-13,098	1370	divinum	140	0.11	FALSE	TRUE	fimbriatum_platyphyllum
236	divinum_fimbriatum_platyphyllum	fimbriatum	0	5.03	0.91	0.09	0.00	0.00	-6,506	-6,510	660	divinum	5	0.02	FALSE	TRUE	divinum_platyphyllum
237	divinum_fimbriatum_platyphyllum	platyphyllum	0	3.83	0.74	0.26	0.00	0.01	-9,876	-9,906	1165	divinum	31	0.10	FALSE	TRUE	divinum_fimbriatum
238	**divinum_compactum_flexuosum**	**divinum**	**0**	**5.49**	**0.93**	**0.07**	**0.00**	**0.00**	**-8,128**	**-8,116**	**809**	**flexuosum**	**-12**	**0.02**	**TRUE**	**TRUE**	**compactum_flexuosum**
239	divinum_compactum_flexuosum	compactum	0	3.61	0.87	0.13	0.00	0.00	-10,062	-10,143	1018	flexuosum	82	0.04	FALSE	TRUE	divinum_flexuosum
240	divinum_compactum_flexuosum	flexuosum	0	3.96	0.87	0.13	0.00	0.00	-12,656	-12,725	1368	flexuosum	69	0.06	FALSE	TRUE	divinum_compactum
241	divinum_compactum_tenellum	divinum	0	5.25	0.92	0.08	0.00	0.00	-8,165	-8,161	817	tenellum	-4	0.02	FALSE	TRUE	compactum_tenellum
242	divinum_compactum_tenellum	compactum	0	3.39	0.86	0.14	0.00	0.00	-10,077	-10,166	1023	tenellum	89	0.04	FALSE	TRUE	divinum_tenellum
243	divinum_compactum_tenellum	tenellum	0	3.65	0.87	0.13	0.00	0.00	-12,547	-12,640	1355	tenellum	93	0.05	FALSE	TRUE	divinum_compactum
244	**divinum_compactum_lindbergii**	**divinum**	**0**	**5.92**	**0.92**	**0.08**	**0.00**	**0.00**	**-9,678**	**-9,642**	**950**	**lindbergii**	**-35**	**0.02**	**TRUE**	**TRUE**	**compactum_lindbergii**
245	divinum_compactum_lindbergii	compactum	0	4.12	0.88	0.12	0.00	0.00	-10,577	-10,629	1064	lindbergii	52	0.04	FALSE	TRUE	divinum_lindbergii
246	divinum_compactum_lindbergii	lindbergii	0	3.65	0.89	0.11	0.00	0.00	-11,677	-11,773	1181	lindbergii	95	0.04	FALSE	TRUE	divinum_compactum
247	divinum_compactum_riparium	divinum	0	4.40	0.90	0.10	0.00	0.00	-8,545	-8,581	852	riparium	36	0.03	FALSE	TRUE	compactum_riparium
248	divinum_compactum_riparium	compactum	0	3.68	0.87	0.13	0.00	0.00	-10,190	-10,265	1030	riparium	75	0.04	FALSE	TRUE	divinum_riparium
249	divinum_compactum_riparium	riparium	0	2.86	0.83	0.17	0.00	0.00	-12,585	-12,724	1313	riparium	139	0.07	FALSE	TRUE	divinum_compactum
250	**divinum_compactum_squarrosum**	**divinum**	**0**	**6.14**	**0.92**	**0.08**	**0.00**	**0.00**	**-9,557**	**-9,506**	**937**	**squarrosum**	**-51**	**0.02**	**TRUE**	**TRUE**	**compactum_squarrosum**
251	divinum_compactum_squarrosum	compactum	0	4.41	0.90	0.10	0.00	0.00	-10,739	-10,779	1077	squarrosum	39	0.03	FALSE	TRUE	divinum_squarrosum
252	divinum_compactum_squarrosum	squarrosum	0	4.16	0.89	0.11	0.00	0.00	-11,672	-11,744	1181	squarrosum	71	0.04	FALSE	TRUE	divinum_compactum
253	divinum_compactum_platyphyllum	divinum	0	4.71	0.90	0.10	0.00	0.00	-8,330	-8,343	828	platyphyllum	12	0.03	FALSE	TRUE	compactum_platyphyllum
254	divinum_compactum_platyphyllum	compactum	0	4.55	0.89	0.11	0.00	0.00	-7,714	-7,737	775	platyphyllum	23	0.03	FALSE	TRUE	divinum_platyphyllum
255	divinum_compactum_platyphyllum	platyphyllum	0	3.87	0.78	0.22	0.00	0.01	-13,608	-13,666	1592	platyphyllum	58	0.11	FALSE	TRUE	divinum_compactum
256	divinum_flexuosum_tenellum	divinum	0	2.13	0.17	0.83	0.00	0.01	-23,678	-22,495	2859	divinum	-1183	0.74	TRUE	TRUE	flexuosum_tenellum
257	divinum_flexuosum_tenellum	flexuosum	0	3.79	0.85	0.15	0.00	0.00	-1,744	-1,766	194	divinum	22	0.01	FALSE	TRUE	divinum_tenellum
258	divinum_flexuosum_tenellum	tenellum	0	4.10	0.79	0.21	0.00	0.00	-1,257	-1,270	142	divinum	12	0.01	FALSE	TRUE	divinum_flexuosum
259	divinum_flexuosum_lindbergii	divinum	0	2.44	0.74	0.26	0.00	0.00	-14,046	-14,200	1466	divinum	154	0.12	FALSE	TRUE	flexuosum_lindbergii
260	divinum_flexuosum_lindbergii	flexuosum	0	4.23	0.85	0.15	0.00	0.00	-9,642	-9,679	1033	divinum	37	0.05	FALSE	TRUE	divinum_lindbergii
261	**divinum_flexuosum_lindbergii**	**lindbergii**	**0**	**5.66**	**0.92**	**0.08**	**0.00**	**0.00**	**-7,083**	**-7,070**	**696**	**divinum**	**-12**	**0.02**	**TRUE**	**TRUE**	**divinum_flexuosum**
262	divinum_flexuosum_riparium	divinum	0	1.95	0.48	0.52	0.00	0.00	-19,177	-19,105	2096	divinum	-72	0.34	TRUE	TRUE	flexuosum_riparium
263	divinum_flexuosum_riparium	flexuosum	0	4.19	0.82	0.18	0.00	0.00	-6,005	-6,027	647	divinum	22	0.04	FALSE	TRUE	divinum_riparium
264	**divinum_flexuosum_riparium**	**riparium**	**0**	**7.22**	**0.94**	**0.06**	**0.00**	**0.00**	**-4,489**	**-4,441**	**452**	**divinum**	**-49**	**0.01**	**TRUE**	**TRUE**	**divinum_flexuosum**
265	divinum_flexuosum_squarrosum	divinum	0	3.02	0.83	0.17	0.00	0.00	-10,120	-10,218	1032	flexuosum	98	0.05	FALSE	TRUE	flexuosum_squarrosum
266	divinum_flexuosum_squarrosum	flexuosum	0	3.86	0.85	0.15	0.00	0.00	-11,478	-11,545	1234	flexuosum	68	0.06	FALSE	TRUE	divinum_squarrosum
267	divinum_flexuosum_squarrosum	squarrosum	0	4.30	0.90	0.10	0.00	0.00	-9,224	-9,264	929	flexuosum	40	0.03	FALSE	TRUE	divinum_flexuosum
268	divinum_flexuosum_platyphyllum	divinum	0	4.85	0.91	0.09	0.00	0.00	-6,456	-6,469	661	flexuosum	13	0.02	FALSE	TRUE	flexuosum_platyphyllum
269	divinum_flexuosum_platyphyllum	flexuosum	0	4.06	0.84	0.16	0.00	0.00	-9,861	-9,901	1072	flexuosum	41	0.05	FALSE	FALSE	divinum_platyphyllum
270	divinum_flexuosum_platyphyllum	platyphyllum	0	3.58	0.75	0.25	0.00	0.01	-12,329	-12,406	1462	flexuosum	76	0.11	FALSE	FALSE	divinum_flexuosum
271	divinum_tenellum_lindbergii	divinum	0	2.50	0.75	0.25	0.00	0.00	-14,147	-14,294	1476	divinum	148	0.12	FALSE	TRUE	tenellum_lindbergii
272	divinum_tenellum_lindbergii	tenellum	0	3.81	0.86	0.14	0.00	0.00	-9,470	-9,532	1013	divinum	62	0.04	FALSE	TRUE	divinum_lindbergii
273	divinum_tenellum_lindbergii	lindbergii	0	4.60	0.91	0.09	0.00	0.00	-7,148	-7,175	706	divinum	27	0.02	FALSE	TRUE	divinum_tenellum
274	divinum_tenellum_riparium	divinum	0	1.92	0.48	0.52	0.00	0.00	-19,271	-19,201	2111	divinum	-70	0.34	TRUE	TRUE	tenellum_riparium
275	divinum_tenellum_riparium	tenellum	0	3.66	0.84	0.16	0.00	0.00	-5,668	-5,717	614	divinum	49	0.03	FALSE	TRUE	divinum_riparium
276	**divinum_tenellum_riparium**	**riparium**	**0**	**7.08**	**0.94**	**0.06**	**0.00**	**0.00**	**-4,672**	**-4,621**	**470**	**divinum**	**-50**	**0.01**	**TRUE**	**TRUE**	**divinum_tenellum**
277	divinum_tenellum_squarrosum	divinum	0	3.05	0.85	0.15	0.00	0.00	-10,129	-10,230	1038	tenellum	101	0.05	FALSE	TRUE	tenellum_squarrosum
278	divinum_tenellum_squarrosum	tenellum	0	3.61	0.86	0.14	0.00	0.00	-11,301	-11,387	1214	tenellum	86	0.05	FALSE	TRUE	divinum_squarrosum
279	divinum_tenellum_squarrosum	squarrosum	0	4.12	0.89	0.11	0.00	0.00	-9,348	-9,401	943	tenellum	53	0.03	FALSE	TRUE	divinum_tenellum
280	divinum_tenellum_platyphyllum	divinum	0	5.03	0.91	0.09	0.00	0.00	-6,554	-6,558	666	tenellum	4	0.02	FALSE	TRUE	tenellum_platyphyllum
281	divinum_tenellum_platyphyllum	tenellum	0	3.78	0.84	0.16	0.00	0.00	-9,754	-9,816	1060	tenellum	62	0.05	FALSE	FALSE	divinum_platyphyllum
282	divinum_tenellum_platyphyllum	platyphyllum	0	3.57	0.75	0.25	0.00	0.01	-12,377	-12,454	1469	tenellum	77	0.12	FALSE	FALSE	divinum_tenellum
283	divinum_lindbergii_riparium	divinum	0	2.44	0.77	0.23	0.00	0.00	-14,575	-14,733	1514	divinum	159	0.11	FALSE	TRUE	lindbergii_riparium
284	divinum_lindbergii_riparium	lindbergii	0	3.72	0.89	0.11	0.00	0.00	-7,423	-7,477	732	divinum	54	0.03	FALSE	TRUE	divinum_riparium
285	divinum_lindbergii_riparium	riparium	0	3.77	0.88	0.12	0.00	0.00	-9,298	-9,367	949	divinum	70	0.04	FALSE	TRUE	divinum_lindbergii
286	divinum_lindbergii_squarrosum	divinum	0	3.76	0.88	0.12	0.00	0.00	-10,674	-10,750	1079	lindbergii	76	0.04	FALSE	FALSE	lindbergii_squarrosum
287	divinum_lindbergii_squarrosum	lindbergii	0	3.31	0.85	0.15	0.00	0.00	-10,638	-10,734	1062	lindbergii	96	0.05	FALSE	FALSE	divinum_squarrosum
288	divinum_lindbergii_squarrosum	squarrosum	0	4.26	0.90	0.10	0.00	0.00	-10,564	-10,613	1054	lindbergii	48	0.03	FALSE	TRUE	divinum_lindbergii
289	**divinum_lindbergii_platyphyllum**	**divinum**	**0**	**5.72**	**0.93**	**0.07**	**0.00**	**0.00**	**-7,353**	**-7,333**	**736**	**lindbergii**	**-20**	**0.02**	**TRUE**	**TRUE**	**lindbergii_platyphyllum**
290	divinum_lindbergii_platyphyllum	lindbergii	0	3.74	0.87	0.13	0.00	0.00	-9,071	-9,137	911	lindbergii	66	0.04	FALSE	FALSE	divinum_platyphyllum
291	divinum_lindbergii_platyphyllum	platyphyllum	0	4.07	0.77	0.23	0.00	0.01	-13,192	-13,215	1548	lindbergii	24	0.11	FALSE	FALSE	divinum_lindbergii
292	divinum_riparium_squarrosum	divinum	0	3.17	0.85	0.15	0.00	0.00	-10,662	-10,763	1085	riparium	101	0.05	FALSE	TRUE	riparium_squarrosum
293	divinum_riparium_squarrosum	riparium	0	3.54	0.85	0.15	0.00	0.00	-11,035	-11,124	1140	riparium	89	0.05	FALSE	TRUE	divinum_squarrosum
294	divinum_riparium_squarrosum	squarrosum	0	3.57	0.87	0.13	0.00	0.00	-9,679	-9,754	970	riparium	75	0.04	FALSE	TRUE	divinum_riparium
295	divinum_riparium_platyphyllum	divinum	0	4.71	0.90	0.10	0.00	0.00	-7,053	-7,073	716	riparium	20	0.02	FALSE	TRUE	riparium_platyphyllum
296	divinum_riparium_platyphyllum	riparium	0	3.19	0.82	0.18	0.00	0.00	-9,636	-9,732	1001	riparium	96	0.06	FALSE	FALSE	divinum_platyphyllum
297	divinum_riparium_platyphyllum	platyphyllum	0	3.64	0.75	0.25	0.00	0.01	-12,510	-12,576	1478	riparium	66	0.12	FALSE	FALSE	divinum_riparium
298	divinum_squarrosum_platyphyllum	divinum	0	3.59	0.86	0.14	0.00	0.00	-9,301	-9,381	946	divinum	81	0.04	FALSE	FALSE	squarrosum_platyphyllum
299	divinum_squarrosum_platyphyllum	squarrosum	0	5.45	0.91	0.09	0.00	0.00	-7,797	-7,789	768	divinum	-7	0.02	FALSE	TRUE	divinum_platyphyllum
300	divinum_squarrosum_platyphyllum	platyphyllum	0	3.84	0.77	0.23	0.00	0.01	-12,647	-12,696	1481	divinum	49	0.11	FALSE	FALSE	divinum_squarrosum
301	fuscum_subnitens_fimbriatum	fuscum	0	4.08	0.87	0.13	0.00	0.00	-7,044	-7,084	710	fimbriatum	41	0.03	FALSE	TRUE	subnitens_fimbriatum
302	fuscum_subnitens_fimbriatum	subnitens	0	3.95	0.86	0.14	0.00	0.00	-7,084	-7,125	707	fimbriatum	42	0.03	FALSE	TRUE	fuscum_fimbriatum
303	fuscum_subnitens_fimbriatum	fimbriatum	0	2.66	0.75	0.25	0.00	0.00	-16,640	-16,810	1778	fimbriatum	170	0.14	FALSE	TRUE	fuscum_subnitens
304	fuscum_subnitens_compactum	fuscum	0	3.95	0.83	0.17	0.00	0.00	-4,017	-4,041	404	compactum	24	0.02	FALSE	TRUE	subnitens_compactum
305	fuscum_subnitens_compactum	subnitens	0	4.02	0.84	0.16	0.00	0.00	-3,590	-3,613	369	compactum	23	0.02	FALSE	TRUE	fuscum_compactum
306	fuscum_subnitens_compactum	compactum	0	2.07	0.48	0.52	0.00	0.00	-21,219	-21,145	2422	compactum	-74	0.39	TRUE	TRUE	fuscum_subnitens
307	fuscum_subnitens_flexuosum	fuscum	0	3.68	0.82	0.18	0.00	0.00	-3,883	-3,918	392	flexuosum	35	0.02	FALSE	TRUE	subnitens_flexuosum
308	fuscum_subnitens_flexuosum	subnitens	0	3.56	0.83	0.17	0.00	0.00	-3,068	-3,100	322	flexuosum	32	0.02	FALSE	TRUE	fuscum_flexuosum
309	fuscum_subnitens_flexuosum	flexuosum	0	2.15	0.56	0.44	0.00	0.01	-20,781	-20,837	2481	flexuosum	55	0.34	FALSE	TRUE	fuscum_subnitens
310	fuscum_subnitens_tenellum	fuscum	0	3.82	0.83	0.17	0.00	0.00	-3,915	-3,944	396	tenellum	29	0.02	FALSE	TRUE	subnitens_tenellum
311	fuscum_subnitens_tenellum	subnitens	0	3.75	0.86	0.14	0.00	0.00	-3,029	-3,060	318	tenellum	30	0.01	FALSE	TRUE	fuscum_tenellum
312	fuscum_subnitens_tenellum	tenellum	0	2.19	0.55	0.45	0.00	0.01	-20,822	-20,870	2481	tenellum	48	0.35	FALSE	TRUE	fuscum_subnitens
313	fuscum_subnitens_lindbergii	fuscum	0	3.93	0.83	0.17	0.00	0.00	-4,013	-4,040	407	lindbergii	27	0.02	FALSE	TRUE	subnitens_lindbergii
314	fuscum_subnitens_lindbergii	subnitens	0	3.55	0.79	0.21	0.00	0.00	-3,519	-3,552	366	lindbergii	32	0.02	FALSE	TRUE	fuscum_lindbergii
315	fuscum_subnitens_lindbergii	lindbergii	0	2.19	0.47	0.53	0.00	0.00	-21,084	-20,987	2422	lindbergii	-97	0.40	TRUE	TRUE	fuscum_subnitens
316	fuscum_subnitens_riparium	fuscum	0	4.32	0.88	0.12	0.00	0.00	-3,964	-3,983	401	riparium	19	0.02	FALSE	TRUE	subnitens_riparium
317	fuscum_subnitens_riparium	subnitens	0	3.75	0.84	0.16	0.00	0.00	-3,283	-3,313	342	riparium	30	0.02	FALSE	TRUE	fuscum_riparium
318	fuscum_subnitens_riparium	riparium	0	2.31	0.50	0.50	0.00	0.01	-21,038	-20,991	2452	riparium	-48	0.38	TRUE	TRUE	fuscum_subnitens
319	fuscum_subnitens_squarrosum	fuscum	0	4.38	0.88	0.12	0.00	0.00	-4,345	-4,363	436	squarrosum	18	0.02	FALSE	TRUE	subnitens_squarrosum
320	fuscum_subnitens_squarrosum	subnitens	0	3.98	0.84	0.16	0.00	0.00	-3,850	-3,876	398	squarrosum	26	0.02	FALSE	TRUE	fuscum_squarrosum
321	fuscum_subnitens_squarrosum	squarrosum	0	2.14	0.51	0.49	0.00	0.00	-20,900	-20,869	2361	squarrosum	-31	0.36	TRUE	TRUE	fuscum_subnitens
322	fuscum_subnitens_platyphyllum	fuscum	0	3.52	0.85	0.15	0.00	0.00	-4,115	-4,155	418	platyphyllum	40	0.02	FALSE	TRUE	subnitens_platyphyllum
323	fuscum_subnitens_platyphyllum	subnitens	0	4.53	0.88	0.12	0.00	0.00	-4,130	-4,146	420	platyphyllum	16	0.02	FALSE	TRUE	fuscum_platyphyllum
324	fuscum_subnitens_platyphyllum	platyphyllum	0	2.95	0.77	0.23	0.00	0.01	-19,521	-19,748	2357	platyphyllum	227	0.17	FALSE	TRUE	fuscum_subnitens
325	fuscum_fimbriatum_compactum	fuscum	0	4.77	0.90	0.10	0.00	0.00	-5,876	-5,889	594	compactum	13	0.02	FALSE	TRUE	fimbriatum_compactum
326	fuscum_fimbriatum_compactum	fimbriatum	0	4.98	0.90	0.10	0.00	0.00	-4,918	-4,922	510	compactum	4	0.02	FALSE	TRUE	fuscum_compactum
327	fuscum_fimbriatum_compactum	compactum	0	2.06	0.58	0.42	0.00	0.00	-19,169	-19,249	2091	compactum	80	0.28	FALSE	TRUE	fuscum_fimbriatum

