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Abstract:	METHODS RADseq analyses were applied to a sample of 384 collections representing the European, North American, and (to a lesser extent) Asian ranges of the complex. The data were subjected to maximum likelihood phylogenetic analyses and analyses of genetic structure using the software, STRUCTURE, and multivariate ordination approaches. RESULTS Defined phylogenetically, the S. recurvum complex includes S. angustifolium , S. fallax , S. flexuosum , S. pacificum , and S. recurvum , as distinct clades with little evidence of admixture within them. In addition, we resolved another clade, sister to either S. pacificum or S. fallax , that is currently unnamed and is referred to in this paper as S. “pseudopacificum.” We confirm that S. balticum , a species not generally included in the S. recurvum complex, and S. obtusum , never associated with the complex by previous authors, are nested within it among the core species. Species with geographic ranges that span Europe, eastern North America, and Western North America exhibit a sister-group relationship between amphi-Atlantic and Pacific clades. European plants within S. flexuosum form a clade that is nested within a paraphyletic group of eastern North American plants; this species does not occur in western North America. CONCLUSIONS We recognize seven species in the amended S. recurvum complex, including S. balticum and S. obtusum , in addition to the informal clade, S. “pseudopacificum”. Although we detected some geographically-correlated phylogenetic structure within widespread morphospecies, our RADseq data support the interpretation that these species have intercontinental geographic ranges.

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Phylogenetic structure in the *Sphagnum recurvum* complex (Bryophyta: Sphagnaceae) relative to taxonomy and geography

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Running Head: Phylogenetic structure in the *Sphagnum recurvum* complex

PREMISE: The *Sphagnum recurvum* complex comprises a group of closely related species of peat mosses that are dominant components of many northern wetland ecosystems. Taxonomic hypotheses for the group range from interpreting the whole complex as one polymorphic species or as 6-10 species. The complex occurs around the Northern Hemisphere and some of the putative species also have intercontinental ranges. Our goals were to circumscribe the complex and assess its phylogenetic structure relative to morphologically defined species and geography.

METHODS: RADseq analyses were applied to a sample of 384 collections representing the European, North American, and (to a lesser extent) Asian ranges of the complex. The data were subjected to maximum likelihood phylogenetic analyses and analyses of genetic structure using the software, STRUCTURE, and multivariate ordination approaches.

RESULTS: Defined phylogenetically, the *S. recurvum* complex includes *S. angustifolium*, *S. fallax*, *S. flexuosum*, *S. pacificum*, and *S. recurvum*, as distinct clades with little evidence of admixture within them. In addition, we resolved another clade, sister to either *S. pacificum* or *S. fallax*, that is currently unnamed and is referred to in this paper as S. "pseudopacificum." We confirm that *S. balticum*, a species not generally included in the *S. recurvum* complex, and *S. obtusum*, never associated with the complex by previous authors, are nested within it among the core species. Within the complex, species with bluntly acute to obtuse stem leaf apices are sister to those with acute to apiculate stem leaves. Species with geographic ranges that span Europe, eastern North America, and Western North America exhibit a sister-group relationship between amphi-Atlantic and Pacific clades. European plants within *S. flexuosum* form a clade that is nested within a paraphyletic group of eastern North American plants; this species does not occur in western North America.

CONCLUSIONS: We recognize seven species in the amended *S. recurvum* complex, including *S. balticum* and *S. obtusum*, in addition to the informal clade, S. "pseudopacificum". Although we detected some geographically-correlated phylogenetic structure within widespread morphospecies,

our RADseq data support the interpretation that these species have intercontinental geographic ranges.

KEY WORDS: biogeography; peat moss; Sphagnaceae; *Sphagnum*; *Sphagnum angustifolium*; *Sphagnum balticum; Sphagnum fallax*; *Sphagnum flexuosum*; *Sphagnum obtusum*; *Sphagnum pacificum*; and *Sphagnum recurvum*

Plants that reproduce with spores rather than seeds, including the bryophytes, lycophytes, and monilophytes, are generally thought to have broad ranges that often span multiple continents (Schofield and Crum, 1972). It has been estimated that approximately 70% of the mosses found in Europe also occur in North America (Frahm and Vitt, 1993). Indeed, a perusal of the bryophyte volumes in the *Flora of North America* project indicate that as presently understood, most temperate and boreal bryophyte species are recorded from multiple continents. Moreover, a substantial number of Neotropical bryophytes are also reported from Africa and/or other tropical continental areas (Gradstein et al., 1983). Consistent with the general pattern of bryophytes having broad, often intercontinental ranges is that many south-temperate bryophyte species are thought to occur disjunctively between Australia/New Zealand and South America, with low rates of endemism in any one area (such as New Zealand) (Muñoz et al., 2004). In contrast, most seed plants are restricted to a single continent; Qian (1999) estimated that only about 6% of vascular plants are shared between North America and Europe. Notwithstanding issues such as how to define what constitutes a species, heterogeneity among plant groups in genetic/phylogenetic architecture, and differences in the approaches of different taxonomists, the general pattern that spore plants have broader ranges than seed plants has not been controversial (but see Vigalondo et al., 2019).

Dated molecular phylogenies have consistently suggested divergence times between intercontinentally disjunct bryophyte populations as being far too recent to be explained by continental drift. Thus, attention has focused on the efficacy of spore dispersal in minimizing or eliminating divergence among distinct populations of bryophytes. At the same time, recent systematic analyses have shown that some species previously thought to have extremely broad intercontinental ranges consist of genetically and sometimes morphologically divergent units that can be interpreted as separate species (Medina et al., 2012, 2013; Heinrichs et al., 2010; Renner et al., 2013, 2017; Hedenäs et al., 2014; Hassel et al 2018, Vigalondo et al., 2019).

In this paper we describe phylogenetic architecture in a small clade of closely related plants in the moss genus *Sphagnum* (peatmosses). *Sphagnum*, with some 200-400 species, is the largest of four genera in the moss class Sphagnopsida (Shaw et al., 2010, 2016). The genus is especially

abundant and diverse in north temperate and boreal regions of the Northern Hemisphere where it grows in and actually creates peatlands – bogs and fens – in many wetland habitats (Rydin and Jeglum, 2013). *Sphagnum*-dominated peatlands have long served as a model for research in community assembly and niche differentiation among closely related sympatric species. Moreover, because some 25% of earth's terrestrial carbon pool is stored in *Sphagnum*-dominated peatlands (Yu et al., 2010), the genus has recently become a model for linking the plants and their traits, ecosystem function, and global climate (Weston et al., 2018).