328	fuscum_fimbriatum_flexuosum	fuscum	0	4.92	0.89	0.11	0.00	0.00	-5,638	-5,636	573	flexuosum	-1	0.02	FALSE	TRUE	fimbriatum_flexuosum
329	fuscum_fimbriatum_flexuosum	fimbriatum	0	5.12	0.90	0.10	0.00	0.00	-4,312	-4,308	448	flexuosum	-4	0.01	FALSE	TRUE	fuscum_flexuosum
330	fuscum_fimbriatum_flexuosum	flexuosum	0	2.29	0.67	0.33	0.00	0.00	-18,906	-19,062	2174	flexuosum	157	0.23	FALSE	TRUE	fuscum_fimbriatum
331	fuscum_fimbriatum_tenellum	fuscum	0	4.68	0.90	0.10	0.00	0.00	-5,695	-5,708	578	tenellum	12	0.02	FALSE	TRUE	fimbriatum_tenellum
332	fuscum_fimbriatum_tenellum	fimbriatum	0	5.42	0.91	0.09	0.00	0.00	-4,246	-4,240	443	tenellum	-5	0.01	FALSE	TRUE	fuscum_tenellum
333	fuscum_fimbriatum_tenellum	tenellum	0	2.31	0.66	0.34	0.00	0.00	-18,945	-19,092	2174	tenellum	147	0.23	FALSE	TRUE	fuscum_fimbriatum
334	fuscum_fimbriatum_lindbergii	fuscum	0	4.16	0.86	0.14	0.00	0.00	-5,718	-5,751	582	lindbergii	33	0.02	FALSE	TRUE	fimbriatum_lindbergii
335	fuscum_fimbriatum_lindbergii	fimbriatum	0	5.19	0.91	0.09	0.00	0.00	-4,853	-4,853	502	lindbergii	0	0.01	FALSE	TRUE	fuscum_lindbergii
336	fuscum_fimbriatum_lindbergii	lindbergii	0	2.20	0.57	0.43	0.00	0.00	-19,263	-19,309	2111	lindbergii	46	0.28	FALSE	TRUE	fuscum_fimbriatum
337	fuscum_fimbriatum_riparium	fuscum	0	4.83	0.89	0.11	0.00	0.00	-5,852	-5,858	589	riparium	6	0.02	FALSE	TRUE	fimbriatum_riparium
338	**fuscum_fimbriatum_riparium**	**fimbriatum**	**0**	**5.46**	**0.90**	**0.10**	**0.00**	**0.00**	**-4,563**	**-4,552**	**473**	**riparium**	**-11**	**0.01**	**TRUE**	**TRUE**	**fuscum_riparium**
339	fuscum_fimbriatum_riparium	riparium	0	2.42	0.61	0.39	0.00	0.00	-19,057	-19,155	2133	riparium	98	0.26	FALSE	TRUE	fuscum_fimbriatum
340	fuscum_fimbriatum_squarrosum	fuscum	0	4.65	0.89	0.11	0.00	0.00	-6,322	-6,340	635	squarrosum	18	0.02	FALSE	TRUE	fimbriatum_squarrosum
341	fuscum_fimbriatum_squarrosum	fimbriatum	0	4.69	0.90	0.10	0.00	0.00	-5,618	-5,634	579	squarrosum	15	0.02	FALSE	TRUE	fuscum_squarrosum
342	fuscum_fimbriatum_squarrosum	squarrosum	0	2.17	0.63	0.37	0.00	0.00	-18,358	-18,479	1981	squarrosum	120	0.23	FALSE	TRUE	fuscum_fimbriatum
343	fuscum_fimbriatum_platyphyllum	fuscum	0	4.02	0.87	0.13	0.00	0.00	-6,273	-6,310	629	platyphyllum	37	0.02	FALSE	TRUE	fimbriatum_platyphyllum
344	**fuscum_fimbriatum_platyphyllum**	**fimbriatum**	**0**	**5.40**	**0.90**	**0.10**	**0.00**	**0.00**	**-6,134**	**-6,123**	**616**	**platyphyllum**	**-10**	**0.02**	**TRUE**	**TRUE**	**fuscum_platyphyllum**
345	fuscum_fimbriatum_platyphyllum	platyphyllum	0	3.99	0.84	0.16	0.00	0.00	-16,778	-16,864	1950	platyphyllum	86	0.10	FALSE	TRUE	fuscum_fimbriatum
346	fuscum_compactum_flexuosum	fuscum	0	3.47	0.83	0.17	0.00	0.00	-11,127	-11,220	1169	flexuosum	93	0.06	FALSE	TRUE	compactum_flexuosum
347	fuscum_compactum_flexuosum	compactum	0	4.58	0.90	0.10	0.00	0.00	-7,356	-7,374	756	flexuosum	18	0.02	FALSE	TRUE	fuscum_flexuosum
348	fuscum_compactum_flexuosum	flexuosum	0	3.99	0.86	0.14	0.00	0.00	-11,710	-11,768	1270	flexuosum	58	0.06	FALSE	TRUE	fuscum_compactum
349	fuscum_compactum_tenellum	fuscum	0	3.52	0.82	0.18	0.00	0.00	-11,307	-11,407	1188	tenellum	100	0.07	FALSE	TRUE	compactum_tenellum
350	fuscum_compactum_tenellum	compactum	0	4.97	0.91	0.09	0.00	0.00	-7,241	-7,248	743	tenellum	7	0.02	FALSE	TRUE	fuscum_tenellum
351	fuscum_compactum_tenellum	tenellum	0	3.65	0.85	0.15	0.00	0.00	-11,683	-11,769	1264	tenellum	86	0.06	FALSE	TRUE	fuscum_compactum
352	fuscum_compactum_lindbergii	fuscum	0	3.65	0.85	0.15	0.00	0.00	-11,942	-12,030	1248	lindbergii	88	0.06	FALSE	FALSE	compactum_lindbergii
353	fuscum_compactum_lindbergii	compactum	0	4.79	0.90	0.10	0.00	0.00	-8,617	-8,631	875	lindbergii	14	0.03	FALSE	TRUE	fuscum_lindbergii
354	fuscum_compactum_lindbergii	lindbergii	0	2.71	0.83	0.17	0.00	0.00	-10,607	-10,717	1072	lindbergii	110	0.06	FALSE	FALSE	fuscum_compactum
355	fuscum_compactum_riparium	fuscum	0	3.13	0.80	0.20	0.00	0.00	-11,366	-11,485	1190	riparium	119	0.08	FALSE	TRUE	compactum_riparium
356	fuscum_compactum_riparium	compactum	0	4.74	0.90	0.10	0.00	0.00	-7,721	-7,731	795	riparium	10	0.02	FALSE	TRUE	fuscum_riparium
357	fuscum_compactum_riparium	riparium	0	3.26	0.83	0.17	0.00	0.00	-11,654	-11,767	1210	riparium	113	0.07	FALSE	TRUE	fuscum_compactum
358	fuscum_compactum_squarrosum	fuscum	0	3.81	0.84	0.16	0.00	0.00	-11,380	-11,447	1169	compactum	67	0.06	FALSE	FALSE	compactum_squarrosum
359	fuscum_compactum_squarrosum	compactum	0	4.28	0.89	0.11	0.00	0.00	-10,823	-10,874	1120	compactum	51	0.04	FALSE	FALSE	fuscum_squarrosum
360	fuscum_compactum_squarrosum	squarrosum	0	4.57	0.89	0.11	0.00	0.00	-9,045	-9,070	906	compactum	25	0.03	FALSE	TRUE	fuscum_compactum
361	fuscum_compactum_platyphyllum	fuscum	0	3.89	0.84	0.16	0.00	0.00	-6,703	-6,740	682	compactum	37	0.03	FALSE	TRUE	compactum_platyphyllum
362	fuscum_compactum_platyphyllum	compactum	0	2.10	0.72	0.28	0.00	0.00	-12,910	-13,026	1366	compactum	116	0.12	FALSE	TRUE	fuscum_platyphyllum
363	fuscum_compactum_platyphyllum	platyphyllum	0	3.80	0.73	0.27	0.00	0.01	-9,729	-9,759	1147	compactum	29	0.10	FALSE	TRUE	fuscum_compactum
364	fuscum_flexuosum_tenellum	fuscum	0	1.99	0.19	0.81	0.00	0.01	-23,039	-22,014	2864	fuscum	-1025	0.72	TRUE	TRUE	flexuosum_tenellum
365	fuscum_flexuosum_tenellum	flexuosum	0	2.86	0.77	0.23	0.00	0.00	-1,570	-1,594	174	fuscum	24	0.01	FALSE	TRUE	fuscum_tenellum
366	fuscum_flexuosum_tenellum	tenellum	0	4.87	0.80	0.20	0.00	0.00	-1,450	-1,449	157	fuscum	0	0.01	FALSE	TRUE	fuscum_flexuosum
367	fuscum_flexuosum_lindbergii	fuscum	0	2.71	0.71	0.29	0.00	0.00	-15,285	-15,428	1666	fuscum	143	0.15	FALSE	TRUE	flexuosum_lindbergii
368	fuscum_flexuosum_lindbergii	flexuosum	0	3.84	0.81	0.19	0.00	0.00	-9,149	-9,194	984	fuscum	45	0.06	FALSE	TRUE	fuscum_lindbergii
369	**fuscum_flexuosum_lindbergii**	**lindbergii**	**0**	**6.63**	**0.93**	**0.07**	**0.00**	**0.00**	**-5,538**	**-5,492**	**545**	**fuscum**	**-46**	**0.01**	**TRUE**	**TRUE**	**fuscum_flexuosum**
370	fuscum_flexuosum_riparium	fuscum	0	2.16	0.54	0.46	0.00	0.00	-19,349	-19,366	2200	fuscum	17	0.32	FALSE	TRUE	flexuosum_riparium
371	fuscum_flexuosum_riparium	flexuosum	0	4.06	0.79	0.21	0.00	0.00	-5,707	-5,730	622	fuscum	23	0.04	FALSE	TRUE	fuscum_riparium
372	**fuscum_flexuosum_riparium**	**riparium**	**0**	**7.12**	**0.93**	**0.07**	**0.00**	**0.00**	**-3,686**	**-3,642**	**373**	**fuscum**	**-44**	**0.01**	**TRUE**	**TRUE**	**fuscum_flexuosum**
373	fuscum_flexuosum_squarrosum	fuscum	0	3.45	0.81	0.19	0.00	0.00	-11,852	-11,949	1251	flexuosum	97	0.08	FALSE	TRUE	flexuosum_squarrosum
374	fuscum_flexuosum_squarrosum	flexuosum	0	3.33	0.80	0.20	0.00	0.00	-12,089	-12,196	1326	flexuosum	107	0.08	FALSE	TRUE	fuscum_squarrosum
375	**fuscum_flexuosum_squarrosum**	**squarrosum**	**0**	**5.32**	**0.89**	**0.11**	**0.00**	**0.00**	**-6,221**	**-6,201**	**618**	**flexuosum**	**-20**	**0.02**	**TRUE**	**TRUE**	**fuscum_flexuosum**
376	fuscum_flexuosum_platyphyllum	fuscum	0	4.28	0.88	0.12	0.00	0.00	-6,119	-6,147	633	flexuosum	28	0.02	FALSE	TRUE	flexuosum_platyphyllum
377	fuscum_flexuosum_platyphyllum	flexuosum	0	3.22	0.80	0.20	0.00	0.00	-13,629	-13,764	1536	flexuosum	136	0.10	FALSE	TRUE	fuscum_platyphyllum
378	fuscum_flexuosum_platyphyllum	platyphyllum	0	3.60	0.70	0.30	0.00	0.01	-8,566	-8,604	1026	flexuosum	38	0.09	FALSE	TRUE	fuscum_flexuosum
379	fuscum_tenellum_lindbergii	fuscum	0	2.88	0.72	0.28	0.00	0.00	-15,451	-15,602	1685	fuscum	151	0.15	FALSE	TRUE	tenellum_lindbergii
380	fuscum_tenellum_lindbergii	tenellum	0	3.81	0.85	0.15	0.00	0.00	-9,056	-9,116	972	fuscum	60	0.05	FALSE	TRUE	fuscum_lindbergii
381	**fuscum_tenellum_lindbergii**	**lindbergii**	**0**	**6.00**	**0.92**	**0.08**	**0.00**	**0.00**	**-5,449**	**-5,420**	**538**	**fuscum**	**-29**	**0.01**	**TRUE**	**TRUE**	**fuscum_tenellum**
382	fuscum_tenellum_riparium	fuscum	0	2.22	0.55	0.45	0.00	0.00	-19,429	-19,455	2214	fuscum	26	0.32	FALSE	TRUE	tenellum_riparium
383	fuscum_tenellum_riparium	tenellum	0	3.18	0.81	0.19	0.00	0.00	-5,461	-5,522	598	fuscum	60	0.03	FALSE	TRUE	fuscum_riparium
384	**fuscum_tenellum_riparium**	**riparium**	**0**	**7.15**	**0.93**	**0.07**	**0.00**	**0.00**	**-3,828**	**-3,781**	**383**	**fuscum**	**-47**	**0.01**	**TRUE**	**TRUE**	**fuscum_tenellum**
385	fuscum_tenellum_squarrosum	fuscum	0	3.47	0.82	0.18	0.00	0.00	-11,934	-12,030	1263	tenellum	96	0.07	FALSE	TRUE	tenellum_squarrosum
386	fuscum_tenellum_squarrosum	tenellum	0	3.14	0.79	0.21	0.00	0.00	-12,068	-12,185	1320	tenellum	117	0.09	FALSE	TRUE	fuscum_squarrosum
387	**fuscum_tenellum_squarrosum**	**squarrosum**	**0**	**5.27**	**0.90**	**0.10**	**0.00**	**0.00**	**-6,158**	**-6,145**	**612**	**tenellum**	**-12**	**0.02**	**TRUE**	**TRUE**	**fuscum_tenellum**
388	fuscum_tenellum_platyphyllum	fuscum	0	4.23	0.86	0.14	0.00	0.00	-6,221	-6,246	638	tenellum	25	0.03	FALSE	TRUE	tenellum_platyphyllum
389	fuscum_tenellum_platyphyllum	tenellum	0	2.94	0.78	0.22	0.00	0.00	-13,672	-13,815	1536	tenellum	143	0.11	FALSE	TRUE	fuscum_platyphyllum
390	fuscum_tenellum_platyphyllum	platyphyllum	0	3.64	0.70	0.30	0.00	0.01	-8,529	-8,560	1021	tenellum	31	0.10	FALSE	TRUE	fuscum_tenellum
391	fuscum_lindbergii_riparium	fuscum	0	3.02	0.76	0.24	0.00	0.00	-15,912	-16,062	1721	fuscum	150	0.13	FALSE	TRUE	lindbergii_riparium
392	fuscum_lindbergii_riparium	lindbergii	0	4.68	0.91	0.09	0.00	0.00	-6,005	-6,017	601	fuscum	12	0.02	FALSE	TRUE	fuscum_riparium
393	fuscum_lindbergii_riparium	riparium	0	3.16	0.84	0.16	0.00	0.00	-8,528	-8,606	873	fuscum	78	0.04	FALSE	TRUE	fuscum_lindbergii
394	fuscum_lindbergii_squarrosum	fuscum	0	3.68	0.83	0.17	0.00	0.00	-12,272	-12,358	1285	lindbergii	86	0.07	FALSE	FALSE	lindbergii_squarrosum
395	fuscum_lindbergii_squarrosum	lindbergii	0	3.11	0.81	0.19	0.00	0.00	-11,079	-11,194	1142	lindbergii	115	0.07	FALSE	FALSE	fuscum_squarrosum
396	**fuscum_lindbergii_squarrosum**	**squarrosum**	**0**	**5.82**	**0.92**	**0.08**	**0.00**	**0.00**	**-7,798**	**-7,760**	**768**	**lindbergii**	**-38**	**0.02**	**TRUE**	**TRUE**	**fuscum_lindbergii**
397	fuscum_lindbergii_platyphyllum	fuscum	0	4.20	0.86	0.14	0.00	0.00	-6,461	-6,491	657	lindbergii	30	0.03	FALSE	TRUE	lindbergii_platyphyllum
398	fuscum_lindbergii_platyphyllum	lindbergii	0	2.02	0.68	0.32	0.00	0.00	-13,328	-13,420	1419	lindbergii	92	0.14	FALSE	TRUE	fuscum_platyphyllum
399	fuscum_lindbergii_platyphyllum	platyphyllum	0	3.79	0.71	0.29	0.00	0.01	-9,437	-9,464	1119	lindbergii	27	0.10	FALSE	TRUE	fuscum_lindbergii
400	fuscum_riparium_squarrosum	fuscum	0	3.65	0.82	0.18	0.00	0.00	-12,261	-12,346	1285	riparium	85	0.07	FALSE	FALSE	riparium_squarrosum
401	fuscum_riparium_squarrosum	riparium	0	3.27	0.80	0.20	0.00	0.00	-11,840	-11,945	1244	riparium	105	0.08	FALSE	FALSE	fuscum_squarrosum
402	**fuscum_riparium_squarrosum**	**squarrosum**	**0**	**5.42**	**0.91**	**0.09**	**0.00**	**0.00**	**-6,718**	**-6,699**	**666**	**riparium**	**-19**	**0.02**	**TRUE**	**TRUE**	**fuscum_riparium**
403	fuscum_riparium_platyphyllum	fuscum	0	4.30	0.86	0.14	0.00	0.00	-6,479	-6,501	659	riparium	22	0.03	FALSE	TRUE	riparium_platyphyllum
404	fuscum_riparium_platyphyllum	riparium	0	2.59	0.71	0.29	0.00	0.00	-13,626	-13,750	1480	riparium	124	0.13	FALSE	TRUE	fuscum_platyphyllum
405	fuscum_riparium_platyphyllum	platyphyllum	0	3.63	0.70	0.30	0.00	0.01	-8,857	-8,889	1056	riparium	32	0.10	FALSE	TRUE	fuscum_riparium
406	fuscum_squarrosum_platyphyllum	fuscum	0	4.58	0.87	0.13	0.00	0.00	-7,139	-7,150	716	squarrosum	11	0.03	FALSE	TRUE	squarrosum_platyphyllum
407	fuscum_squarrosum_platyphyllum	squarrosum	0	2.39	0.75	0.25	0.00	0.00	-12,191	-12,313	1268	squarrosum	122	0.10	FALSE	TRUE	fuscum_platyphyllum
408	fuscum_squarrosum_platyphyllum	platyphyllum	0	3.78	0.74	0.26	0.00	0.01	-10,265	-10,301	1211	squarrosum	36	0.10	FALSE	TRUE	fuscum_squarrosum
409	subnitens_fimbriatum_compactum	subnitens	0	4.81	0.89	0.11	0.00	0.00	-5,808	-5,817	587	compactum	9	0.02	FALSE	TRUE	fimbriatum_compactum
410	subnitens_fimbriatum_compactum	fimbriatum	0	5.26	0.91	0.09	0.00	0.00	-5,249	-5,248	536	compactum	-2	0.01	FALSE	TRUE	subnitens_compactum
411	subnitens_fimbriatum_compactum	compactum	0	1.98	0.57	0.43	0.00	0.00	-18,919	-18,994	2072	compactum	75	0.28	FALSE	TRUE	subnitens_fimbriatum
412	subnitens_fimbriatum_flexuosum	subnitens	0	4.26	0.86	0.14	0.00	0.00	-5,267	-5,289	543	flexuosum	22	0.02	FALSE	TRUE	fimbriatum_flexuosum
413	subnitens_fimbriatum_flexuosum	fimbriatum	0	4.83	0.90	0.10	0.00	0.00	-4,630	-4,633	476	flexuosum	3	0.02	FALSE	TRUE	subnitens_flexuosum
414	subnitens_fimbriatum_flexuosum	flexuosum	0	2.35	0.68	0.32	0.00	0.00	-18,876	-19,047	2176	flexuosum	171	0.22	FALSE	TRUE	subnitens_fimbriatum
415	subnitens_fimbriatum_tenellum	subnitens	0	4.33	0.88	0.12	0.00	0.00	-5,287	-5,312	544	tenellum	25	0.02	FALSE	TRUE	fimbriatum_tenellum
416	subnitens_fimbriatum_tenellum	fimbriatum	0	5.10	0.90	0.10	0.00	0.00	-4,594	-4,596	476	tenellum	2	0.01	FALSE	TRUE	subnitens_tenellum
417	subnitens_fimbriatum_tenellum	tenellum	0	2.35	0.67	0.33	0.00	0.00	-18,905	-19,065	2175	tenellum	161	0.23	FALSE	TRUE	subnitens_fimbriatum
418	subnitens_fimbriatum_lindbergii	subnitens	0	3.99	0.86	0.14	0.00	0.00	-5,669	-5,705	579	lindbergii	36	0.03	FALSE	TRUE	fimbriatum_lindbergii
419	subnitens_fimbriatum_lindbergii	fimbriatum	0	4.71	0.90	0.10	0.00	0.00	-5,011	-5,022	517	lindbergii	11	0.02	FALSE	TRUE	subnitens_lindbergii
420	subnitens_fimbriatum_lindbergii	lindbergii	0	2.17	0.57	0.43	0.00	0.00	-19,069	-19,120	2099	lindbergii	51	0.28	FALSE	TRUE	subnitens_fimbriatum
421	subnitens_fimbriatum_riparium	subnitens	0	4.60	0.88	0.12	0.00	0.00	-5,461	-5,480	556	riparium	19	0.02	FALSE	TRUE	fimbriatum_riparium
422	subnitens_fimbriatum_riparium	fimbriatum	0	4.93	0.89	0.11	0.00	0.00	-4,845	-4,842	499	riparium	-2	0.02	FALSE	TRUE	subnitens_riparium
423	subnitens_fimbriatum_riparium	riparium	0	2.35	0.61	0.39	0.00	0.00	-19,091	-19,196	2140	riparium	105	0.26	FALSE	TRUE	subnitens_fimbriatum
424	subnitens_fimbriatum_squarrosum	subnitens	0	4.40	0.90	0.10	0.00	0.00	-6,045	-6,071	615	squarrosum	26	0.02	FALSE	TRUE	fimbriatum_squarrosum
425	subnitens_fimbriatum_squarrosum	fimbriatum	0	4.91	0.90	0.10	0.00	0.00	-5,844	-5,851	597	squarrosum	8	0.02	FALSE	TRUE	subnitens_squarrosum
426	subnitens_fimbriatum_squarrosum	squarrosum	0	2.22	0.65	0.35	0.00	0.00	-18,298	-18,426	1983	squarrosum	128	0.22	FALSE	TRUE	subnitens_fimbriatum
427	subnitens_fimbriatum_platyphyllum	subnitens	0	4.26	0.89	0.11	0.00	0.00	-6,115	-6,143	620	platyphyllum	28	0.02	FALSE	TRUE	fimbriatum_platyphyllum
428	subnitens_fimbriatum_platyphyllum	fimbriatum	0	4.88	0.90	0.10	0.00	0.00	-6,286	-6,290	632	platyphyllum	4	0.02	FALSE	TRUE	subnitens_platyphyllum
429	subnitens_fimbriatum_platyphyllum	platyphyllum	0	3.91	0.83	0.17	0.00	0.00	-16,621	-16,722	1943	platyphyllum	101	0.10	FALSE	TRUE	subnitens_fimbriatum
430	subnitens_compactum_flexuosum	subnitens	0	3.84	0.85	0.15	0.00	0.00	-11,148	-11,222	1170	flexuosum	74	0.06	FALSE	TRUE	compactum_flexuosum
431	subnitens_compactum_flexuosum	compactum	0	4.53	0.89	0.11	0.00	0.00	-7,392	-7,413	761	flexuosum	21	0.03	FALSE	TRUE	subnitens_flexuosum
432	subnitens_compactum_flexuosum	flexuosum	0	3.92	0.85	0.15	0.00	0.00	-11,636	-11,700	1264	flexuosum	64	0.06	FALSE	TRUE	subnitens_compactum
433	subnitens_compactum_tenellum	subnitens	0	3.85	0.84	0.16	0.00	0.00	-11,285	-11,358	1184	tenellum	73	0.06	FALSE	TRUE	compactum_tenellum
434	subnitens_compactum_tenellum	compactum	0	4.42	0.89	0.11	0.00	0.00	-7,311	-7,338	754	tenellum	27	0.03	FALSE	TRUE	subnitens_tenellum
435	subnitens_compactum_tenellum	tenellum	0	3.67	0.85	0.15	0.00	0.00	-11,609	-11,695	1257	tenellum	86	0.06	FALSE	TRUE	subnitens_compactum
436	subnitens_compactum_lindbergii	subnitens	0	3.69	0.84	0.16	0.00	0.00	-12,149	-12,233	1264	lindbergii	85	0.06	FALSE	FALSE	compactum_lindbergii
437	subnitens_compactum_lindbergii	compactum	0	4.58	0.90	0.10	0.00	0.00	-8,347	-8,368	851	lindbergii	21	0.03	FALSE	TRUE	subnitens_lindbergii
438	subnitens_compactum_lindbergii	lindbergii	0	2.54	0.82	0.18	0.00	0.00	-10,732	-10,845	1080	lindbergii	113	0.06	FALSE	FALSE	subnitens_compactum
439	subnitens_compactum_riparium	subnitens	0	3.70	0.83	0.17	0.00	0.00	-11,349	-11,438	1186	riparium	89	0.06	FALSE	TRUE	compactum_riparium
440	subnitens_compactum_riparium	compactum	0	4.51	0.89	0.11	0.00	0.00	-7,676	-7,693	794	riparium	17	0.03	FALSE	TRUE	subnitens_riparium
441	subnitens_compactum_riparium	riparium	0	3.32	0.83	0.17	0.00	0.00	-11,723	-11,836	1215	riparium	113	0.07	FALSE	TRUE	subnitens_compactum
442	subnitens_compactum_squarrosum	subnitens	0	3.89	0.84	0.16	0.00	0.00	-11,209	-11,267	1155	compactum	58	0.06	FALSE	FALSE	compactum_squarrosum
443	subnitens_compactum_squarrosum	compactum	0	4.38	0.89	0.11	0.00	0.00	-10,949	-10,997	1129	compactum	48	0.04	FALSE	FALSE	subnitens_squarrosum
444	subnitens_compactum_squarrosum	squarrosum	0	1.02	0.86	0.14	0.00	0.00	-9,079	-9,125	911	compactum	46	0.04	FALSE	TRUE	subnitens_compactum

445	subnitens_compactum_platyphyllum	subnitens	0	4.39	0.86	0.14	0.00	0.00	-6,537	-6,564	672	compactum	26	0.03	FALSE	TRUE	compactum_platyphyllum
446	subnitens_compactum_platyphyllum	compactum	0	2.30	0.73	0.27	0.00	0.00	-12,897	-13,026	1368	compactum	129	0.11	FALSE	TRUE	subnitens_platyphyllum
447	subnitens_compactum_platyphyllum	platyphyllum	0	3.81	0.74	0.26	0.00	0.01	-9,779	-9,818	1155	compactum	39	0.10	FALSE	TRUE	subnitens_compactum
448	subnitens_flexuosum_tenellum	subnitens	0	1.90	0.19	0.81	0.00	0.01	-23,062	-22,028	2865	subnitens	-1033	0.73	TRUE	TRUE	flexuosum_tenellum
449	subnitens_flexuosum_tenellum	flexuosum	0	3.27	0.82	0.18	0.00	0.00	-1,609	-1,634	179	subnitens	25	0.01	FALSE	TRUE	subnitens_tenellum
450	subnitens_flexuosum_tenellum	tenellum	0	5.09	0.80	0.20	0.00	0.00	-1,387	-1,385	151	subnitens	-2	0.01	FALSE	TRUE	subnitens_flexuosum
451	subnitens_flexuosum_lindbergii	subnitens	0	2.88	0.72	0.28	0.00	0.00	-15,308	-15,457	1669	subnitens	149	0.14	FALSE	TRUE	flexuosum_lindbergii
452	subnitens_flexuosum_lindbergii	flexuosum	0	4.17	0.84	0.16	0.00	0.00	-9,078	-9,113	977	subnitens	35	0.05	FALSE	TRUE	subnitens_lindbergii
453	**subnitens_flexuosum_lindbergii**	**lindbergii**	**0**	**5.86**	**0.91**	**0.09**	**0.00**	**0.00**	**-5,547**	**-5,522**	**549**	**subnitens**	**-25**	**0.02**	**TRUE**	**TRUE**	**subnitens_flexuosum**
454	subnitens_flexuosum_riparium	subnitens	0	2.10	0.54	0.46	0.00	0.00	-19,399	-19,429	2205	subnitens	30	0.32	FALSE	TRUE	flexuosum_riparium
455	subnitens_flexuosum_riparium	flexuosum	0	3.89	0.79	0.21	0.00	0.00	-5,610	-5,643	615	subnitens	33	0.04	FALSE	TRUE	subnitens_riparium
456	**subnitens_flexuosum_riparium**	**riparium**	**0**	**7.33**	**0.93**	**0.07**	**0.00**	**0.00**	**-3,721**	**-3,672**	**375**	**subnitens**	**-50**	**0.01**	**TRUE**	**TRUE**	**subnitens_flexuosum**
457	subnitens_flexuosum_squarrosum	subnitens	0	3.53	0.80	0.20	0.00	0.00	-11,675	-11,764	1236	flexuosum	88	0.08	FALSE	TRUE	flexuosum_squarrosum
458	subnitens_flexuosum_squarrosum	flexuosum	0	3.31	0.80	0.20	0.00	0.00	-12,235	-12,345	1338	flexuosum	110	0.08	FALSE	TRUE	subnitens_squarrosum
459	subnitens_flexuosum_squarrosum	squarrosum	0	5.11	0.90	0.10	0.00	0.00	-6,210	-6,210	621	flexuosum	-1	0.02	FALSE	TRUE	subnitens_flexuosum
460	subnitens_flexuosum_platyphyllum	subnitens	0	4.14	0.90	0.10	0.00	0.00	-5,896	-5,929	618	flexuosum	33	0.02	FALSE	TRUE	flexuosum_platyphyllum
461	subnitens_flexuosum_platyphyllum	flexuosum	0	2.99	0.78	0.22	0.00	0.00	-13,512	-13,656	1527	flexuosum	144	0.10	FALSE	TRUE	subnitens_platyphyllum
462	subnitens_flexuosum_platyphyllum	platyphyllum	0	3.59	0.70	0.30	0.00	0.01	-8,788	-8,826	1050	flexuosum	38	0.10	FALSE	TRUE	subnitens_flexuosum
463	subnitens_tenellum_lindbergii	subnitens	0	2.94	0.74	0.26	0.00	0.00	-15,453	-15,601	1684	subnitens	148	0.14	FALSE	TRUE	tenellum_lindbergii
464	subnitens_tenellum_lindbergii	tenellum	0	3.74	0.86	0.14	0.00	0.00	-8,963	-9,026	963	subnitens	63	0.04	FALSE	TRUE	subnitens_lindbergii
465	**subnitens_tenellum_lindbergii**	**lindbergii**	**0**	**5.90**	**0.92**	**0.08**	**0.00**	**0.00**	**-5,539**	**-5,513**	**548**	**subnitens**	**-25**	**0.01**	**TRUE**	**TRUE**	**subnitens_tenellum**
466	subnitens_tenellum_riparium	subnitens	0	2.13	0.55	0.45	0.00	0.00	-19,538	-19,576	2224	subnitens	38	0.32	FALSE	TRUE	tenellum_riparium
467	subnitens_tenellum_riparium	tenellum	0	3.09	0.81	0.19	0.00	0.00	-5,355	-5,415	589	subnitens	60	0.04	FALSE	TRUE	subnitens_riparium
468	**subnitens_tenellum_riparium**	**riparium**	**0**	**6.92**	**0.93**	**0.07**	**0.00**	**0.00**	**-3,794**	**-3,752**	**382**	**subnitens**	**-41**	**0.01**	**TRUE**	**TRUE**	**subnitens_tenellum**
469	subnitens_tenellum_squarrosum	subnitens	0	3.58	0.81	0.19	0.00	0.00	-11,670	-11,759	1240	tenellum	89	0.07	FALSE	TRUE	tenellum_squarrosum
470	subnitens_tenellum_squarrosum	tenellum	0	3.12	0.79	0.21	0.00	0.00	-12,220	-12,340	1332	tenellum	121	0.09	FALSE	TRUE	subnitens_squarrosum
471	subnitens_tenellum_squarrosum	squarrosum	0	5.17	0.91	0.09	0.00	0.00	-6,232	-6,228	623	tenellum	-3	0.02	FALSE	TRUE	subnitens_tenellum
472	subnitens_tenellum_platyphyllum	subnitens	0	4.29	0.88	0.12	0.00	0.00	-5,944	-5,971	619	tenellum	27	0.02	FALSE	TRUE	tenellum_platyphyllum
473	subnitens_tenellum_platyphyllum	tenellum	0	2.79	0.76	0.24	0.00	0.00	-13,570	-13,712	1528	tenellum	142	0.11	FALSE	TRUE	subnitens_platyphyllum
474	subnitens_tenellum_platyphyllum	platyphyllum	0	3.53	0.70	0.30	0.00	0.01	-8,752	-8,796	1048	tenellum	43	0.10	FALSE	TRUE	subnitens_tenellum
475	subnitens_lindbergii_riparium	subnitens	0	3.04	0.75	0.25	0.00	0.00	-16,087	-16,239	1736	subnitens	152	0.13	FALSE	TRUE	lindbergii_riparium
476	subnitens_lindbergii_riparium	lindbergii	0	5.29	0.92	0.08	0.00	0.00	-5,939	-5,936	596	subnitens	-3	0.01	FALSE	TRUE	subnitens_riparium
477	subnitens_lindbergii_riparium	riparium	0	3.05	0.85	0.15	0.00	0.00	-8,419	-8,500	863	subnitens	81	0.04	FALSE	TRUE	subnitens_lindbergii
478	subnitens_lindbergii_squarrosum	subnitens	0	3.71	0.83	0.17	0.00	0.00	-12,248	-12,329	1282	lindbergii	80	0.07	FALSE	FALSE	lindbergii_squarrosum
479	subnitens_lindbergii_squarrosum	lindbergii	0	2.98	0.81	0.19	0.00	0.00	-11,284	-11,401	1156	lindbergii	117	0.07	FALSE	FALSE	subnitens_squarrosum
480	**subnitens_lindbergii_squarrosum**	**squarrosum**	**0**	**5.72**	**0.92**	**0.08**	**0.00**	**0.00**	**-7,668**	**-7,638**	**757**	**lindbergii**	**-31**	**0.02**	**TRUE**	**TRUE**	**subnitens_lindbergii**
481	subnitens_lindbergii_platyphyllum	subnitens	0	4.36	0.88	0.12	0.00	0.00	-6,456	-6,482	659	lindbergii	25	0.02	FALSE	TRUE	lindbergii_platyphyllum
482	subnitens_lindbergii_platyphyllum	lindbergii	0	2.08	0.67	0.33	0.00	0.00	-13,313	-13,407	1418	lindbergii	94	0.15	FALSE	TRUE	subnitens_platyphyllum
483	subnitens_lindbergii_platyphyllum	platyphyllum	0	3.71	0.71	0.29	0.00	0.01	-9,406	-9,439	1118	lindbergii	33	0.10	FALSE	TRUE	subnitens_lindbergii
484	subnitens_riparium_squarrosum	subnitens	0	3.64	0.81	0.19	0.00	0.00	-12,079	-12,160	1270	riparium	81	0.08	FALSE	FALSE	riparium_squarrosum
485	subnitens_riparium_squarrosum	riparium	0	3.14	0.79	0.21	0.00	0.00	-12,064	-12,174	1262	riparium	110	0.08	FALSE	FALSE	subnitens_squarrosum
486	subnitens_riparium_squarrosum	squarrosum	0	5.12	0.90	0.10	0.00	0.00	-6,618	-6,618	663	riparium	0	0.02	FALSE	TRUE	subnitens_riparium
487	subnitens_riparium_platyphyllum	subnitens	0	3.95	0.86	0.14	0.00	0.00	-6,162	-6,199	637	riparium	36	0.03	FALSE	TRUE	riparium_platyphyllum
488	subnitens_riparium_platyphyllum	riparium	0	2.50	0.69	0.31	0.00	0.00	-13,691	-13,809	1486	riparium	118	0.14	FALSE	TRUE	subnitens_platyphyllum
489	subnitens_riparium_platyphyllum	platyphyllum	0	3.62	0.70	0.30	0.00	0.01	-8,988	-9,021	1072	riparium	33	0.10	FALSE	TRUE	subnitens_riparium
490	subnitens_squarrosum_platyphyllum	subnitens	0	3.97	0.86	0.14	0.00	0.00	-6,815	-6,854	696	squarrosum	39	0.03	FALSE	TRUE	squarrosum_platyphyllum
491	subnitens_squarrosum_platyphyllum	squarrosum	0	2.36	0.74	0.26	0.00	0.00	-12,236	-12,360	1274	squarrosum	124	0.10	FALSE	TRUE	subnitens_platyphyllum
492	subnitens_squarrosum_platyphyllum	platyphyllum	0	3.89	0.75	0.25	0.00	0.01	-10,407	-10,437	1225	squarrosum	30	0.10	FALSE	TRUE	subnitens_squarrosum
493	fimbriatum_compactum_flexuosum	fimbriatum	0	4.08	0.88	0.12	0.00	0.00	-10,967	-11,031	1149	flexuosum	63	0.04	FALSE	TRUE	compactum_flexuosum
494	fimbriatum_compactum_flexuosum	compactum	0	3.82	0.87	0.13	0.00	0.00	-7,734	-7,786	799	flexuosum	52	0.03	FALSE	TRUE	fimbriatum_flexuosum
495	fimbriatum_compactum_flexuosum	flexuosum	0	4.04	0.86	0.14	0.00	0.00	-11,474	-11,527	1247	flexuosum	53	0.06	FALSE	TRUE	fimbriatum_compactum
496	fimbriatum_compactum_tenellum	fimbriatum	0	4.05	0.86	0.14	0.00	0.00	-11,093	-11,160	1164	tenellum	67	0.05	FALSE	TRUE	compactum_tenellum
497	fimbriatum_compactum_tenellum	compactum	0	3.74	0.87	0.13	0.00	0.00	-7,614	-7,669	786	tenellum	55	0.03	FALSE	TRUE	fimbriatum_tenellum
498	fimbriatum_compactum_tenellum	tenellum	0	3.77	0.85	0.15	0.00	0.00	-11,488	-11,562	1245	tenellum	74	0.06	FALSE	TRUE	fimbriatum_compactum
499	fimbriatum_compactum_lindbergii	fimbriatum	0	3.82	0.86	0.14	0.00	0.00	-11,848	-11,938	1238	lindbergii	90	0.05	FALSE	FALSE	compactum_lindbergii
500	fimbriatum_compactum_lindbergii	compactum	0	3.94	0.88	0.12	0.00	0.00	-8,677	-8,731	885	lindbergii	54	0.03	FALSE	TRUE	fimbriatum_lindbergii
501	fimbriatum_compactum_lindbergii	lindbergii	0	2.74	0.84	0.16	0.00	0.00	-10,611	-10,720	1072	lindbergii	109	0.05	FALSE	FALSE	fimbriatum_compactum
502	fimbriatum_compactum_riparium	fimbriatum	0	3.06	0.85	0.15	0.00	0.00	-11,131	-11,243	1168	riparium	112	0.06	FALSE	TRUE	compactum_riparium
503	fimbriatum_compactum_riparium	compactum	0	4.37	0.89	0.11	0.00	0.00	-8,251	-8,285	846	riparium	34	0.03	FALSE	TRUE	fimbriatum_riparium