There has arguably been more molecular work on inter- and intraspecific genetic/phylogenetic structure on *Sphagnum* than on any other genus of bryophytes. Most Northern Hemisphere species of *Sphagnum*, like other bryophytes, are thought to have geographic ranges that span multiple continents (McQueen and Andrus, 2007). Genetic analyses have supported these interpretations that most species are widespread and that endemism, even at the continental scale, is low. Most of the North American species are found in Europe; some occur in both eastern and western North America, although some intercontinental species have amphi-Atlantic or amphi-Pacific ranges (Shaw et al., 2004, 2014; Kyrkjeeide et al., 2015, 2016a, b; Yousefi et al., 2017)

In their revision of *Sphagnum* for the *Flora of North America* project, McQueen and Andrus (2007) recognized 91 species. The genus is comprised of five major clades, each recognized as a subgenus (Shaw et al., 2016). The focus of this study, the so-called *S. recurvum* complex (Flatberg 1992a), falls within the subgenus *Cuspidata*. Taxonomy of the *S. recurvum* complex has been highly variable; Crum (1984) considered it a single species, *S. recurvum* P. Beauv., but McQueen and Andrus (2007) recognized 5-7 distinct species (depending on precisely how the complex is delimited). Flatberg (1992a) recognized five "core" species. Most of the putative species are widespread in both North America and Europe, excluding *S. rubroflexuosum* Andrus, endemic to a few sites in eastern North America, and *S. recurvum* s. str., which is restricted to the New World other than one confirmed report from the Azores. While most of the species are common and widespread across North America and Europe, some are not strictly circumboreal. *Sphagnum fallax*, for example, is common in Europe and eastern North America but appears to be absent from western North America. A related species,

S. pacificum, is limited in North America to the Pacific coast and is not known from eastern North America nor Europe. *Sphagnum angustifolium*, perhaps the most common species in the complex, occurs in Europe, Asia, and both eastern and western North America.

Our goals in this research were to assess phylogenetic architecture of this complex, and address the following questions. (1) How many phylogenetically distinguishable species are there in the complex? (2) Is there genetic differentiation between plants on different continents such additional allopatric species are resolved, contrary to the interpretation that these species have intercontinental ranges? (3) If the species do have intercontinental ranges, is there detectable differentiation among metapopulation systems on different continents (or between eastern and western North American systems)? This group is especially appropriate to address these questions because the traditionally defined species are difficult to distinguish and have been variously interpreted at the taxonomic level, and they occupy wet microsites near the water table within peatland communities, possibly facilitating interspecific hybridization since sperm are released into the water and the taxa frequently co-occur in close proximity. Most of the putative species are currently thought to have intercontinental ranges.

MATERIALS AND METHODS

Taxon sampling – A total of 384 plants were sampled for the genomic analyses. These included plants generally considered part of the complex, two other taxa not generally included within the complex but sometimes considered close (*S. balticum*, *S. obtusum*), four other species from outside the complex but within the subg. *Cuspidata* (*S. annulatum, S. majus, S. pulchrum, S. riparium*), and one other more distant outgroup from the subg. *Subsecunda* (*S. missouricum*). Of these, 90 were excluded because of poor data quality. The remaining 294 samples that were included in the final analyses comprised 113 samples from Europe (of which 89 were from Norway, one from Portugal [Azores]), and 23 from European Russia), 134 from eastern North America, and 47 from western North America.

Voucher specimens are archived in the Duke University herbarium (DUKE). Specimen information and voucher data are included in Appendix S1. The central portion of a single capitulum was sampled for the molecular work and the remaining tissue from that stem was placed in a small packet and returned to the herbarium specimen.

DNA isolation, library preparation, and sequencing – Genomic DNA was extracted from dried samples using tissue from the capitulum of the gametophytes, each with a mass of approximately 100mg. Extractions followed the CTAB protocol outlined in Shaw et al. (2003). DNA concentrations were measured using a Qubit 2.0 Fluorometer (Life Technologies) and standardized to 20ng/µL. Genomic libraries were made following the double digestion restriction site-associated DNA sequencing (ddRADseq) protocol of Parchman et al. (2012) with modifications described here. Restriction digest of 10µL of the genomic DNA sample was performed in a 25µL reaction containing 0.5µL restriction enzyme EcoRI, 1µL restriction enzyme MseI, and 2.5 µL Cutsmart buffer (New England BioLabs) over three hours at 37°C, followed by 10 minutes at 65°C for permanent inactivation of the enzymes. Digested fragments of each sample were ligated to uniquely barcoded oligonucleotide adapters in 12µL reactions containing 9µL digested DNA, 1µL barcoded EcoRI adapter, 1µL MseI adapter, 0.2µL T4 DNA ligase enzyme, and 0.12µL 10X ligase buffer (New England BioLabs) at 23°C for one hour. Amplification of ligated DNA fragments containing both ligated adapters was performed in 20µL reactions containing 2µL ligated DNA, 4µL 1mM dNTP, 4µL 5X buffer, 1.3µL 5µM premixed PCR primers, 0.4µL $MgCl_2$, 0.15µL DMSO, and 0.2µL iProof Taq polymerase (Bio-Rad). PCR product concentrations were measured using a Qubit 2.0 Fluorometer and pooled into four libraries, each containing 10ng of 96 PCR products. Each library was cleaned and size-selected for fragments around 350bp using AMPur XPbeads (Beckman Coulter), checked for quality on a BioAnalyzer (Agilent) and sequenced on a single lane of Illumina HiSeq 2000 with 100bp single-end reads or a single lane of NextSeq 500 with 150bp single-ended reads at the Genome Sequencing Shared resource operated by the Duke Center for Genomic and Computational Biology (https://oit.duke.edu/comp-print/research/).

RADseq data pipeline – Raw illumina reads were checked for quality with FastQC (Andrews, 2010) and reads from the NextSeq 500 runs were trimmed to match the length of reads from the HiSeq 2000 runs. SNP discovery was performed with ipyrad v.0.7.29 (Eaton, 2014) using default parameters except as noted here. Reads were processed as datatype "ddrad" to match the library preparation method and samples were treated as haploid, since all except six samples of one outgroup species were expected to have haploid gametophytes. A maximum of two mismatched bases were allowed in the barcode during demultiplexing, Illumina adapter sequences and low-quality bases were trimmed from the reads, and trimmed reads less than 42 bases long or with more than five low quality bases were discarded. Multiple ipyrad runs were performed using a range of read clustering thresholds to identify the clustering threshold (0.90) that maximized the number of variable and parsimony informative loci and to verify that the results of downstream analyses are not sensitive to clustering threshold. Low-read samples and samples with low numbers of loci identified in these exploratory analyses were removed. Only loci present in at least 80% of the remaining samples were kept for the final analyses, and additional runs using different minimum sample coverage values were performed to ensure that inferences are not sensitive to the number of loci and level of missing data.