504	fimbriatum_compactum_riparium	riparium	0	3.24	0.85	0.15	0.00	0.00	-11,315	-11,419	1181	riparium	104	0.06	FALSE	TRUE	fimbriatum_compactum
505	fimbriatum_compactum_squarrosum	fimbriatum	0	3.43	0.86	0.14	0.00	0.00	-10,755	-10,852	1121	compactum	97	0.05	FALSE	TRUE	compactum_squarrosum
506	fimbriatum_compactum_squarrosum	compactum	0	3.87	0.88	0.12	0.00	0.00	-11,133	-11,210	1148	compactum	76	0.04	FALSE	TRUE	fimbriatum_squarrosum
507	fimbriatum_compactum_squarrosum	squarrosum	0	4.82	0.90	0.10	0.00	0.00	-9,234	-9,247	926	compactum	13	0.03	FALSE	TRUE	fimbriatum_compactum
508	fimbriatum_compactum_platyphyllum	fimbriatum	0	4.69	0.90	0.10	0.00	0.00	-6,423	-6,437	657	compactum	14	0.02	FALSE	TRUE	compactum_platyphyllum
509	fimbriatum_compactum_platyphyllum	compactum	0	2.27	0.72	0.28	0.00	0.00	-12,837	-12,963	1359	compactum	126	0.12	FALSE	TRUE	fimbriatum_platyphyllum
510	fimbriatum_compactum_platyphyllum	platyphyllum	0	4.00	0.74	0.26	0.00	0.01	-10,064	-10,079	1179	compactum	15	0.10	FALSE	TRUE	fimbriatum_compactum
511	fimbriatum_flexuosum_tenellum	fimbriatum	0	1.92	0.19	0.81	0.00	0.01	-22,982	-21,959	2854	fimbriatum	-1023	0.72	TRUE	TRUE	flexuosum_tenellum
512	fimbriatum_flexuosum_tenellum	flexuosum	0	3.12	0.76	0.24	0.00	0.00	-1,661	-1,684	182	fimbriatum	24	0.01	FALSE	TRUE	fimbriatum_tenellum
513	fimbriatum_flexuosum_tenellum	tenellum	0	4.78	0.81	0.19	0.00	0.00	-1,451	-1,455	159	fimbriatum	4	0.01	FALSE	TRUE	fimbriatum_flexuosum
514	fimbriatum_flexuosum_lindbergii	fimbriatum	0	2.40	0.71	0.29	0.00	0.00	-15,077	-15,224	1645	fimbriatum	148	0.15	FALSE	TRUE	flexuosum_lindbergii
515	fimbriatum_flexuosum_lindbergii	flexuosum	0	3.71	0.81	0.19	0.00	0.00	-8,976	-9,034	970	fimbriatum	58	0.06	FALSE	TRUE	fimbriatum_lindbergii
516	**fimbriatum_flexuosum_lindbergii**	**lindbergii**	**0**	**6.32**	**0.92**	**0.08**	**0.00**	**0.00**	**-5,852**	**-5,800**	**580**	**fimbriatum**	**-52**	**0.02**	**TRUE**	**TRUE**	**fimbriatum_flexuosum**
517	fimbriatum_flexuosum_riparium	fimbriatum	0	2.07	0.54	0.46	0.00	0.00	-19,232	-19,270	2185	fimbriatum	38	0.31	FALSE	TRUE	flexuosum_riparium
518	fimbriatum_flexuosum_riparium	flexuosum	0	4.17	0.82	0.18	0.00	0.00	-5,837	-5,857	630	fimbriatum	19	0.04	FALSE	TRUE	fimbriatum_riparium
519	**fimbriatum_flexuosum_riparium**	**riparium**	**0**	**6.38**	**0.92**	**0.08**	**0.00**	**0.00**	**-3,718**	**-3,691**	**380**	**fimbriatum**	**-27**	**0.01**	**TRUE**	**TRUE**	**fimbriatum_flexuosum**
520	fimbriatum_flexuosum_squarrosum	fimbriatum	0	3.47	0.84	0.16	0.00	0.00	-11,605	-11,704	1225	flexuosum	99	0.06	FALSE	TRUE	flexuosum_squarrosum
521	fimbriatum_flexuosum_squarrosum	flexuosum	0	3.42	0.82	0.18	0.00	0.00	-12,005	-12,104	1311	flexuosum	99	0.07	FALSE	TRUE	fimbriatum_squarrosum
522	fimbriatum_flexuosum_squarrosum	squarrosum	0	4.92	0.88	0.12	0.00	0.00	-6,606	-6,603	659	flexuosum	-3	0.02	FALSE	TRUE	fimbriatum_flexuosum
523	fimbriatum_flexuosum_platyphyllum	fimbriatum	0	5.02	0.92	0.08	0.00	0.00	-5,800	-5,807	601	flexuosum	7	0.02	FALSE	TRUE	flexuosum_platyphyllum
524	fimbriatum_flexuosum_platyphyllum	flexuosum	0	3.21	0.81	0.19	0.00	0.00	-13,526	-13,663	1523	flexuosum	138	0.09	FALSE	TRUE	fimbriatum_platyphyllum
525	fimbriatum_flexuosum_platyphyllum	platyphyllum	0	3.65	0.70	0.30	0.00	0.01	-8,987	-9,018	1071	flexuosum	31	0.10	FALSE	TRUE	fimbriatum_flexuosum
526	fimbriatum_tenellum_lindbergii	fimbriatum	0	2.43	0.73	0.27	0.00	0.00	-15,204	-15,350	1660	fimbriatum	146	0.14	FALSE	TRUE	tenellum_lindbergii
527	fimbriatum_tenellum_lindbergii	tenellum	0	3.72	0.85	0.15	0.00	0.00	-8,885	-8,951	958	fimbriatum	66	0.04	FALSE	TRUE	fimbriatum_lindbergii
528	**fimbriatum_tenellum_lindbergii**	**lindbergii**	**0**	**6.18**	**0.92**	**0.08**	**0.00**	**0.00**	**-5,841**	**-5,796**	**577**	**fimbriatum**	**-45**	**0.02**	**TRUE**	**TRUE**	**fimbriatum_tenellum**
529	fimbriatum_tenellum_riparium	fimbriatum	0	2.09	0.55	0.45	0.00	0.00	-19,412	-19,451	2208	fimbriatum	39	0.31	FALSE	TRUE	tenellum_riparium
530	fimbriatum_tenellum_riparium	tenellum	0	3.44	0.85	0.15	0.00	0.00	-5,597	-5,652	607	fimbriatum	55	0.03	FALSE	TRUE	fimbriatum_riparium
531	**fimbriatum_tenellum_riparium**	**riparium**	**0**	**6.99**	**0.93**	**0.07**	**0.00**	**0.00**	**-3,761**	**-3,723**	**380**	**fimbriatum**	**-37**	**0.01**	**TRUE**	**TRUE**	**fimbriatum_tenellum**
532	fimbriatum_tenellum_squarrosum	fimbriatum	0	3.40	0.85	0.15	0.00	0.00	-11,601	-11,700	1231	tenellum	99	0.06	FALSE	TRUE	tenellum_squarrosum
533	fimbriatum_tenellum_squarrosum	tenellum	0	3.33	0.82	0.18	0.00	0.00	-11,994	-12,103	1307	tenellum	109	0.07	FALSE	TRUE	fimbriatum_squarrosum
534	fimbriatum_tenellum_squarrosum	squarrosum	0	4.86	0.88	0.12	0.00	0.00	-6,596	-6,601	657	tenellum	5	0.02	FALSE	TRUE	fimbriatum_tenellum
535	fimbriatum_tenellum_platyphyllum	fimbriatum	0	4.69	0.90	0.10	0.00	0.00	-5,852	-5,863	605	tenellum	11	0.02	FALSE	TRUE	tenellum_platyphyllum
536	fimbriatum_tenellum_platyphyllum	tenellum	0	3.02	0.79	0.21	0.00	0.00	-13,533	-13,683	1522	tenellum	150	0.10	FALSE	TRUE	fimbriatum_platyphyllum
537	fimbriatum_tenellum_platyphyllum	platyphyllum	0	3.73	0.71	0.29	0.00	0.01	-8,961	-8,991	1068	tenellum	30	0.10	FALSE	TRUE	fimbriatum_tenellum
538	fimbriatum_lindbergii_riparium	fimbriatum	0	2.68	0.75	0.25	0.00	0.00	-15,763	-15,927	1707	fimbriatum	164	0.13	FALSE	TRUE	lindbergii_riparium
539	**fimbriatum_lindbergii_riparium**	**lindbergii**	**0**	**5.74**	**0.92**	**0.08**	**0.00**	**0.00**	**-6,412**	**-6,390**	**635**	**fimbriatum**	**-22**	**0.02**	**TRUE**	**TRUE**	**fimbriatum_riparium**
540	fimbriatum_lindbergii_riparium	riparium	0	3.14	0.85	0.15	0.00	0.00	-8,275	-8,355	853	fimbriatum	80	0.04	FALSE	TRUE	fimbriatum_lindbergii
541	fimbriatum_lindbergii_squarrosum	fimbriatum	0	3.73	0.86	0.14	0.00	0.00	-11,974	-12,066	1259	lindbergii	92	0.06	FALSE	FALSE	lindbergii_squarrosum
542	fimbriatum_lindbergii_squarrosum	lindbergii	0	2.55	0.79	0.21	0.00	0.00	-11,345	-11,460	1160	lindbergii	114	0.08	FALSE	FALSE	fimbriatum_squarrosum
543	fimbriatum_lindbergii_squarrosum	squarrosum	0	4.91	0.90	0.10	0.00	0.00	-7,813	-7,817	776	lindbergii	4	0.02	FALSE	TRUE	fimbriatum_lindbergii
544	fimbriatum_lindbergii_platyphyllum	fimbriatum	0	4.74	0.91	0.09	0.00	0.00	-6,285	-6,301	642	lindbergii	16	0.02	FALSE	TRUE	lindbergii_platyphyllum
545	fimbriatum_lindbergii_platyphyllum	lindbergii	0	2.30	0.70	0.30	0.00	0.00	-13,243	-13,365	1413	lindbergii	121	0.13	FALSE	TRUE	fimbriatum_platyphyllum
546	fimbriatum_lindbergii_platyphyllum	platyphyllum	0	3.81	0.73	0.27	0.00	0.01	-9,622	-9,654	1140	lindbergii	32	0.10	FALSE	TRUE	fimbriatum_lindbergii
547	fimbriatum_riparium_squarrosum	fimbriatum	0	3.47	0.83	0.17	0.00	0.00	-11,914	-12,014	1254	riparium	100	0.07	FALSE	FALSE	riparium_squarrosum
548	fimbriatum_riparium_squarrosum	riparium	0	3.02	0.78	0.22	0.00	0.00	-11,661	-11,777	1224	riparium	116	0.08	FALSE	FALSE	fimbriatum_squarrosum
549	fimbriatum_riparium_squarrosum	squarrosum	0	4.97	0.90	0.10	0.00	0.00	-7,276	-7,280	717	riparium	3	0.02	FALSE	TRUE	fimbriatum_riparium
550	fimbriatum_riparium_platyphyllum	fimbriatum	0	4.79	0.91	0.09	0.00	0.00	-6,113	-6,125	628	riparium	12	0.02	FALSE	TRUE	riparium_platyphyllum
551	fimbriatum_riparium_platyphyllum	riparium	0	2.60	0.72	0.28	0.00	0.00	-13,428	-13,560	1462	riparium	132	0.13	FALSE	TRUE	fimbriatum_platyphyllum
552	fimbriatum_riparium_platyphyllum	platyphyllum	0	3.74	0.70	0.30	0.00	0.01	-9,338	-9,364	1105	riparium	26	0.10	FALSE	TRUE	fimbriatum_riparium
553	fimbriatum_squarrosum_platyphyllum	fimbriatum	0	4.04	0.90	0.10	0.00	0.00	-6,853	-6,891	694	squarrosum	39	0.02	FALSE	TRUE	squarrosum_platyphyllum
554	fimbriatum_squarrosum_platyphyllum	squarrosum	0	2.49	0.77	0.23	0.00	0.00	-12,228	-12,355	1269	squarrosum	127	0.09	FALSE	TRUE	fimbriatum_platyphyllum
555	fimbriatum_squarrosum_platyphyllum	platyphyllum	0	3.95	0.76	0.24	0.00	0.01	-10,518	-10,546	1232	squarrosum	28	0.09	FALSE	TRUE	fimbriatum_squarrosum
556	compactum_flexuosum_tenellum	compactum	0	2.17	0.17	0.83	0.00	0.01	-23,331	-22,187	2844	compactum	-1144	0.73	TRUE	TRUE	flexuosum_tenellum
557	compactum_flexuosum_tenellum	flexuosum	0	2.87	0.77	0.23	0.00	0.00	-1,813	-1,841	201	compactum	27	0.01	FALSE	TRUE	compactum_tenellum
558	compactum_flexuosum_tenellum	tenellum	0	4.20	0.76	0.24	0.00	0.00	-1,354	-1,363	150	compactum	8	0.01	FALSE	TRUE	compactum_flexuosum
559	compactum_flexuosum_lindbergii	compactum	0	2.41	0.72	0.28	0.00	0.00	-14,408	-14,546	1526	compactum	137	0.14	FALSE	TRUE	flexuosum_lindbergii
560	compactum_flexuosum_lindbergii	flexuosum	0	3.94	0.84	0.16	0.00	0.00	-9,691	-9,744	1042	compactum	53	0.05	FALSE	TRUE	compactum_lindbergii
561	**compactum_flexuosum_lindbergii**	**lindbergii**	**0**	**5.77**	**0.92**	**0.08**	**0.00**	**0.00**	**-6,306**	**-6,292**	**627**	**compactum**	**-14**	**0.02**	**TRUE**	**TRUE**	**compactum_flexuosum**

562	compactum_flexuosum_riparium	compactum	0	2.07	0.46	0.54	0.00	0.00	-19,277	-19,172	2128	compactum	-105	0.36	TRUE	TRUE	flexuosum_riparium
563	compactum_flexuosum_riparium	flexuosum	0	4.13	0.81	0.19	0.00	0.00	-5,977	-5,999	645	compactum	22	0.04	FALSE	TRUE	compactum_riparium
564	**compactum_flexuosum_riparium**	**riparium**	**0**	**6.95**	**0.93**	**0.07**	**0.00**	**0.00**	**-4,153**	**-4,106**	**422**	**compactum**	**-47**	**0.01**	**TRUE**	**TRUE**	**compactum_flexuosum**
565	compactum_flexuosum_squarrosum	compactum	0	3.00	0.82	0.18	0.00	0.00	-10,929	-11,043	1126	flexuosum	114	0.06	FALSE	TRUE	flexuosum_squarrosum
566	compactum_flexuosum_squarrosum	flexuosum	0	3.99	0.86	0.14	0.00	0.00	-11,135	-11,191	1197	flexuosum	56	0.05	FALSE	TRUE	compactum_squarrosum
567	compactum_flexuosum_squarrosum	squarrosum	0	4.68	0.91	0.09	0.00	0.00	-8,729	-8,750	872	flexuosum	21	0.02	FALSE	TRUE	compactum_flexuosum
568	compactum_flexuosum_platyphyllum	compactum	0	4.77	0.92	0.08	0.00	0.00	-6,533	-6,547	679	flexuosum	13	0.02	FALSE	TRUE	flexuosum_platyphyllum
569	compactum_flexuosum_platyphyllum	flexuosum	0	4.00	0.84	0.16	0.00	0.00	-10,463	-10,517	1138	flexuosum	54	0.06	FALSE	FALSE	compactum_platyphyllum
570	compactum_flexuosum_platyphyllum	platyphyllum	0	3.76	0.76	0.24	0.00	0.01	-11,622	-11,678	1378	flexuosum	57	0.10	FALSE	FALSE	compactum_flexuosum
571	compactum_tenellum_lindbergii	compactum	0	2.37	0.72	0.28	0.00	0.00	-14,404	-14,538	1526	compactum	134	0.14	FALSE	TRUE	tenellum_lindbergii
572	compactum_tenellum_lindbergii	tenellum	0	3.82	0.87	0.13	0.00	0.00	-9,603	-9,667	1027	compactum	63	0.04	FALSE	TRUE	compactum_lindbergii
573	compactum_tenellum_lindbergii	lindbergii	0	4.89	0.90	0.10	0.00	0.00	-6,460	-6,461	642	compactum	1	0.02	FALSE	TRUE	compactum_tenellum
574	compactum_tenellum_riparium	compactum	0	2.00	0.46	0.54	0.00	0.00	-19,269	-19,163	2133	compactum	-106	0.36	TRUE	TRUE	tenellum_riparium
575	compactum_tenellum_riparium	tenellum	0	3.62	0.85	0.15	0.00	0.00	-5,600	-5,648	608	compactum	48	0.03	FALSE	TRUE	compactum_riparium
576	**compactum_tenellum_riparium**	**riparium**	**0**	**6.63**	**0.93**	**0.07**	**0.00**	**0.00**	**-4,484**	**-4,446**	**454**	**compactum**	**-38**	**0.01**	**TRUE**	**TRUE**	**compactum_tenellum**
577	compactum_tenellum_squarrosum	compactum	0	2.86	0.83	0.17	0.00	0.00	-10,907	-11,023	1128	tenellum	116	0.06	FALSE	TRUE	tenellum_squarrosum
578	compactum_tenellum_squarrosum	tenellum	0	3.75	0.86	0.14	0.00	0.00	-11,083	-11,157	1187	tenellum	74	0.05	FALSE	TRUE	compactum_squarrosum
579	compactum_tenellum_squarrosum	squarrosum	0	4.39	0.90	0.10	0.00	0.00	-8,781	-8,816	880	tenellum	35	0.03	FALSE	TRUE	compactum_tenellum
580	compactum_tenellum_platyphyllum	compactum	0	4.87	0.91	0.09	0.00	0.00	-6,589	-6,595	679	tenellum	6	0.02	FALSE	TRUE	tenellum_platyphyllum
581	compactum_tenellum_platyphyllum	tenellum	0	3.69	0.84	0.16	0.00	0.00	-10,419	-10,493	1130	tenellum	74	0.06	FALSE	FALSE	compactum_platyphyllum
582	compactum_tenellum_platyphyllum	platyphyllum	0	3.73	0.75	0.25	0.00	0.01	-11,684	-11,743	1386	tenellum	59	0.11	FALSE	FALSE	compactum_tenellum
583	compactum_lindbergii_riparium	compactum	0	2.47	0.73	0.27	0.00	0.00	-14,939	-15,091	1572	compactum	152	0.13	FALSE	TRUE	lindbergii_riparium
584	compactum_lindbergii_riparium	lindbergii	0	5.15	0.92	0.08	0.00	0.00	-6,701	-6,706	662	compactum	5	0.02	FALSE	TRUE	compactum_riparium
585	compactum_lindbergii_riparium	riparium	0	3.53	0.88	0.12	0.00	0.00	-9,431	-9,509	961	compactum	78	0.04	FALSE	TRUE	compactum_lindbergii
586	compactum_lindbergii_squarrosum	compactum	0	3.78	0.87	0.13	0.00	0.00	-11,329	-11,403	1158	lindbergii	74	0.05	FALSE	FALSE	lindbergii_squarrosum
587	compactum_lindbergii_squarrosum	lindbergii	0	2.81	0.85	0.15	0.00	0.00	-10,232	-10,333	1020	lindbergii	100	0.05	FALSE	FALSE	compactum_squarrosum
588	compactum_lindbergii_squarrosum	squarrosum	0	4.84	0.91	0.09	0.00	0.00	-10,235	-10,244	1017	lindbergii	9	0.03	FALSE	TRUE	compactum_lindbergii
589	compactum_lindbergii_platyphyllum	compactum	0	4.91	0.91	0.09	0.00	0.00	-7,464	-7,470	755	lindbergii	6	0.02	FALSE	TRUE	lindbergii_platyphyllum
590	compactum_lindbergii_platyphyllum	lindbergii	0	3.10	0.85	0.15	0.00	0.00	-9,506	-9,601	960	lindbergii	96	0.04	FALSE	FALSE	compactum_platyphyllum
591	compactum_lindbergii_platyphyllum	platyphyllum	0	3.84	0.77	0.23	0.00	0.01	-12,576	-12,635	1480	lindbergii	59	0.11	FALSE	FALSE	compactum_lindbergii
592	compactum_riparium_squarrosum	compactum	0	3.02	0.84	0.16	0.00	0.00	-11,402	-11,516	1171	riparium	114	0.06	FALSE	FALSE	riparium_squarrosum
593	compactum_riparium_squarrosum	riparium	0	2.99	0.82	0.18	0.00	0.00	-10,823	-10,935	1115	riparium	112	0.06	FALSE	FALSE	compactum_squarrosum
594	compactum_riparium_squarrosum	squarrosum	0	4.86	0.91	0.09	0.00	0.00	-9,177	-9,191	909	riparium	14	0.03	FALSE	TRUE	compactum_riparium
595	compactum_riparium_platyphyllum	compactum	0	4.66	0.91	0.09	0.00	0.00	-7,060	-7,074	727	riparium	14	0.02	FALSE	TRUE	riparium_platyphyllum
596	compactum_riparium_platyphyllum	riparium	0	2.66	0.79	0.21	0.00	0.00	-10,335	-10,449	1075	riparium	113	0.07	FALSE	FALSE	compactum_platyphyllum
597	compactum_riparium_platyphyllum	platyphyllum	0	3.83	0.77	0.23	0.00	0.01	-11,775	-11,830	1393	riparium	55	0.10	FALSE	FALSE	compactum_riparium
598	compactum_squarrosum_platyphyllum	compactum	0	3.76	0.86	0.14	0.00	0.00	-9,265	-9,335	953	compactum	70	0.04	FALSE	FALSE	squarrosum_platyphyllum
599	compactum_squarrosum_platyphyllum	squarrosum	0	5.28	0.91	0.09	0.00	0.00	-8,266	-8,264	822	compactum	-2	0.02	FALSE	TRUE	compactum_platyphyllum
600	compactum_squarrosum_platyphyllum	platyphyllum	0	4.04	0.79	0.21	0.00	0.01	-12,142	-12,180	1420	compactum	38	0.09	FALSE	FALSE	compactum_squarrosum
601	flexuosum_tenellum_lindbergii	flexuosum	0	2.88	0.81	0.19	0.00	0.00	-1,937	-1,966	212	lindbergii	29	0.01	FALSE	TRUE	tenellum_lindbergii
602	flexuosum_tenellum_lindbergii	tenellum	0	4.66	0.77	0.23	0.00	0.00	-1,566	-1,565	168	lindbergii	-1	0.01	FALSE	TRUE	flexuosum_lindbergii
603	flexuosum_tenellum_lindbergii	lindbergii	0	1.91	0.19	0.81	0.00	0.01	-23,847	-22,843	2815	lindbergii	-1004	0.71	TRUE	TRUE	flexuosum_tenellum
604	flexuosum_tenellum_riparium	flexuosum	0	4.35	0.88	0.12	0.00	0.00	-2,465	-2,485	267	riparium	20	0.01	FALSE	TRUE	tenellum_riparium
605	flexuosum_tenellum_riparium	tenellum	0	5.17	0.86	0.14	0.00	0.00	-2,009	-2,008	212	riparium	-1	0.01	FALSE	TRUE	flexuosum_riparium
606	flexuosum_tenellum_riparium	riparium	0	1.79	0.28	0.72	0.00	0.01	-23,842	-23,260	2716	riparium	-581	0.61	TRUE	TRUE	flexuosum_tenellum
607	flexuosum_tenellum_squarrosum	flexuosum	0	4.91	0.89	0.11	0.00	0.00	-1,802	-1,807	198	squarrosum	6	0.01	FALSE	TRUE	tenellum_squarrosum
608	flexuosum_tenellum_squarrosum	tenellum	0	4.85	0.83	0.17	0.00	0.00	-1,428	-1,431	155	squarrosum	3	0.01	FALSE	TRUE	flexuosum_squarrosum
609	flexuosum_tenellum_squarrosum	squarrosum	0	1.95	0.18	0.82	0.00	0.01	-23,533	-22,434	2842	squarrosum	-1099	0.73	TRUE	TRUE	flexuosum_tenellum
610	flexuosum_tenellum_platyphyllum	flexuosum	0	4.50	0.87	0.13	0.00	0.00	-1,546	-1,557	171	platyphyllum	10	0.01	FALSE	TRUE	tenellum_platyphyllum
611	flexuosum_tenellum_platyphyllum	tenellum	0	4.47	0.83	0.17	0.00	0.00	-1,252	-1,261	142	platyphyllum	9	0.01	FALSE	TRUE	flexuosum_platyphyllum
612	flexuosum_tenellum_platyphyllum	platyphyllum	0	1.47	0.30	0.70	0.01	0.01	-21,832	-21,264	2882	platyphyllum	-567	0.63	TRUE	TRUE	flexuosum_tenellum
613	flexuosum_lindbergii_riparium	flexuosum	0	3.76	0.82	0.18	0.00	0.00	-7,458	-7,505	792	lindbergii	47	0.04	FALSE	TRUE	lindbergii_riparium
614	flexuosum_lindbergii_riparium	lindbergii	0	2.13	0.62	0.38	0.00	0.00	-16,780	-16,890	1781	lindbergii	110	0.21	FALSE	TRUE	flexuosum_riparium
615	flexuosum_lindbergii_riparium	riparium	0	5.09	0.91	0.09	0.00	0.00	-6,248	-6,246	622	lindbergii	-2	0.02	FALSE	TRUE	flexuosum_lindbergii
616	flexuosum_lindbergii_squarrosum	flexuosum	0	4.03	0.83	0.17	0.00	0.00	-9,749	-9,799	1045	squarrosum	49	0.06	FALSE	TRUE	lindbergii_squarrosum
617	flexuosum_lindbergii_squarrosum	lindbergii	0	4.48	0.89	0.11	0.00	0.00	-7,613	-7,643	756	squarrosum	29	0.03	FALSE	TRUE	flexuosum_squarrosum
618	flexuosum_lindbergii_squarrosum	squarrosum	0	2.82	0.78	0.22	0.00	0.00	-13,340	-13,478	1394	squarrosum	138	0.10	FALSE	TRUE	flexuosum_lindbergii
619	flexuosum_lindbergii_platyphyllum	flexuosum	0	3.91	0.81	0.19	0.00	0.00	-8,133	-8,172	876	platyphyllum	38	0.05	FALSE	TRUE	lindbergii_platyphyllum
620	**flexuosum_lindbergii_platyphyllum**	**lindbergii**	**0**	**6.10**	**0.93**	**0.07**	**0.00**	**0.00**	**-4,948**	**-4,926**	**500**	**platyphyllum**	**-22**	**0.01**	**TRUE**	**TRUE**	**flexuosum_platyphyllum**
621	flexuosum_lindbergii_platyphyllum	platyphyllum	0	3.81	0.81	0.19	0.00	0.01	-15,249	-15,330	1819	platyphyllum	82	0.11	FALSE	TRUE	flexuosum_lindbergii
622	flexuosum_riparium_squarrosum	flexuosum	0	4.08	0.82	0.18	0.00	0.00	-6,446	-6,477	691	squarrosum	32	0.04	FALSE	TRUE	riparium_squarrosum
623	**flexuosum_riparium_squarrosum**	**riparium**	**0**	**7.54**	**0.94**	**0.06**	**0.00**	**0.00**	**-4,775**	**-4,721**	**474**	**squarrosum**	**-54**	**0.01**	**TRUE**	**TRUE**	**flexuosum_squarrosum**
624	flexuosum_riparium_squarrosum	squarrosum	0	2.10	0.54	0.46	0.00	0.00	-18,565	-18,568	2030	squarrosum	3	0.29	FALSE	TRUE	flexuosum_riparium
625	flexuosum_riparium_platyphyllum	flexuosum	0	4.12	0.78	0.22	0.00	0.00	-5,252	-5,268	575	platyphyllum	16	0.04	FALSE	TRUE	riparium_platyphyllum
626	**flexuosum_riparium_platyphyllum**	**riparium**	**0**	**6.79**	**0.92**	**0.08**	**0.00**	**0.00**	**-3,360**	**-3,324**	**347**	**platyphyllum**	**-36**	**0.01**	**TRUE**	**TRUE**	**flexuosum_platyphyllum**
627	flexuosum_riparium_platyphyllum	platyphyllum	0	3.09	0.77	0.23	0.00	0.01	-18,456	-18,648	2273	platyphyllum	192	0.16	FALSE	TRUE	flexuosum_riparium
628	flexuosum_squarrosum_platyphyllum	flexuosum	0	3.49	0.81	0.19	0.00	0.00	-10,296	-10,376	1131	flexuosum	81	0.07	FALSE	FALSE	squarrosum_platyphyllum
629	**flexuosum_squarrosum_platyphyllum**	**squarrosum**	**0**	**6.26**	**0.94**	**0.06**	**0.00**	**0.00**	**-5,809**	**-5,779**	**582**	**flexuosum**	**-30**	**0.01**	**TRUE**	**TRUE**	**flexuosum_platyphyllum**
630	flexuosum_squarrosum_platyphyllum	platyphyllum	0	3.90	0.79	0.21	0.00	0.01	-12,551	-12,606	1482	flexuosum	55	0.10	FALSE	FALSE	flexuosum_squarrosum
631	tenellum_lindbergii_riparium	tenellum	0	3.95	0.86	0.14	0.00	0.00	-7,206	-7,255	762	lindbergii	49	0.03	FALSE	TRUE	lindbergii_riparium
632	tenellum_lindbergii_riparium	lindbergii	0	2.15	0.61	0.39	0.00	0.00	-16,889	-17,000	1796	lindbergii	111	0.22	FALSE	TRUE	tenellum_riparium
633	tenellum_lindbergii_riparium	riparium	0	5.07	0.91	0.09	0.00	0.00	-6,414	-6,412	637	lindbergii	-1	0.02	FALSE	TRUE	tenellum_lindbergii
634	tenellum_lindbergii_squarrosum	tenellum	0	3.59	0.85	0.15	0.00	0.00	-9,602	-9,681	1028	squarrosum	79	0.05	FALSE	TRUE	lindbergii_squarrosum
635	tenellum_lindbergii_squarrosum	lindbergii	0	5.03	0.92	0.08	0.00	0.00	-7,663	-7,670	763	squarrosum	7	0.02	FALSE	TRUE	tenellum_squarrosum
636	tenellum_lindbergii_squarrosum	squarrosum	0	2.83	0.78	0.22	0.00	0.00	-13,432	-13,566	1404	squarrosum	133	0.10	FALSE	TRUE	tenellum_lindbergii
637	tenellum_lindbergii_platyphyllum	tenellum	0	3.78	0.85	0.15	0.00	0.00	-8,038	-8,093	865	platyphyllum	55	0.04	FALSE	TRUE	lindbergii_platyphyllum
638	**tenellum_lindbergii_platyphyllum**	**lindbergii**	**0**	**5.67**	**0.90**	**0.10**	**0.00**	**0.00**	**-5,031**	**-5,009**	**505**	**platyphyllum**	**-22**	**0.02**	**TRUE**	**TRUE**	**tenellum_platyphyllum**
639	tenellum_lindbergii_platyphyllum	platyphyllum	0	3.79	0.81	0.19	0.00	0.01	-15,278	-15,360	1825	platyphyllum	83	0.11	FALSE	TRUE	tenellum_lindbergii
640	tenellum_riparium_squarrosum	tenellum	0	3.46	0.83	0.17	0.00	0.00	-6,141	-6,200	660	squarrosum	58	0.03	FALSE	TRUE	riparium_squarrosum
641	**tenellum_riparium_squarrosum**	**riparium**	**0**	**6.94**	**0.94**	**0.06**	**0.00**	**0.00**	**-4,901**	**-4,860**	**490**	**squarrosum**	**-41**	**0.01**	**TRUE**	**TRUE**	**tenellum_squarrosum**
642	tenellum_riparium_squarrosum	squarrosum	0	2.08	0.53	0.47	0.00	0.00	-18,670	-18,670	2045	squarrosum	0	0.30	FALSE	TRUE	tenellum_riparium
643	tenellum_riparium_platyphyllum	tenellum	0	3.29	0.81	0.19	0.00	0.00	-5,005	-5,060	551	platyphyllum	55	0.03	FALSE	TRUE	riparium_platyphyllum
644	**tenellum_riparium_platyphyllum**	**riparium**	**0**	**7.21**	**0.92**	**0.08**	**0.00**	**0.00**	**-3,509**	**-3,461**	**355**	**platyphyllum**	**-48**	**0.01**	**TRUE**	**TRUE**	**tenellum_platyphyllum**
645	tenellum_riparium_platyphyllum	platyphyllum	0	3.10	0.77	0.23	0.00	0.01	-18,569	-18,767	2289	platyphyllum	197	0.17	FALSE	TRUE	tenellum_riparium
646	tenellum_squarrosum_platyphyllum	tenellum	0	3.32	0.83	0.17	0.00	0.00	-10,345	-10,436	1131	tenellum	91	0.06	FALSE	FALSE	squarrosum_platyphyllum
647	**tenellum_squarrosum_platyphyllum**	**squarrosum**	**0**	**5.96**	**0.92**	**0.08**	**0.00**	**0.00**	**-5,795**	**-5,767**	**577**	**tenellum**	**-27**	**0.01**	**TRUE**	**TRUE**	**tenellum_platyphyllum**
648	tenellum_squarrosum_platyphyllum	platyphyllum	0	3.87	0.79	0.21	0.00	0.01	-12,569	-12,626	1487	tenellum	58	0.10	FALSE	FALSE	tenellum_squarrosum
649	lindbergii_riparium_squarrosum	lindbergii	0	5.24	0.92	0.08	0.00	0.00	-8,180	-8,175	806	squarrosum	-4	0.02	FALSE	TRUE	riparium_squarrosum
650	lindbergii_riparium_squarrosum	riparium	0	3.43	0.86	0.14	0.00	0.00	-9,261	-9,343	945	squarrosum	82	0.04	FALSE	TRUE	lindbergii_squarrosum
651	lindbergii_riparium_squarrosum	squarrosum	0	2.91	0.79	0.21	0.00	0.00	-13,937	-14,075	1444	squarrosum	138	0.09	FALSE	TRUE	lindbergii_riparium
652	lindbergii_riparium_platyphyllum	lindbergii	0	5.39	0.92	0.08	0.00	0.00	-5,460	-5,455	550	platyphyllum	-5	0.01	FALSE	TRUE	riparium_platyphyllum
653	lindbergii_riparium_platyphyllum	riparium	0	3.11	0.85	0.15	0.00	0.00	-7,514	-7,590	768	platyphyllum	75	0.04	FALSE	TRUE	lindbergii_platyphyllum
654	lindbergii_riparium_platyphyllum	platyphyllum	0	4.01	0.82	0.18	0.00	0.01	-15,859	-15,929	1877	platyphyllum	70	0.11	FALSE	TRUE	lindbergii_riparium
655	lindbergii_squarrosum_platyphyllum	lindbergii	0	2.83	0.81	0.19	0.00	0.00	-9,558	-9,659	980	lindbergii	101	0.06	FALSE	FALSE	squarrosum_platyphyllum
656	**lindbergii_squarrosum_platyphyllum**	**squarrosum**	**0**	**5.66**	**0.92**	**0.08**	**0.00**	**0.00**	**-6,746**	**-6,725**	**666**	**lindbergii**	**-21**	**0.02**	**TRUE**	**TRUE**	**lindbergii_platyphyllum**
657	lindbergii_squarrosum_platyphyllum	platyphyllum	0	4.09	0.80	0.20	0.00	0.01	-13,222	-13,259	1549	lindbergii	36	0.10	FALSE	FALSE	lindbergii_squarrosum
658	riparium_squarrosum_platyphyllum	riparium	0	2.89	0.77	0.23	0.00	0.00	-10,209	-10,306	1067	riparium	96	0.08	FALSE	FALSE	squarrosum_platyphyllum
659	**riparium_squarrosum_platyphyllum**	**squarrosum**	**0**	**6.06**	**0.93**	**0.07**	**0.00**	**0.00**	**-6,270**	**-6,241**	**621**	**riparium**	**-28**	**0.01**	**TRUE**	**TRUE**	**riparium_platyphyllum**
660	riparium_squarrosum_platyphyllum	platyphyllum	0	3.84	0.79	0.21	0.00	0.01	-12,792	-12,852	1507	riparium	60	0.10	FALSE	FALSE	riparium_squarrosum