Phylogenetic analyses – RAxML version 8.2.12 (Stamatakis, 2014) was used to estimate phylogenetic relationships among sequences under maximum likelihood (ML) using concatenated loci identified by ipyrad. The ML tree was estimated using random starting trees, the rapid bootstrap analysis and best scoring ML tree search, and the GTRGAMMA nucleotide substitution model. The rapid hill-climbing search algorithm was used to estimate the best ML tree using 100 bootstrap replicates to determine support for branches.

Phylogenetic relationships among species were also estimated under the multispecies coalescent model using singular value decomposition scores for species quartets (SVDquartets) as implemented in PAUP* Version 4.0a, build 165 (Chifman and Kubatko, 2014; Chifman and Kubatko,

2015; Swofford, 2003). Ten million random quartets were sampled (22.28% of total distinct quartets) with 200 bootstrap replicates to determine branch support.

Cluster analyses – Each locus identified by ipyrad may contain multiple SNPs, so to avoid using tightly linked SNPs one randomly selected SNP per locus was used for clustering analyses. Genetic structure within the *Sphagnum recurvum* complex was explored using Bayesian model-based cluster analysis with STRUCTURE Version 2.3.2.1 (Pritchard et al., 2000). The most likely number of clusters (K) was evaluated using the method of Evanno et al. (2005) based on ten independent runs using an admixture model with correlated allele frequencies for each K from one to 10 with 50000 steps of burn-in and 500000 steps per run. Regardless of how this method evaluated the "optimal" K, we explored higher levels of K to assess the possibility of additional structure in the data. Matrices of membership coefficients across the independent runs were used to search for the optimal alignment with CLUMPP, version 1.1.2 (Jakobsson and Rosenberg, 2007). In addition to the entire *Sphagnum recurvum* complex, STRUCTURE was also used on subsets of the samples to explore finer-scale genetic structure within major clades identified in the phylogenetic analyses and within individual species when sufficient samples were available.

Principal Components Analysis (PCA) of scaled allele frequencies using the R package 'adagenet' (Jombart, 2011) was used to further explore genetic structure in the entire complex, in major clades, and within individual species.

Genetic diversity analyses – Genetic diversity patterns were explored by calculating diversity statistics and estimating pairwise Nei's unbiased genetic distance with GenAlEx 6.5 (Peakall and Smouse, 2006; Peakall and Smouse, 2012) and estimating pairwise Fst with the R package 'hierfstat' (Goudet, 2005). Genetic diversity statistics and distances were calculated for the entire complex, for major clades, and for individual species.

RESULTS

Data characterization – Four lanes of Illumina sequencing yielded 652 million reads. After trimming, removing barcodes and adapter sequences, filtering for quality, and removing samples with low readcounts, 448 million reads of 42 to 92 bp were retained across 294 individual plant samples, with the number of reads per individual ranging from 375,249 to 2,878,373 (median ± SD = 1,518,724 ± 531,416). The assembly pipeline produced 6170 loci shared among at least 80% of the individuals. 6148 of those loci contained one or more SNPs and 6100 contained one or more parsimony informative SNPs. The mean locus coverage per individual was 88.2%.

Phylogenetic analyses – Phylogenetic relationships among all individuals are provided in Appendix S2; relationships among species are summarized in Fig. 1. Rooted by a series of increasingly distant *Sphagnum* species, the *S. recurvum* complex is resolved as monophyletic with 100% bootstrap (BS) support (identified by asterisks in Figs 1 and S1). The complex, defined phylogenetically, includes two species, *S. balticum* and *S. obtusum*, that have not generally been identified as closely related to the core species. The complex is sister to a clade that includes *S. majus*, *S. annulatum*, and *S. pulchrum*. *Sphagnum majus* has been shown to be an allopolyploid species (i.e., diploid gametophytes, tetraploid sporophytes) derived from a cross between *S. cuspidatum* (also in subg. *Cuspidata*) and *S. annulatum*.

Two reciprocally monophyletic groups are resolved (each with 100% BS) within the *S. recurvum* complex, hereafter referred to as the “Pointed Leaf” and “Rounded Leaf” groups (clades). These labels refer to the stem leaves, which tend to be acute to apiculate in the Pointed Leaf and are obtuse to broadly acute in the Rounded Leaf clade (Fig. 2). These informal labels are not perfectly descriptive (for example, *S. balticum*, phylogenetically part of the Pointed Leaf group, has stem leaves that are barely pointed), but they apply in general. Stem leaf shapes and their apices are generally used for distinguishing species in this complex. *Sphagnum fallax* (Fig. 2:1-6), S. ‘pseudopacificum” [see below] (Fig. 2:7-12), and *S. pacificum* (Fig. 2:13-18) have acute to apiculate leaves whereas *S. balticum*, as noted, has broadly acute to more or less obtuse leaves. Species in the *S. angustifolium*

clade, *S. angustifolium* (Fig. 2: 25-31), *S. obtusum* (Fig. 2: 32-37), and *S. flexuosum* (Fig. 2: 38-43) have broadly obtuse leaves that are often resorbed across the apex. Occasional stem leaves of *S. angustifolium* are more acute (e.g., Fig. 2: 31), causing confusion with *S. fallax*, with which is often co-occurs.

Support for species relationships within the complex differ between maximum likelihood (ML) analyses of the concatenated dataset and the quartet analyses (Fig. 1). Based on ML, four taxa are resolved, all with 100% BS, within the Pointed Leaf clade. These include *S. fallax*, *S. pacificum*, and *S. balticum*, plus a currently unnamed taxon that we refer to as S. "pseudopacificum." All samples identified morphologically as *S. brevifolium* or *S. isoviitae*, recognized as species by McQueen and Andrus (2007), Flatberg (2002, 2013), and Laine et al. (2018), are scattered within the *S. fallax* clade with no hint that either forms a monophyletic group (Appendix S2). In the Rounded Leaf clade, *S. angustifolium* itself is sister to *S. obtusum*, *S. flexuosum*, and *S. recurvum* in the ML analyses, but relationships of *S. obtusum* to *S. flexuosum* and *S. recurvum* are more ambiguous (Fig. 1). In the quartet analysis, *S. obtusum* plus *S. angustifolium* are resolved as sister to *S. flexuosum* plus *S. recurvum*. Ambiguity within and between the analyses relates mainly to the position of *S. obtusum*; the sister group relationship between *S. flexuosum* and *S. recurvum* is consistent and strongly supported in both (Fig. 1).

ML analyses of relationships among all accessions suggest geographically correlated genetic structure within species that have intercontinental ranges. Reciprocally monophyletic groups comprised of European versus eastern North American plants are resolved within *S. fallax* (Appendix S2). The European clade is supported at 100% BS whereas the North American clade is unsupported, although there is a perfect geographic segregation of plants between the clades. *Sphagnum fallax* does not occur in western North America.