Table S10. Average total introgression proportion per species pair in the QuIBL analysis

Pair	Mean total non-ILS proportion
capillifolium,flexuosum	0.011
capillifolium,riparium	0.013
capillifolium,tenellum	0.012
compactum,flexuosum	0.014
compactum,lindbergii	0.024
compactum,squarrosum	0.022
compactum,tenellum	0.009
divinum,flexuosum	0.013
divinum,fuscum	0.015
divinum,tenellum	0.009
fimbriatum,flexuosum	0.012
fimbriatum,riparium	0.015
fimbriatum,tenellum	0.012
flexuosum,platyphyllum	0.010
flexuosum,squarrosum	0.009
fuscum,flexuosum	0.014
fuscum,lindbergii	0.019
platyphyllum,fuscum	0.018
fuscum,riparium	0.016
fuscum,tenellum	0.014
lindbergii,platyphyllum	0.017
riparium,platyphyllum	0.014
subnitens,flexuosum	0.012
subnitens,lindbergii	0.019
subnitens,tenellum	0.011
tenellum,platyphyllum	0.013
tenellum,squarrosum	0.010

Table S11. Summary statistics for trees used in the QuIBL analysis

Parameter	Mean	Median	SD	SE	Minimum	Maximum	Upper Quantile 75%	Lower Quartile 25%	Coefficient of Variation	Sample size
Number of distinct site patterns	526	492	191	3	152	1,058	671	364	0.36	3195
Number of parsimony informative sites	36	35	10	0	10	83	42	29	0.28	3195
Number of singleton sites	131	131	22	0	32	203	145	118	0.17	3195
Number of constant sites	1,833	1,833	27	0	1,743	1,953	1,849	1,816	0.01	3195
cAIC	7,944	8,056	582	10	2,780	9,397	8,293	7,744	0.07	3195
AIC	7,943	8,055	582	10	2,779	9,396	8,292	7,743	0.07	3195
BIC	8,113	8,245	655	12	1,029	9,592	8,487	7,929	0.08	3195
Mean node bootstrap support	61	62	9	0	20	87	68	56	0.14	3195

Table S12. Summary of D_{FOIL} analysis per 5-taxon phylogeny.

Proportion of introgressed windows is calculated as the ratio of the number of windows with significant evidence (p<0.001) for introgression to the total number of windows with data

Columns 1-12:

1 Proportion of windows supporting P1→P3, 2 Proportion of windows supporting P3→P1, 3 Proportion of windows supporting P1→P4, 4 Proportion of windows supporting P4→P1, 5 Proportion of windows supporting P2→P3, 6 Proportion of windows supporting P3→P2, 7 Proportion of windows supporting P2→P4, 8 Proportion of windows supporting P4→P2, 9 Proportion of windows supporting P1,2→P3, 10 Proportion of windows supporting P3→P1,2, 11 Proportion of windows supporting P1,2→P4, 12 Proportion of windows supporting P4→P1,2

5-taxon phylogeny (P1,P2,P3,P4,O)	1	2	3	4	5	6	7	8	9	10	11	12	# of windows with no data	# windows supporting no introgression	Total # of windows	P1	P2	P3	P4
capillifolium,fimbriatum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0007	NA	0.0082	NA	1346	1331	2689	capillifolium	fimbriatum	divinum	compactum
capillifolium,fimbriatum,flexuosum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0397	NA	NA	NA	1304	1329	2688	capillifolium	fimbriatum	flexuosum	lindbergii
capillifolium,fimbriatum,flexuosum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.1157	NA	NA	NA	1303	1223	2686	capillifolium	fimbriatum	flexuosum	riparium
capillifolium,fimbriatum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0059	NA	1321	1358	2687	capillifolium	fimbriatum	riparium	lindbergii
capillifolium,fimbriatum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0014	NA	NA	NA	1306	1380	2688	capillifolium	fimbriatum	tenellum	lindbergii
capillifolium,fimbriatum,tenellum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0094	NA	NA	NA	1303	1372	2688	capillifolium	fimbriatum	tenellum	riparium
capillifolium,platyphyllum,divinum,compactum,sericeum	NA	NA	NA	0.0006	NA	NA	NA	NA	NA	NA	0.0049	NA	1063	1609	2681	capillifolium	platyphyllum	divinum	compactum
capillifolium,platyphyllum,flexuosum,lindbergii,sericeum	0.0012	NA	NA	NA	NA	NA	NA	NA	0.0279	NA	NA	NA	1031	1602	2681	capillifolium	platyphyllum	flexuosum	lindbergii
capillifolium,platyphyllum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0054	NA	1015	1654	2679	capillifolium	platyphyllum	riparium	lindbergii
capillifolium,platyphyllum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0036	NA	NA	NA	1021	1652	2679	capillifolium	platyphyllum	tenellum	lindbergii
capillifolium,squarrosum,divinum,compactum,sericeum	NA	NA	0.0006	0.0006	NA	NA	NA	NA	0.0006	NA	0.0035	NA	973	1705	2687	capillifolium	squarrosum	divinum	compactum
capillifolium,squarrosum,flexuosum,lindbergii,sericeum	0.0017	0.0023	NA	NA	NA	NA	NA	NA	0.0217	NA	NA	NA	933	1703	2681	capillifolium	squarrosum	flexuosum	lindbergii
capillifolium,squarrosum,riparium,lindbergii,sericeum	NA	NA	NA	0.0005	NA	NA	NA	NA	NA	NA	0.0016	NA	853	1829	2686	capillifolium	squarrosum	riparium	lindbergii
capillifolium,squarrosum,tenellum,lindbergii,sericeum	0.0006	0.0006	NA	NA	NA	NA	NA	NA	0.0011	NA	NA	NA	879	1797	2680	capillifolium	squarrosum	tenellum	lindbergii
capillifolium,subnitens,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0076	NA	1643	1044	2695	capillifolium	subnitens	divinum	compactum
capillifolium,subnitens,flexuosum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0485	NA	NA	NA	1592	1040	2685	capillifolium	subnitens	flexuosum	lindbergii
capillifolium,subnitens,flexuosum,riparium,sericeum	0.0009	NA	NA	NA	NA	NA	NA	NA	0.1192	NA	NA	NA	1580	974	2687	capillifolium	subnitens	flexuosum	riparium
capillifolium,subnitens,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0009	NA	0.0056	NA	1627	1055	2689	capillifolium	subnitens	riparium	lindbergii
capillifolium,subnitens,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0037	NA	NA	NA	1608	1076	2688	capillifolium	subnitens	tenellum	lindbergii
capillifolium,subnitens,tenellum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0128	NA	NA	NA	1598	1077	2689	capillifolium	subnitens	tenellum	riparium
fimbriatum,platyphyllum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0060	NA	1013	1660	2684	fimbriatum	platyphyllum	divinum	compactum
fimbriatum,platyphyllum,flexuosum,lindbergii,sericeum	0.0006	NA	NA	NA	NA	NA	NA	NA	0.0274	NA	NA	NA	977	1667	2692	fimbriatum	platyphyllum	flexuosum	lindbergii
fimbriatum,platyphyllum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0052	NA	939	1737	2685	fimbriatum	platyphyllum	riparium	lindbergii
fimbriatum,platyphyllum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0017	NA	NA	NA	953	1733	2689	fimbriatum	platyphyllum	tenellum	lindbergii
fimbriatum,squarrosum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0046	NA	938	1746	2693	fimbriatum	squarrosum	divinum	compactum
fimbriatum,squarrosum,flexuosum,lindbergii,sericeum	0.0006	0.0006	NA	NA	NA	NA	NA	NA	0.0246	NA	NA	NA	907	1739	2692	fimbriatum	squarrosum	flexuosum	lindbergii
fimbriatum,squarrosum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0037	NA	820	1866	2693	fimbriatum	squarrosum	riparium	lindbergii
fimbriatum,squarrosum,tenellum,lindbergii,sericeum	0.0005	NA	NA	NA	NA	NA	NA	NA	0.0011	NA	NA	NA	845	1846	2694	fimbriatum	squarrosum	tenellum	lindbergii
flexuosum,tenellum,capillifolium,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0076	NA	NA	NA	1505	1169	2683	flexuosum	tenellum	capillifolium	fimbriatum
flexuosum,tenellum,capillifolium,platyphyllum,sericeum	0.0008	NA	NA	NA	NA	NA	NA	NA	0.0360	NA	NA	NA	1460	1176	2681	flexuosum	tenellum	capillifolium	platyphyllum
flexuosum,tenellum,capillifolium,squarrosum,sericeum	0.0025	NA	NA	NA	NA	NA	NA	NA	0.1191	NA	NA	NA	1467	1069	2684	flexuosum	tenellum	capillifolium	squarrosum
flexuosum,tenellum,compactum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0016	NA	0.0066	NA	1466	1207	2683	flexuosum	tenellum	compactum	capillifolium
flexuosum,tenellum,compactum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0096	NA	0.0016	NA	1431	1239	2684	flexuosum	tenellum	compactum	fimbriatum
flexuosum,tenellum,compactum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0008	NA	0.0113	NA	1452	1223	2690	flexuosum	tenellum	compactum	fuscum
flexuosum,tenellum,compactum,platyphyllum,sericeum	0.0008	NA	NA	NA	NA	NA	NA	NA	0.0304	NA	0.0008	NA	1434	1212	2686	flexuosum	tenellum	compactum	platyphyllum
flexuosum,tenellum,compactum,squarrosum,sericeum	0.0024	0.0008	NA	NA	NA	NA	NA	NA	0.1033	NA	NA	NA	1457	1099	2687	flexuosum	tenellum	compactum	squarrosum
flexuosum,tenellum,compactum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0047	NA	0.0016	NA	1418	1260	2686	flexuosum	tenellum	compactum	subnitens
flexuosum,tenellum,divinum,capillifolium,sericeum	NA	NA	NA	0.0008	NA	NA	NA	NA	NA	NA	0.0049	NA	1454	1224	2685	flexuosum	tenellum	divinum	capillifolium
flexuosum,tenellum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0008	NA	0.0056	NA	1443	1238	2689	flexuosum	tenellum	divinum	compactum
flexuosum,tenellum,divinum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1439	1251	2690	flexuosum	tenellum	divinum	fimbriatum

flexuosum,tenellum,divinum,fuscum,sericeum	NA	NA	0.0008	NA	NA	NA	NA	NA	NA	NA	0.0119	NA	1436	1243	2695	flexuosum	tenellum	divinum	fuscum
flexuosum,tenellum,divinum,platyphyllum,sericeum	0.0008	NA	NA	NA	NA	NA	NA	NA	0.0088	NA	0.0008	NA	1433	1244	2690	flexuosum	tenellum	divinum	platyphyllum
flexuosum,tenellum,divinum,squarrosum,sericeum	0.0024	NA	NA	NA	NA	NA	NA	NA	0.0482	NA	NA	NA	1448	1181	2692	flexuosum	tenellum	divinum	squarrosum
flexuosum,tenellum,divinum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0024	NA	1419	1265	2687	flexuosum	tenellum	divinum	subnitens
flexuosum,tenellum,fimbriatum,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0056	NA	NA	NA	1438	1244	2689	flexuosum	tenellum	fimbriatum	platyphyllum
flexuosum,tenellum,fimbriatum,squarrosum,sericeum	0.0016	NA	NA	NA	NA	NA	NA	NA	0.0303	NA	NA	NA	1437	1213	2690	flexuosum	tenellum	fimbriatum	squarrosum
flexuosum,tenellum,fuscum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2124	567	2691	flexuosum	tenellum	fuscum	capillifolium
flexuosum,tenellum,fuscum,fimbriatum,sericeum	NA	0.0008	NA	NA	NA	NA	NA	NA	0.0239	NA	NA	NA	1482	1181	2693	flexuosum	tenellum	fuscum	fimbriatum
flexuosum,tenellum,fuscum,platyphyllum,sericeum	0.0008	0.0016	NA	NA	NA	NA	NA	NA	0.0701	NA	NA	NA	1437	1164	2692	flexuosum	tenellum	fuscum	platyphyllum
flexuosum,tenellum,fuscum,squarrosum,sericeum	0.0024	0.0016	NA	NA	NA	NA	NA	NA	0.1949	NA	NA	NA	1442	1003	2694	flexuosum	tenellum	fuscum	squarrosum
flexuosum,tenellum,platyphyllum,squarrosum,sericeum	0.0008	NA	NA	NA	NA	NA	NA	NA	0.0040	NA	NA	NA	1441	1239	2686	flexuosum	tenellum	platyphyllum	squarrosum
flexuosum,tenellum,subnitens,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0049	NA	1656	1022	2683	flexuosum	tenellum	subnitens	capillifolium
flexuosum,tenellum,subnitens,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0008	NA	0.0016	NA	1436	1251	2690	flexuosum	tenellum	subnitens	fimbriatum
flexuosum,tenellum,subnitens,fuscum,sericeum	NA	NA	NA	0.0010	NA	NA	NA	NA	NA	NA	0.0095	NA	1648	1037	2696	flexuosum	tenellum	subnitens	fuscum
flexuosum,tenellum,subnitens,platyphyllum,sericeum	NA	0.0008	NA	NA	NA	NA	NA	NA	0.0071	NA	NA	NA	1426	1251	2687	flexuosum	tenellum	subnitens	platyphyllum
flexuosum,tenellum,subnitens,squarrosum,sericeum	0.0016	0.0008	NA	NA	NA	NA	NA	NA	0.0397	NA	NA	NA	1428	1207	2688	flexuosum	tenellum	subnitens	squarrosum
fuscum,capillifolium,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0058	NA	2180	513	2696	fuscum	capillifolium	divinum	compactum
fuscum,capillifolium,flexuosum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0766	NA	NA	NA	2140	506	2688	fuscum	capillifolium	flexuosum	lindbergii
fuscum,capillifolium,flexuosum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.1646	NA	NA	NA	2130	472	2695	fuscum	capillifolium	flexuosum	riparium
fuscum,capillifolium,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0095	NA	2165	522	2692	fuscum	capillifolium	riparium	lindbergii
fuscum,capillifolium,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0037	NA	NA	NA	2154	535	2691	fuscum	capillifolium	tenellum	lindbergii
fuscum,capillifolium,tenellum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0165	NA	NA	NA	2151	536	2696	fuscum	capillifolium	tenellum	riparium
fuscum,fimbriatum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0007	NA	0.0082	NA	1356	1325	2693	fuscum	fimbriatum	divinum	compactum
fuscum,fimbriatum,flexuosum,lindbergii,sericeum	0.0014	NA	NA	NA	NA	NA	NA	NA	0.0432	NA	NA	NA	1309	1328	2699	fuscum	fimbriatum	flexuosum	lindbergii
fuscum,fimbriatum,flexuosum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.1204	NA	NA	NA	1290	1235	2694	fuscum	fimbriatum	flexuosum	riparium
fuscum,fimbriatum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0051	NA	1339	1353	2699	fuscum	fimbriatum	riparium	lindbergii
fuscum,fimbriatum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0015	NA	NA	NA	1318	1375	2695	fuscum	fimbriatum	tenellum	lindbergii
fuscum,fimbriatum,tenellum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0115	NA	NA	NA	1301	1381	2698	fuscum	fimbriatum	tenellum	riparium
fuscum,platyphyllum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0049	NA	1069	1610	2687	fuscum	platyphyllum	divinum	compactum
fuscum,platyphyllum,flexuosum,lindbergii,sericeum	0.0018	0.0024	NA	NA	NA	NA	NA	NA	0.0308	NA	NA	NA	1036	1600	2694	fuscum	platyphyllum	flexuosum	lindbergii
fuscum,platyphyllum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0054	NA	1027	1650	2687	fuscum	platyphyllum	riparium	lindbergii
fuscum,platyphyllum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0036	NA	NA	NA	1023	1662	2691	fuscum	platyphyllum	tenellum	lindbergii
fuscum,squarrosum,divinum,compactum,sericeum	NA	NA	0.0012	0.0012	NA	NA	NA	NA	NA	NA	0.0012	NA	966	1726	2698	fuscum	squarrosum	divinum	compactum
fuscum,squarrosum,flexuosum,lindbergii,sericeum	0.0011	0.0051	NA	NA	NA	NA	NA	NA	0.0204	NA	NA	NA	925	1720	2692	fuscum	squarrosum	flexuosum	lindbergii
fuscum,squarrosum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0016	NA	867	1826	2696	fuscum	squarrosum	riparium	lindbergii
fuscum,squarrosum,tenellum,lindbergii,sericeum	NA	0.0006	NA	NA	NA	NA	NA	NA	0.0006	NA	NA	NA	878	1812	2692	fuscum	squarrosum	tenellum	lindbergii
fuscum,subnitens,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0106	NA	1667	1022	2700	fuscum	subnitens	divinum	compactum
fuscum,subnitens,flexuosum,lindbergii,sericeum	0.0009	NA	NA	NA	NA	NA	NA	NA	0.0460	NA	NA	NA	1609	1037	2697	fuscum	subnitens	flexuosum	lindbergii
fuscum,subnitens,flexuosum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.1284	NA	NA	NA	1610	950	2700	fuscum	subnitens	flexuosum	riparium
fuscum,subnitens,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0009	NA	0.0066	NA	1646	1048	2702	fuscum	subnitens	riparium	lindbergii
fuscum,subnitens,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0065	NA	NA	NA	1610	1078	2695	fuscum	subnitens	tenellum	lindbergii
fuscum,subnitens,tenellum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0093	NA	NA	NA	1626	1064	2700	fuscum	subnitens	tenellum	riparium
lindbergii,flexuosum,compactum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0012	NA	0.0042	NA	1007	1664	2680	lindbergii	flexuosum	compactum	capillifolium
lindbergii,flexuosum,compactum,fimbriatum,sericeum	NA	NA	NA	NA	0.0006	NA	NA	NA	0.0052	NA	0.0012	NA	952	1722	2686	lindbergii	flexuosum	compactum	fimbriatum
lindbergii,flexuosum,compactum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	NA	0.0078	NA	1015	1661	2690	lindbergii	flexuosum	compactum	fuscum
lindbergii,flexuosum,compactum,platyphyllum,sericeum	NA	NA	NA	NA	0.0017	NA	NA	NA	0.0215	NA	0.0011	NA	920	1721	2684	lindbergii	flexuosum	compactum	platyphyllum
lindbergii,flexuosum,compactum,squarrosum,sericeum	NA	NA	NA	NA	0.0011	0.0006	NA	NA	0.0599	NA	NA	NA	903	1675	2688	lindbergii	flexuosum	compactum	squarrosum
lindbergii,flexuosum,compactum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	0.0006	0.0011	NA	0.0011	NA	944	1736	2685	lindbergii	flexuosum	compactum	subnitens
lindbergii,flexuosum,divinum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	NA	0.0071	NA	992	1678	2683	lindbergii	flexuosum	divinum	capillifolium
lindbergii,flexuosum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0029	NA	957	1721	2683	lindbergii	flexuosum	divinum	compactum
lindbergii,flexuosum,divinum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0011	NA	0.0006	NA	943	1746	2692	lindbergii	flexuosum	divinum	fimbriatum
lindbergii,flexuosum,divinum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	0.0006	NA	NA	NA	0.0088	NA	988	1691	2695	lindbergii	flexuosum	divinum	fuscum
lindbergii,flexuosum,divinum,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0056	NA	NA	NA	913	1765	2688	lindbergii	flexuosum	divinum	platyphyllum
lindbergii,flexuosum,divinum,squarrosum,sericeum	NA	NA	NA	NA	0.0011	0.0006	NA	NA	0.0290	NA	NA	NA	897	1737	2689	lindbergii	flexuosum	divinum	squarrosum
lindbergii,flexuosum,divinum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0006	NA	932	1756	2690	lindbergii	flexuosum	divinum	subnitens
lindbergii,riparium,compactum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0012	NA	0.0042	NA	999	1677	2685	lindbergii	riparium	compactum	capillifolium
lindbergii,riparium,compactum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0062	NA	0.0011	NA	921	1755	2689	lindbergii	riparium	compactum	fimbriatum