Geographic structure within *S. angustifolium* is complex (Appendix S2). Most Alaskan samples are resolved as a separate (unsupported) clade sister to all the other samples. But a well-supported smaller second group of samples from Alaska (and British Columbia) appears to be more closely related to plants from northern Europe (Norway, Russia) (Appendix S2). Eastern North American

plants also form a single clade that spans at least from Wisconsin and Pennsylvania to subarctic Quebec. All European plants (including those from western Russia) form a clade nested within the overall North American paraphyletic group. Similarly, all European (Norwegian) samples of *S. flexuosum* form a clade that is nested within North American samples of that species. *Sphagnum recurvum* is restricted to eastern North America with the exception of one recorded occurrence in the Azores (Dias et al., 2009). A plant from that single European population is resolved as closely related to samples of *S. recurvum* from the southeastern U.S. (Appendix S2). Among outgroup taxa, samples of *S. majus* from the eastern U.S. are nested within European samples, but this pattern, opposite to that resolved within *S. angustifolium* and *S. flexuosum*, is based on more limited sampling.

Sampling within continents was too limited to thoroughly assess geographic structure on more local scales, but several species were sampled sufficiently from within eastern North America to suggest that some geographic structure is likely. Within *S. fallax*, for example, samples collected from the same or proximate sites within states generally group together (Appendix S2). As previously noted, Alaskan samples of *S. angustifolium* fall into two clades, both distinct from samples collected in temperate eastern U.S. Some grouping of geographically proximate samples is also evident within *S. recurvum* and *S. flexuosum* (Appendix S2).

Cluster Analyses – Results of cluster analyses based on STRUCTURE parallel those from the phylogenetic analyses (Fig. 3). When all samples were analyzed as a group, at K=2 (evaluated as "optimal") the Pointed Leaf and Rounded Leaf groups were resolved, with *S. balticum* showing substantial admixture between the two. *Sphagnum pacificum* and *S. obtusum* also showed admixture, but to a very limited extent (Fig. 2). As with the phylogenetic analyses, no distinction is evident between *S. fallax, S. brevifolium*, and *S. isoviitae*.

Separate analyses of the Pointed and Rounded Leaf groups (left and right, respectively, in Fig. 3) reveal additional genetic structure. For the Pointed Leaf group, at K=3 (optimal), two genotype groups are resolved within the phylogenetic species, *S. fallax*. Norwegian samples identified as *S. brevifolium* and *S. isoviitae* all belong to one of those two groups (Fig. 2), but the group also includes

plants that appeared to be unambiguous *S. fallax* s. str. North American samples identified as *S. brevifolium* or *S. isoviitae* are scattered across the same *S. fallax* genotype groups. *Sphagnum pacificum* and S. “pseudopacificum”, in contrast, are genetically divergent from both of the two *S. fallax* genotype groups. In an analysis of *S. fallax* alone (including *S. brevifolium* and *S. isoviitae*), K=2 was considered optimal, and this resolves European and North American samples of this species but does not resolve *S. fallax*, *S. brevifolium*, and *S. isoviitae* (which all occur on both continents; Fig. 2). Even at K=3 or K=4, we found no additional genetic structure to support separating *S. brevifolium* or *S. isoviitae* from *S. fallax* (results not shown).

In a separate analysis of the Rounded Leaf group, the optimal K=2. One of the genotype groups is fixed within *S. angustifolium* and the other in *S. flexuosum*, with *S. recurvum* and *S. obtusum* showing different patterns of admixture for the two genotype groups. At K=4, each of the four morphospecies, *S. angustifolium*, *S. flexuosum*, *S. recurvum*, and *S. obtusum*, are resolved as different clusters. Within *S. angustifolium,* at K=2, eastern North American and European samples belong to the same genetic group (light grey in Fig. 2) and the western North American (mainly Alaskan) plants mostly belong to a different genetic group but with some admixture. Moreover, five Alaskan plants belong to the light grey genotype group, otherwise restricted to eastern North American and European plants. At increasing levels of K, additional genetic structure is suggested within *S. angustifolium*, but also with increasing evidence of admixture (Appendix S3). At K=4, the two phylogenetically resolved groups of Alaskan plants belong to separate clusters. Within *S. flexuosum*, European and eastern North American plants belong to different genotype groups, with a limited amount of admixture (Fig. 2).

Genetic patterns resolved by phylogenetic and STRUCTURE analyses are corroborated by principal components analyses (PCA) (Appendix S4). Differentiation between the Rounded and Pointed Leaf groups is strong (Appendix S4A), as are morphospecies within those groups (Appendix S4B, C). Differentiation between European and North American plants within *S. fallax* (Appendix S4D) and *S. flexuosum* (Appendix S4G) is also evident. Moreover, the greater genetic similarity between *S. angustifolium* plants from eastern North America and Europe compared to either with western North

American plants is clear, as is the occurrence of two genetically divergent groups of *S. angustifolium* plants from Alaska (Appendix S4E). The PCA also corroborates differentiation of S. “pseudopacificum” and *S. pacificum* (Appendix S4F).

Genetic differentiation and diversity – Genetic differentiation (estimated by Nei’s D and Fst) among species in the *S. recurvum* complex is generally low, corroborating the view that this is a group of very closely related species (Table 1). In fact, differentiation is also low (Fst < 0.4) between the Rounded and Pointed groups of species within the complex, and some species within those two groups are more differentiated than are the groups.

For all estimated statistics, the Rounded Leaf group of species contains higher genetic diversity, and more private alleles, than the Pointed Leaf group, although the sample size was somewhat larger for the latter than the former (Table 2). Within the Pointed Leaf group, the most common species (and most sampled), *S. fallax*, contains the highest levels of genetic diversity; similarly, *S. angustifolium*, which is the most common species (and most abundantly sampled), is more genetically diverse than any other Rounded Leaf species (Table 2).

DISCUSSION

Systematic/taxonomic implications – Both circumscription of the *S. recurvum* complex and the numbers of species within it have been disputed, and our results inform both issues. The core species comprising the complex (Flatberg 1989, 1992a,b; Laine et al., 2018; McQueen and Andrus, 2007) are *S. brevifolium*, *S. fallax*, *S. flexuosum*, *S. isoviitae*, *S. pacificum*, and *S. recurvum*. It is referred to as the *S. recurvum* complex because that species was the first described. Members of the complex typically have two side by side branch buds in the lower parts of the capitula whereas most Sphagna have them one above the other or single. These species are further characterized (though not unique to these within subg. *Cuspidata*) by the arrangement of pores on the branch leaves: few other than a single conspicuous pore near the distal end of each hyaline cell on the outer (convex or abaxial)

surface, and more numerous, larger round pores on the inner (convex, adaxial) surface. Finally, compared to other taxa in the subg. *Cuspidata*, species in the *S. recurvum* group are generally characterized by relatively short stem leaves, sometimes barely longer than wide, although this trait is somewhat variable (as shown in Fig. 2).