lindbergii,riparium,compactum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	NA	0.0006	0.0006	NA	0.0072	NA	1020	1660	2694	lindbergii	riparium	compactum	fuscum
lindbergii,riparium,compactum,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0248	NA	0.0011	NA	868	1766	2681	lindbergii	riparium	compactum	platyphyllum
lindbergii,riparium,compactum,squarrosum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0642	NA	NA	NA	818	1749	2687	lindbergii	riparium	compactum	squarrosum
lindbergii,riparium,compactum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0034	NA	0.0011	NA	917	1763	2688	lindbergii	riparium	compactum	subnitens
lindbergii,riparium,divinum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0052	NA	958	1719	2686	lindbergii	riparium	divinum	capillifolium
lindbergii,riparium,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0040	NA	931	1746	2684	lindbergii	riparium	divinum	compactum
lindbergii,riparium,divinum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0006	NA	883	1807	2692	lindbergii	riparium	divinum	fimbriatum
lindbergii,riparium,divinum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0081	NA	975	1706	2695	lindbergii	riparium	divinum	fuscum
lindbergii,riparium,divinum,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0076	NA	NA	NA	840	1829	2683	lindbergii	riparium	divinum	platyphyllum
lindbergii,riparium,divinum,squarrosum,sericeum	0.0005	NA	NA	NA	NA	NA	NA	NA	0.0255	NA	NA	NA	808	1836	2693	lindbergii	riparium	divinum	squarrosum
lindbergii,riparium,divinum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0006	NA	895	1799	2696	lindbergii	riparium	divinum	subnitens
lindbergii,tenellum,compactum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0012	NA	0.0041	NA	984	1690	2683	lindbergii	tenellum	compactum	capillifolium
lindbergii,tenellum,compactum,fimbriatum,sericeum	NA	NA	NA	NA	0.0006	NA	NA	NA	0.0045	NA	0.0011	NA	920	1757	2688	lindbergii	tenellum	compactum	fimbriatum
lindbergii,tenellum,compactum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0071	NA	1010	1671	2693	lindbergii	tenellum	compactum	fuscum
lindbergii,tenellum,compactum,platyphyllum,sericeum	NA	NA	NA	NA	0.0006	NA	NA	NA	0.0228	NA	0.0011	NA	880	1757	2681	lindbergii	tenellum	compactum	platyphyllum
lindbergii,tenellum,compactum,squarrosum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0656	NA	NA	NA	844	1723	2688	lindbergii	tenellum	compactum	squarrosum
lindbergii,tenellum,compactum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0028	NA	0.0011	NA	924	1758	2689	lindbergii	tenellum	compactum	subnitens
lindbergii,tenellum,divinum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0070	NA	968	1707	2687	lindbergii	tenellum	divinum	capillifolium
lindbergii,tenellum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0029	NA	937	1744	2686	lindbergii	tenellum	divinum	compactum
lindbergii,tenellum,divinum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	902	1790	2693	lindbergii	tenellum	divinum	fimbriatum
lindbergii,tenellum,divinum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0076	NA	978	1703	2694	lindbergii	tenellum	divinum	fuscum
lindbergii,tenellum,divinum,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0077	NA	NA	NA	856	1816	2686	lindbergii	tenellum	divinum	platyphyllum
lindbergii,tenellum,divinum,squarrosum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0286	NA	NA	NA	835	1803	2691	lindbergii	tenellum	divinum	squarrosum
lindbergii,tenellum,divinum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0006	NA	892	1795	2689	lindbergii	tenellum	divinum	subnitens
platyphyllum,squarrosum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0051	NA	933	1742	2684	platyphyllum	squarrosum	divinum	compactum
platyphyllum,squarrosum,flexuosum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0233	NA	NA	NA	885	1761	2688	platyphyllum	squarrosum	flexuosum	lindbergii
platyphyllum,squarrosum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0005	NA	0.0021	NA	780	1898	2683	platyphyllum	squarrosum	riparium	lindbergii
platyphyllum,squarrosum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0016	NA	NA	NA	812	1868	2683	platyphyllum	squarrosum	tenellum	lindbergii
riparium,flexuosum,capillifolium,platyphyllum,sericeum	NA	NA	NA	NA	0.0012	0.0006	NA	NA	0.0268	NA	NA	NA	1042	1594	2683	riparium	flexuosum	capillifolium	platyphyllum
riparium,flexuosum,capillifolium,squarrosum,sericeum	NA	NA	NA	NA	0.0040	0.0023	NA	NA	0.0713	NA	NA	NA	943	1605	2683	riparium	flexuosum	capillifolium	squarrosum
riparium,flexuosum,compactum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	0.0006	0.0012	NA	0.0061	NA	1032	1638	2683	riparium	flexuosum	compactum	capillifolium
riparium,flexuosum,compactum,fimbriatum,sericeum	NA	NA	NA	NA	0.0006	NA	NA	NA	0.0059	NA	0.0012	NA	985	1688	2686	riparium	flexuosum	compactum	fimbriatum
riparium,flexuosum,compactum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0006	NA	0.0096	NA	1031	1641	2690	riparium	flexuosum	compactum	fuscum
riparium,flexuosum,compactum,platyphyllum,sericeum	NA	NA	NA	NA	0.0017	0.0006	NA	NA	0.0202	NA	0.0006	NA	952	1694	2686	riparium	flexuosum	compactum	platyphyllum
riparium,flexuosum,compactum,squarrosum,sericeum	NA	NA	NA	NA	0.0040	0.0017	NA	NA	0.0600	NA	0.0006	NA	936	1635	2687	riparium	flexuosum	compactum	squarrosum
riparium,flexuosum,compactum,subnitens,sericeum	NA	NA	NA	NA	NA	0.0006	NA	NA	0.0047	NA	0.0006	NA	979	1699	2688	riparium	flexuosum	compactum	subnitens
riparium,flexuosum,divinum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0042	NA	1004	1675	2686	riparium	flexuosum	divinum	capillifolium
riparium,flexuosum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0041	NA	986	1692	2686	riparium	flexuosum	divinum	compactum
riparium,flexuosum,divinum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	959	1728	2687	riparium	flexuosum	divinum	fimbriatum
riparium,flexuosum,divinum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	0.0012	0.0006	NA	NA	0.0071	NA	1004	1676	2695	riparium	flexuosum	divinum	fuscum
riparium,flexuosum,divinum,platyphyllum,sericeum	NA	NA	NA	NA	0.0006	0.0006	NA	NA	0.0046	NA	NA	NA	935	1744	2689	riparium	flexuosum	divinum	platyphyllum
riparium,flexuosum,divinum,squarrosum,sericeum	NA	NA	NA	NA	0.0017	0.0006	NA	NA	0.0238	NA	0.0006	NA	930	1715	2692	riparium	flexuosum	divinum	squarrosum
riparium,flexuosum,divinum,subnitens,sericeum	NA	NA	NA	NA	NA	0.0006	NA	NA	0.0006	NA	0.0012	NA	952	1735	2691	riparium	flexuosum	divinum	subnitens
riparium,flexuosum,fimbriatum,platyphyllum,sericeum	NA	NA	NA	NA	0.0012	NA	NA	NA	0.0018	NA	NA	NA	989	1696	2690	riparium	flexuosum	fimbriatum	platyphyllum
riparium,flexuosum,fimbriatum,squarrosum,sericeum	NA	NA	NA	NA	0.0011	0.0006	NA	NA	0.0205	NA	NA	NA	930	1719	2688	riparium	flexuosum	fimbriatum	squarrosum
riparium,flexuosum,fuscum,platyphyllum,sericeum	NA	NA	NA	NA	0.0042	0.0054	NA	NA	0.0459	NA	NA	NA	1039	1562	2693	riparium	flexuosum	fuscum	platyphyllum
riparium,flexuosum,fuscum,squarrosum,sericeum	NA	NA	NA	NA	0.0057	0.0040	NA	NA	0.1232	NA	NA	NA	948	1513	2693	riparium	flexuosum	fuscum	squarrosum
riparium,flexuosum,platyphyllum,squarrosum,sericeum	NA	NA	NA	NA	0.0006	NA	NA	NA	0.0011	NA	0.0006	NA	915	1767	2686	riparium	flexuosum	platyphyllum	squarrosum
riparium,flexuosum,subnitens,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0058	NA	NA	NA	981	1702	2693	riparium	flexuosum	subnitens	platyphyllum
riparium,flexuosum,subnitens,squarrosum,sericeum	NA	NA	NA	NA	NA	0.0006	NA	NA	0.0228	NA	NA	NA	941	1710	2692	riparium	flexuosum	subnitens	squarrosum
riparium,tenellum,capillifolium,platyphyllum,sericeum	NA	NA	NA	NA	NA	0.0006	NA	NA	0.0263	NA	NA	NA	1007	1626	2678	riparium	tenellum	capillifolium	platyphyllum
riparium,tenellum,capillifolium,squarrosum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0812	NA	NA	NA	901	1640	2686	riparium	tenellum	capillifolium	squarrosum
riparium,tenellum,compactum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0018	NA	0.0053	NA	1000	1673	2685	riparium	tenellum	compactum	capillifolium
riparium,tenellum,compactum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0074	NA	0.0011	NA	940	1732	2687	riparium	tenellum	compactum	fimbriatum
riparium,tenellum,compactum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0071	NA	1014	1666	2693	riparium	tenellum	compactum	fuscum
riparium,tenellum,compactum,platyphyllum,sericeum	NA	NA	NA	NA	0.0006	NA	NA	NA	0.0223	NA	0.0011	NA	887	1749	2679	riparium	tenellum	compactum	platyphyllum
riparium,tenellum,compactum,squarrosum,sericeum	NA	NA	NA	NA	0.0006	NA	NA	NA	0.0700	NA	0.0006	NA	876	1684	2689	riparium	tenellum	compactum	squarrosum

riparium,tenellum,compactum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0051	NA	0.0006	NA	924	1752	2686	riparium	tenellum	compactum	subnitens
riparium,tenellum,divinum,capillifolium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0041	NA	980	1705	2692	riparium	tenellum	divinum	capillifolium
riparium,tenellum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0046	NA	954	1726	2689	riparium	tenellum	divinum	compactum
riparium,tenellum,divinum,fimbriatum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0011	NA	909	1781	2692	riparium	tenellum	divinum	fimbriatum
riparium,tenellum,divinum,fuscum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0133	NA	973	1702	2698	riparium	tenellum	divinum	fuscum
riparium,tenellum,divinum,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0077	NA	NA	NA	871	1799	2684	riparium	tenellum	divinum	platyphyllum
riparium,tenellum,divinum,squarrosum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0291	NA	NA	NA	874	1768	2695	riparium	tenellum	divinum	squarrosum
riparium,tenellum,divinum,subnitens,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0011	NA	902	1789	2694	riparium	tenellum	divinum	subnitens
riparium,tenellum,fimbriatum,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0040	NA	NA	NA	945	1728	2680	riparium	tenellum	fimbriatum	platyphyllum
riparium,tenellum,fimbriatum,squarrosum,sericeum	NA	NA	NA	NA	0.0005	NA	NA	NA	0.0192	NA	NA	NA	872	1784	2692	riparium	tenellum	fimbriatum	squarrosum
riparium,tenellum,fuscum,platyphyllum,sericeum	NA	NA	NA	NA	0.0012	NA	NA	NA	0.0508	NA	NA	NA	1011	1586	2684	riparium	tenellum	fuscum	platyphyllum
riparium,tenellum,fuscum,squarrosum,sericeum	NA	NA	NA	NA	0.0011	NA	NA	NA	0.1468	NA	NA	NA	905	1526	2696	riparium	tenellum	fuscum	squarrosum
riparium,tenellum,platyphyllum,squarrosum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0016	NA	0.0005	NA	828	1850	2682	riparium	tenellum	platyphyllum	squarrosum
riparium,tenellum,subnitens,platyphyllum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0057	NA	NA	NA	936	1738	2684	riparium	tenellum	subnitens	platyphyllum
riparium,tenellum,subnitens,squarrosum,sericeum	NA	NA	NA	NA	NA	0.0005	NA	NA	0.0273	NA	NA	NA	863	1779	2693	riparium	tenellum	subnitens	squarrosum
subnitens,fimbriatum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0007	NA	0.0082	NA	1224	1456	2693	subnitens	fimbriatum	divinum	compactum
subnitens,fimbriatum,flexuosum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0329	NA	NA	NA	1171	1472	2693	subnitens	fimbriatum	flexuosum	lindbergii
subnitens,fimbriatum,flexuosum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.1066	NA	NA	NA	1169	1358	2689	subnitens	fimbriatum	flexuosum	riparium
subnitens,fimbriatum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0060	NA	1199	1486	2694	subnitens	fimbriatum	riparium	lindbergii
subnitens,fimbriatum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0020	NA	NA	NA	1176	1513	2692	subnitens	fimbriatum	tenellum	lindbergii
subnitens,fimbriatum,tenellum,riparium,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0113	NA	NA	NA	1183	1493	2693	subnitens	fimbriatum	tenellum	riparium
subnitens,platyphyllum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0048	NA	1009	1668	2686	subnitens	platyphyllum	divinum	compactum
subnitens,platyphyllum,flexuosum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0250	NA	NA	NA	973	1676	2692	subnitens	platyphyllum	flexuosum	lindbergii
subnitens,platyphyllum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0046	NA	939	1738	2686	subnitens	platyphyllum	riparium	lindbergii
subnitens,platyphyllum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0029	NA	NA	NA	942	1742	2689	subnitens	platyphyllum	tenellum	lindbergii
subnitens,squarrosum,divinum,compactum,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0006	NA	0.0040	NA	939	1747	2694	subnitens	squarrosum	divinum	compactum
subnitens,squarrosum,flexuosum,lindbergii,sericeum	0.0006	NA	NA	NA	NA	NA	NA	NA	0.0206	NA	NA	NA	901	1754	2693	subnitens	squarrosum	flexuosum	lindbergii
subnitens,squarrosum,riparium,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0032	NA	813	1874	2693	subnitens	squarrosum	riparium	lindbergii
subnitens,squarrosum,tenellum,lindbergii,sericeum	NA	NA	NA	NA	NA	NA	NA	NA	0.0027	NA	NA	NA	831	1855	2691	subnitens	squarrosum	tenellum	lindbergii

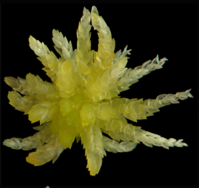
Table S13. Summary statistics for each type of introgression based on D_{FOIL} analysis

Calculated on proportion of windows showing significant signal for introgression of a certain type to the total number of windows

Type of introgression	Mean	Median	SD	SE	Minimum	Maximum	Upper Quantile 75%	Lower Quartile 25%	Coefficient of Variation	Number of 5-taxon phylogenies
P1→P3	0.0012	0.0009	0.0007	0.0001	0.0005	0.0025	0.0016	0.0007	0.55	24
P3→P1	0.0015	0.0008	0.0013	0.0004	0.0006	0.0051	0.0018	0.0007	0.88	12
P1→P4	0.0008	0.0008	0.0003	0.0002	0.0006	0.0012	0.0010	0.0007	0.34	3
P4→P1	0.0008	0.0007	0.0002	0.0001	0.0005	0.0012	0.0009	0.0006	0.31	6
P2→P3	0.0016	0.0011	0.0015	0.0003	0.0005	0.0057	0.0017	0.0006	0.92	23
P3→P2	0.0013	0.0006	0.0015	0.0004	0.0005	0.0054	0.0009	0.0006	1.15	16
P2→P4	0.0008	0.0006	0.0003	0.0002	0.0006	0.0012	0.0009	0.0006	0.43	3
P4→P2	0.0006	0.0006	0.0000	0.0000	0.0006	0.0006	0.0006	0.0006	0.02	6
P1,2→P3	0.0245	0.0073	0.0370	0.0031	0.0005	0.1949	0.0284	0.0012	1.51	142
P3→P1,2	NA	NA	NA	NA	NA	NA	NA	NA	NA	0
P1,2→P4	0.0041	0.0041	0.0031	0.0003	0.0005	0.0133	0.0060	0.0011	0.76	97
P4→P1,2	NA	NA	NA	NA	NA	NA	NA	NA	NA	0

Table S14. Number of blocks with consecutive 100-Kbp introgressed windows per 5-taxon combination based on D_{FOIL} analysis

Number of consecutive introgressed windows in a block	Mean	Median	SD	Minimum	Maximum	Number of 5-taxon phylogenies
1	29.32	11.00	39.60	1.00	208.00	179.00
2	4.27	2.50	5.24	1.00	24.00	56.00
3	2.00	2.00	1.07	1.00	4.00	8.00
4	1.50	1.50	0.71	1.00	2.00	2.00



Paper III

Kjell Ivar Flatberg
NTNU Vitenskapsmuseet

Genome-wide patterns of diversification are shaped by selection, ancient introgression and incomplete lineage sorting in a rapidly radiated genus of peatmoss

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction

1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two workplaces with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher

1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*

1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos	Population responses of Arctic charr (*Salvelinus alpi-*

		Zoology	*nus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:

1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control

2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in three-spine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Bi-	Studies on antifreeze proteins

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2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis*

			virescens
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution

2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding re-

			gime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis*): Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms:

	Hovland		Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad	PhD Biology	Invasive species: Genetics, characteristics and trait

	Acharya		variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.
2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park

2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh
2019	Knut Jørgen Egelie	Phd Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
			Adaptive responses to enviromental stochasticity on different evolutionary time-scales
2019	Thomas Ray Haaland	Phd Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Kwaslema Malle Hariohay	Phd Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Mari Engvig Løseth	Phd Biology	
2019	Joseph Mbyati Mukeka	Phd Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	Phd Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
			Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field

2019	Nathalie Briels	Phd Biology	studies
2019	Anders L.Kolstad	Phd Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	Phd Biology	Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer
2019	Alex Kojo Datsomor	Phd Biology	The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon (*Salmo salar L*): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes
2020	Ingun Næve	Phd Biology	Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon (*Salmo Salar*) production and reproduction
2020	Rachael Morgan	Phd Biology	Physiological plasticity and evolution of thermal performance in zebrafish
2020	Mahsa Jalili	Phd Biology	Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon (*Salmo salar L.):* possible nutriomics approaches
2020	Haiqing Wang	Phd Biology	Utilization of the polychaete Hediste diversicolor (O.F. Millier, 1776) in recycling waste nutrients from land-based fish farms for valueadding applications'
2020	Louis Hunninck	Phd Biology	Physiological and behavioral adaptations of impala to anthropogenic disturbances in the Serengeti ecosystems
2020	Kate Layton-Matthews	Phd Biology	Demographic consequences of rapid climate change and density dependence in migratory Arctic geese
2020	Amit Kumar Sharma	Phd Biology	Genome editing of marine algae: Technology development and use of the CRISPR/Cas9 system for studies of light harvesting complexes and regulation of phosphate homeostasis
2020	Lars Rød-Eriksen	Phd Biology	Drivers of change in meso-carnivore distributions in a northern ecosystem
2020	Lone Sunniva Jevne	Phd Biology	Development and dispersal of salmon lice (*Lepeophtheirus salmonis Krøyer*, 1837) in commercial salmon farming localities
2020	Sindre Håvarstein Eldøy	Phd Biology	The influence of physiology, life history and environmental conditions on the marine migration patters of sea trout
2020	Vasundra Touré	Ph Biology	Improving the FAIRness of causal interactions in systems biology: data curation and standardisation to support systems modelling applications
2020	Silje Forbord	Phd Biology	Cultivation of Saccharina latissima (Phaeophyceae) in temperate marine waters; nitrogen uptake kinetics, growth characteristics and chemical composition
2020	Jørn Olav Løkken	Phd Biology	Change in vegetation composition and growth in the forest-tundra ecotone – effects of climate warming and herbivory
2020	Kristin Odden Nystuen	Phd Biology	Drivers of plant recruitment in alpine vegetation
2021	Sam Perrin	Phd Biology	Freshwater Fish Community Responses to Climate Change and Invasive Species
2021	Lara Veylit	Phd Biology	Causes and consequences of body growth variation in hunted wild boar populations
2021	Semona Issa	Phd Biology	Combined effects of environmental variation and pollution on zooplankton life history and population dynamics

ISBN 978-82-326-5439-0 (trykt utg.)
ISBN 978-82-326-5605-9 (elektr. utg.)
ISSN 1503-8181 (trykt utg.)
ISSN 2703-8084 (online ver.)

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