Flatberg (1992a) noted that *S. balticum* and *S. pulchrum* appear to be closely related to the *S. recurvum* complex and that the decision to exclude them from his taxonomic studies on this group was largely arbitrary. Based on phylogenetic analyses of organellar (plastid, mitochondrial) genome sequences, *S. balticum* is nested within the *S. recurvum* complex (Shaw et. al., 2016), and our results corroborate that conclusion. *Sphagnum balticum* lacks the paired branch buds generally characteristic of the core species, and the stem leaves are somewhat longer than in the other species (Fig. 2). They also spread widely from the stem, unlike the more pendent-spreading stem leaves of most *S. recurvum* complex species. The branch leaf pore pattern, typically with one prominent distal pore on the outer surface of each hyaline cell and more numerous, round, larger pores inside, is similar to that of the core species. *Sphagnum obtusum*, also shown here to be part of the *S. recurvum* complex, has a somewhat different branch leaf pore structure than the others. Outer pores are more numerous, sometimes in commissural rows, and are often faint and poorly defined.

Sphagnum pulchrum, in contrast, falls outside the *S. recurvum* complex, in a clade that includes the gametophytically haploid *S. annulatum*. That clade also includes two allopolyploid species (i.e., diploid gametophytes, tetraploid sporophytes) that share *S. annulatum* as one of their parents. *Sphagnum majus* is derived from a cross between *S. annulatum* and *S. cuspidatum* (Såstad et al., 2000), and *S. jensenii* derives from a cross between *S. annulatum* and *S. balticum* (Såstad et al., 1999a). Both *S. annulatum, S. majus* and *S. jensenii* differ morphologically by numerous pores on the convex surface of branch leaves, stem leaves much longer than broad, and stem cortex 2-3 cells wide (except in *S. annulatum*). Flatberg (1992a), based on morphology, noted that *S. pulchrum* appears to bridge the *S. recurvum* and *S. annulatum* complexes; our results indicate that *S. pulchrum* shares a recent common ancestor with *S. annulatum* and is not in any way phylogenetically intermediate between the two groups.

Several species in the *S. recurvum* complex are reported from South America and/or other tropical areas and genetic analyses are needed to determine if in fact those plants are conspecific with the temperate and boreal (to subarctic) samples included in this study. Some northern *Sphagnum* species definitely do occur at low latitudes but some samples from South America identified as *S. recurvum*, for example, are allopolyploids (unlike northern *S. recurvum*) and are clearly not conspecific (unpublished data). Flatberg (1992a) speculated that *S. recurvum* could be conspecific with two tropical species, *S. pulchricoma* and *S. cuspidatulum*, which would imply that *S. recurvum* has a pantropical range that includes South America, Africa, and Asia. This view is not supported by genetic information from microsatellites, however, which indicates that both *S. pulchricoma* and *S. cuspidatulum* are distinct from *S. recurvum* (Karlin et al., 2014). We can only confirm the occurrence of *S. recurvum* is eastern North America, with a single known European locality, in the Azores (Dias et al., 2009). That collection from the Azores falls within the *S. recurvum* clade in our analyses (Appendix S2), closely related to collections from the southeastern U.S. Nevertheless, in addition to cases of northern species possibly occurring in tropical regions, there could be other, distinct, tropical species that would fall within the *S. recurvum* complex. The current circumscription of the complex, limited to the northern species included in this study, is necessarily a work-in-progress.

Our analyses resolve eight clades within the *S. recurvum* complex, seven corresponding to widely recognized species, plus S. “pseudopacificum”. Crum (1984) considered plants that we attribute to *S. angustifolium*, *S. fallax*, *S. flexuosum*, and *S. recurvum* as conspecific (*S. recurvum* s. lat.). *Sphagnum pacificum* had not been described at the time, and Crum did not consider *S. balticum* or *S. obtusum* as part of the *S. recurvum* complex. McQueen and Andrus (2007) recognized all of the taxa we resolve here as distinct species and added S. *rubruflexuosum*, describing this new species from a few sites in Pennsylvania and Maryland (Andrus, 1988). Plants that we included in the present analyses from the type locality for *S. rubroflexuosum* were genetically indistinguishable from *S. flexuosum*.

The two major clades within the *S. recurvum* complex, referred to here as the Rounded and Pointed Leaf groups, correspond more or less to groups recognized previously (Flatberg 1992a). The

Pointed leaf group contains *S. fallax* (including *S. brevifolium* and *S. isoviitae*) and *S. pacificum*, plus the clade resolved as S. "pseudopacificum" in our analyses. These species are characterized by acute to apiculate stem leaves (Fig. 2), and also share yellow spores and somewhat differentiated stem cortical cells. Our results show that *S. balticum* is part of this clade as well; it has broadly and bluntly acute stems leaves, but does have yellow spores and a more or less differentiated cortex (Flatberg 1992a). Species in the Rounded Leaf group, including *S. angustifolium*, *S. flexuosum*, *S. obtusum*, and *S. recurvum*, have brown spores, stem cortex little or not differentiated, and rounded stem leaf apices that are obviously and characteristically resorbed. That apical resorption is minimal in *S. angustifolium* compared to the other species in this subgroup (Fig.2: 25-49). Our results show that these morphological traits generally track phylogenetic relationships within the complex with regard to the grouping of species into more inclusive clades.

In terms of species delineation, the most controversial issue in the complex pertains to the delineation of *S. fallax*, *S. isoviitae*, and *S. brevifolium*. Both *S. fallax* and *S. brevifolium* were described in the 19th century (*S. cuspidatum* var. *fallax* Klinggräff and *S. cuspidatum* var. *brevifolium* Röll, respectively). Flatberg (1992a) described *S. isoviitae* from central Norway as part of his taxonomic studies on the *S. recurvum* complex. These three species are closely related morphotypes within the Pointed Leaf group and frequently grow intimately mixed (Fig. 4). Flatberg and collaborators (Flatberg, 1992a, b; Såstad and Flatberg, 1994; Stenøien et al., 1997; Såstad et al., 1999b) have conducted a series of morphometric, experimental, and genetic studies to test the occurrence and degree of discontinuity among them and concluded that the three can be distinguished morphologically (although weakly so, at best, for *S. fallax* vs. *S. isoviitae*). They are frequently distinguishable in the field and/or as dried specimens, and differ in color, capitulum shape, branch leaf shape and arrangement (e.g., the degree of ranking [running in rows]), and the extent to which the branch leaves of the inner part of the capitula recurve when dry. They can also differ subtly in microscopic characters including the shape of the chlorophyllose cells in transverse section. Såstad et al (1999a) showed that whereas isozyme and RAPD markers evidenced genetic differentiation among *S. recurvum*, *S. angustifolium*, and *S. flexuosum* in the Rounded Leaf group, no such

differentiation was detected among *S. fallax*, *S. brevifolium*, and *S. isoviitae* in the Pointed Leaf group. Using microsatellites, Szurdoki et al. (2014) showed that *S. angustifolium*, *S. fallax*, and *S. flexuosum* are genetically distinct, but they did not address the issue of *S. fallax* vs. *S. isoviitae* or *S. brevifolium*.

Neither North American nor Norwegian samples in our data set that had been identified morphologically as *S. brevifolium* or *S. isoviitae* were distinguishable from *S. fallax* based on the RADseq data. Our data provide no hint of genetic divergence within *S. fallax* that could be construed as evidence in favor of separating *S. brevifolium*, *S. isoviitae*, or *S. rubroflexuosum*. Analyses using STRUCTURE identified two genotype groups within *S. fallax*, but these groups do not correspond to these morphotypes. Our results strongly suggest that neither *S. brevifolium* nor *S. isoviitae* represent phylogenetically distinct species, but are rather morphotypes nested within *S. fallax*.

The absence of differentiation using the molecular markers employed here does not bear on the question of whether the morphological characters used to distinguish them as species are genetically based. Indeed, the fact that morphs corresponding to *S. brevifolium* and *S. isoviitae* are often distinguishable in both Scandinavia and eastern North America suggest that they may well represent genetic variants. It could be that a limited number of genes control those morphological traits, and that they are polymorphic within *S. fallax*.

Szurdoki et al. (2014) found that *S. angustifolium*, *S. fallax*, and *S. flexuosum* could be distinguished by molecular data, but suggested that their genetic delineation was sometimes incongruent with morphological patterns. We also first found that some of our plant identifications for these taxa conflicted with subsequent molecular phylogenetic results, but reexamination of all specimens included in the project indicated that essentially every case of morphological-genetic incongruence involved initial misidentifications (by us). One result of our reexaminations was that *S. fallax* turned out to be more common in eastern North America than *S. angustifolium*, and occupies a broader niche range than we (or others; Johnson et al., 2014) had realized. *Sphagnum angustifolium* is generally thought to form hummocks whereas *S. fallax* typically grows in lawns and carpets closer to the water table. Our study suggests that not only is *S. fallax* more common than *S. angustifolium* in eastern North America, it forms low hummocks rather commonly.

Genetic admixture – STRUCTURE software identified genotypic groups within the complex and by conducting hierarchical analyses at different phylogenetic levels (within and between clades) we found some evidence of genotypic admixture within plants. This admixture can reflect retention of ancestral polymorphism and/or introgression. *Sphagnum balticum* is the only species that appeared to have a substantially admixed structure combining genetic attributes of the Rounded and Pointed Leaf clades (Fig. 3). This species is especially variable morphologically, combines stem leaf structure of the two groups (i.e., bluntly acute to rounded stem leaves in the Pointed Leaf clade), and was involved as the paternal parent in hybridization (with another species of the subg. *Cuspidata*, *S. tenellum*) that yielded the allopolyploid species, S. *troendelagicum* (Stenøien et al., 2010). As such, *S. balticum* is a species that invites additional study of genetic structure and the possibility of interspecific introgression across its broad intercontinental range. It may be a central figure facilitating genetic exchange between members of the *S. recurvum* complex, and beyond, in the subg. *Cuspidata*. Despite the fact that other species in the complex grow mixed in wet microsites that could facilitate interspecific hybridization, we found surprisingly little evidence of interspecific admixture. Additional analyses are needed, however, since STRUCTURE may not reveal introgression if it occurred long enough in the past for subsequent coalescence within species that are largely reproductively isolated.

Geographic patterns – Low but non-zero levels of migration/gene flow have been detected between North American and European plants of several *Sphagnum* species (Szövényi et al., 2008; Stenøien et al., 2011), and similarly between western North American and eastern Asian plants (Shaw et al., 2014, 2015). Dating of divergences between European and North American conspecifics have generally inferred Pleistocene time scales (Szövényi et al., 2008; Stenøien et al., 2011).

Both the Rounded Leaf and Pointed Leaf groups within the *S. recurvum* complex have intercontinental ranges that include Europe, Asia, and North America. We detected geographic structure within the three species that have the broadest geographic ranges: *S. fallax* in the Pointed Leaf group; *S. angustifolium* and *S. flexuosum* in the Rounded Leaf group. In *S. fallax*, eastern North

American and European clades are reciprocally monophyletic. This species does not occur in western North America. *Sphagnum angustifolium* does occur in all three regions and its phylogenetic structure is complex. There are multiple, geographically correlated clades. Alaska alone harbors plants representing genetically and phylogenetically divergent *S.angustifolium* plants. In *S. flexuosum*, European plants form a clade that is nested within a paraphyletic group of North American samples.

Vigalondo et al. (2019) found that a species generally interpreted as having a broad intercontinental distribution in the moss family Orthotrichaceae consists of more or less allopatric clades that also differ in multivariate patterns of morphological variation. Citing other recent studies that have found similar phylogenetic structure within supposedly widespread species, Vigalondo et al. (2019) suggested that species diversity in mosses and liverworts may be significantly underestimated. Evidence to support this broad conclusion is currently limited to fewer than a half dozen bryophyte species/complexes (with a total of some 20,000 species in the combined phyla), and it is noteworthy that all are tropical to temperate groups. The situation in *Sphagnum*, as an example of common and widespread temperate to boreal bryophytes, may be different. As data accumulate, we see a pattern in *Sphagnum* of detectable but minimal divergence among metapopulation systems on different continents. This pattern may be generally true among species that are ecologically abundant community dominants around the Northern Hemisphere. Life history correlates of differing phylogenetic structure need to be investigated. For example, the species of Orthotrichaceae studied by Vigalondo et al. (2019) may be less clonal and more short-lived than are *Sphagnum* species.

Key to species in the S. recurvum complex –

As our species delineations differ from those in other recent treatments of the group, we provide the key below to distinguish the seven species we resolve with RADseq data. The clade we identify as S. “pseudopacificum” requires further work, especially additional collections. It is not included in the key and would likely key out by collectors as *S. pacificum*. Because the three morphs of *S. fallax* are often distinguishable we also provide a key to distinguish them in order to encourage further research into their genetics and ecology. The brevifolium and isoviitae morphs are formally recognized by Lönnell

and Hassel (2018) as varieties of *S. fallax*; i.e. *S. fallax* var. *brevifolium* (Lindb. ex Braithw.) Lönnell & Hassel and *S. fallax* var. *isoviitae* (Flatberg) Lönnell & Hassel.

Key to species in the *Sphagnum recurvum* complex

1. Stem leaves bluntly acute, obtuse-truncate or truncate 2

1. Stem leaves acute or apiculate 6

2. Stem leaves rounded-obtuse, ± narrowly eroded at apex 3

2. Stem leaves obtuse-truncate to truncate, narrowly to widely eroded/fimbriate at apex 5

3. Stem leaves wide spreading; upper stem leaf cells fibrillose; branch fascicles usually with one pendent branch ..... *S. balticum*

3. Stem leaves appressed to slightly spreading; stem leaf cells efibrillose (very rarely with rudimentary fibrils); branch fascicles with 2(-3) pendent branches 4

4. Capitula green to brownish, convex, with straight branches; stem leaves not or little longer than wide, scarcely or not eroded apically ..... *S. angustifolium*

4. Capitula usually greenish, rather flat with a knoblike inner part of short concentrically crowded branches; stem leaves slightly but definitely longer than wide; eroded apically ..... *S. flexuosum*

5. Capitula flat; branch leaves non-recurved when dry, unranked, branch leaf cells on outer surface with numerous small pores often in two rows; chlorophyllose cells of branch leaves in transverse section isosceles-triangular, slightly enclosed on inner surface ..... *S. obtusum*

5. Capitula +/- convex; branch leaves sharply recurved when dry, often conspicuously ranked; branch leaf cells on outer surface usually with one apical end pore; chlorophyllose cells of branch leaves in transverse section equilateral-triangular and broadly enclosed on inner surface ..... *S. recurvum*

6. Stem leaves acute-apiculate to apiculate; branch leaf tips strongly subulate-involute above; chlorophyllose cells of branch leaves in transverse section equilateral-triangular, broadly enclosed on inner surface ..... *S. pacificum*

6. Stem leaves varyingly acute-obtuse, acute to acute-apiculate; branch leaf tips weakly subulate-involute above; chlorophyllose cells of branch leaves in transverse section varyingly isosceles-triangular and narrowly enclosed on inner surface to equilateral-triangular and broadly enclosed on inner surface ..... *S. fallax*

Key to *Sphagnum fallax* morphs

1. Capitula green to yellow-brown; central capitulum branches nearly straight to slightly curved laterally, inner capitulum branches with markedly recurved leaf tips (45-90º, often >90º) when dry; stem leaves obtuse-acute; outer stem cortical cells indistinctly enlarged; chlorophyllose cells of branch leaves in transverse section isosceles-triangular and narrowly enclosed on inner surface ..... S. fallax morph
1. Capitula yellow-green, yellow-brown to brown; central capitulum branches markedly curved laterally, inner capitulum branches with little to moderately recurved leaf tips (<45º) when dry; stem leaves acute-apiculate to apiculate; outer layer stem cortical cells enlarged; chlorophyllose cells of branch leaves in transverse section isosceles triangular to ovate-triangular and broadly enclosed on the inner surface 2

    2. Capitula rather flat and clearly 5-radiate, central curved branches more or less sharply differentiated from outer branches and rather straight; branch leaves markedly 5-ranked ……..… S. isoviitae morph

    2. Capitula somewhat convex and indistinctly 5-radiate, central curved branches not clearly differentiated from outer branches; branch leaves indistinctly 5-ranked .... S. brevifolium morph

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AUTHOR CONTRIBUTIONS

A.J.S. and B.A. developed the project, conducted most of the field work, examined all plants microscopically, and participated in the lab work and data analysis. A.D. conducted the analyses and prepared the paper. H.S., K.I.F, and M.S.I. participated in field work and preparation of the paper.

DATA AVAILABILITY

The sequences and alignment analyzed in this study are available in Dryad ([TO BE UPLOADED UPON ACCEPTANCE]

SUPPORTING INFORMATION

Appendix S1. Voucher information for accessions included in the RADseq analyses.

Appendix S2. Phylogenetic relationships among samples of *Sphagnum recurvum* complex species and related species based on RADseq loci. Nodes with bootstrap support >50% are labeled.

Appendix S3. Genetic structure of *S. angustifolium* revealed by STRUCTURE analyses at increasing levels of K.

Appendix S4. Principal Components Analysis (PCA) of variation in RADseq loci among samples of (A) all *Sphagnum recurvum* complex species, (B) Pointed Leaf species, (C) Rounded Leaf species, (D) *S. fallax*, *S. isoviitae*, and *S. brevifolium*, (E) *S. angustifolium*, (F) *S. pacificum*, (G) *S. flexuosum*.

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Figure Legends

Fig. 1. Summary of phylogenetic relationships among *Sphagnum recurvum* complex species and related species based on RADseq loci. Relationships were estimated using maximum likelihood (left) and singular value decomposition scores for species quartets (right). Nodes are labeled with bootstrap support values.

Fig 2. Stem leaf variation in the *S. recurvum* complex. All photos at same magnification; scale bar = 200 µm. 1-6 = *S. fallax*, 1-2 SB5051 (*BS19013*, PE), 3-4 SB5083 (*Ignatov 2015-14*, Russia), 5-6 SB5112 (*Garrett A149*, PE same site as img 1-2). 7-12 = *S*. “pseudopacificum”, 7-8 SB5225 (*Garrett AG541*, AK-Matanuska-Susitna), 9-10 SB5212 (*Garrett AG500*, AK-Alyeska), 11-12 SB5220 (*Garrett AG525*, AK-Kenai). 13-18 = *S. pacificum,* 13-14 SB5152 (*JS 2016-26A*, AK-Juneau), 15-16 SB5154 (*JS 2016-30*, AK-Whittier), 17-18 SB5179 (*Piatkowski 2017-60*, AK-Yakutat). 19-24 =*S. balticum,* 19-20 AG237 (*Garrett A225*, Norway), 21-22 AG249 (*Garrett A248*, Norway), 23-24 AG235 (*Garrett A220*, Norway). 25-31 = *S. angustifolium,* 25-26 SB5250 (*Piatkowski BP2018_145B*, WI), 27-28 SB5077 (*Ignatov 2015-6*, Russia), 29-30 SB5230 (*Garrett AG569*, AK-Fairbanks), 31 SB5252 (*Garrett AG586*, AK-Fairbanks), 32-37 = *S. obtusum,* 32-33 SB5229 (*Garrett AG579*, AK-Fairbanks), 34-35

SB5189 (*Piatkowski BP2017_264*, AK-Anchorage), 36-37 SB5215 (*Garrett AG513*, AK-Kenai) 38-43 = *S. flexuosum,* 38-39 SB4985 (*BS18906*, MD), 40-41 SB4976 (*Garrett A033*, MD), 42-43 SB5009 (*Garrett A075*, PA) 44-49 = *S. recurvum,* 44-45 SB4995 (*Garrett A064*, MD), 46-47 SB5109 (*Garrett A142*, PA), 48-49 SB5234 (*BA19605*, NC)

Fig. 3. Results of STRUCTURE analyses of RADseq loci for all *Sphagnum recurvum* complex species, for the Rounded Leaf and Pointed Leaf species separately, and for individual species. For each analysis, the optimal K-value is presented along with a higher K-value when it provides additional clustering information. *S. balticum* and *S. obtusum* were not analyzed separately due to small sample sizes, and a separate analysis of *S. recurvum* samples did not provide additional clustering information.

Fig. 4. Field-derived photographs of three morphologically distinguishable morphs within the phylogenetic species, *S. fallax*. These morphs are not distinguished by our molecular results but may warrant further study because of subtle morphological and ecological differences. A. fallax morph. B. brevifolium morph. C. isoviitae morph. Photos: Kjell Ivar Flatberg. License: CC BY 4.0 (Norwegian Environmental Specimen Bank).

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The Department of Biology

Duke University
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Durham, NC, USA 27708

6 February 2020

Dear Editor:

I herewith submit a Research Article manuscript entitled **Phylogenetic structure in the *Sphagnum recurvum* complex (Bryophyta: Sphagnaceae) relative to taxonomy and geography** for consideration by the AJB.

Note: the data associated with this paper is available in a Dropbox folder with the Phylip format alignment of concatenated loci, and the one-snp-per-locus data in Structure format. If the paper is accepted for publication we will put them on Dryad along with the demultiplexed reads.

https://www.dropbox.com/sh/yem1lklg7gjkj4b/AAAV9otbHPuzp5-w1bJAunJAa?dl=0

The *Sphagnum recuvum* complex is a group of closely related peatmoss species (Bryophyta) who's phylogenetic/taxonomic structure has been controversial for more than a century. The species have great ecological significance because they are important components of peat-forming wetland ecosystems that currently store some 25-30% of the total terrestrial carbon pool, and are therefore critical determinants of global climate. Moreover, peatmosses in the genus *Sphagnum* have long been utilized in research on community ecology, and more recently they have been developed as an exciting model system for comparative and ecological genomics. One species (*S. fallax*) in the *S. recurvum* complex, the focus of the current paper, has been sequenced to provide a high-quality reference genome for these purposes (supported by the JGI; paper in prep.), but its relationships to a suite of closely related species has remained ambiguous.

The specific questions this paper addresses are: (1) How many phylogenetically distinguishable species are there in the *S. recurvum* complex? (2) Is there genetic differentiation between plants on different continents such additional allopatric species are resolved, contrary to the interpretation that these species have intercontinental ranges? (3) If the species do have intercontinental ranges, is there detectable differentiation among metapopulation systems on different continents (or between eastern and western North American systems)?

The major contribution of this research is to resolve phylogenetic relationships, using a variety of approaches, and based on genome-scale data, in a widespread complex of

closely related spore-producing plants. We address global biogeographic patterns and document inter- and intraspecific variation within and between Northern Hemisphere continental areas. The research resolves important systematic and evolutionary questions, *and* deals formally with the taxonomic implications of those patterns. We document morphological variation and provide keys that will be important tools for ecologists and botanists working in wetland ecosystems, and more broadly, on embryophyte plants. As such, this research will be of interest to a very broad audience and can serve as a model for linking genome variation, morphology, and taxonomy.

Thank you for considering this paper for publication in the *American Journal of Botany*.

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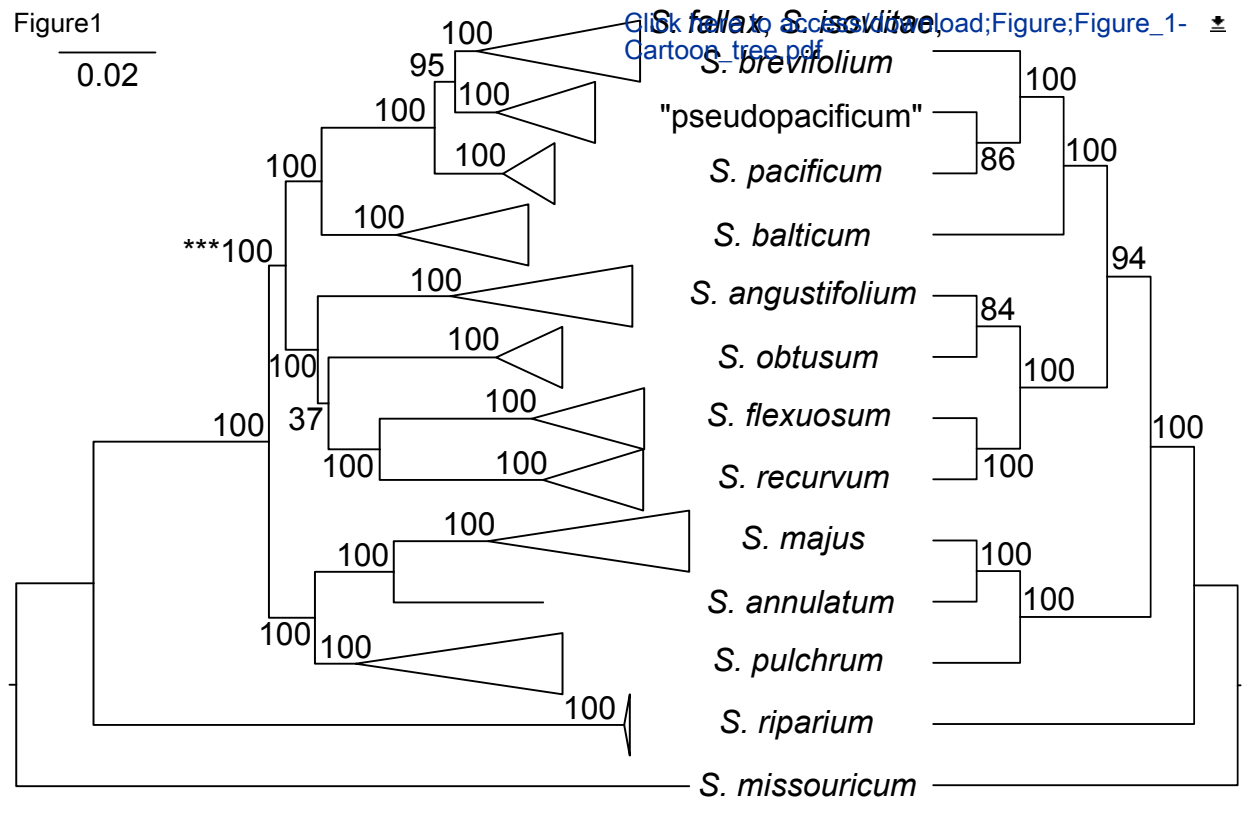
Figure1



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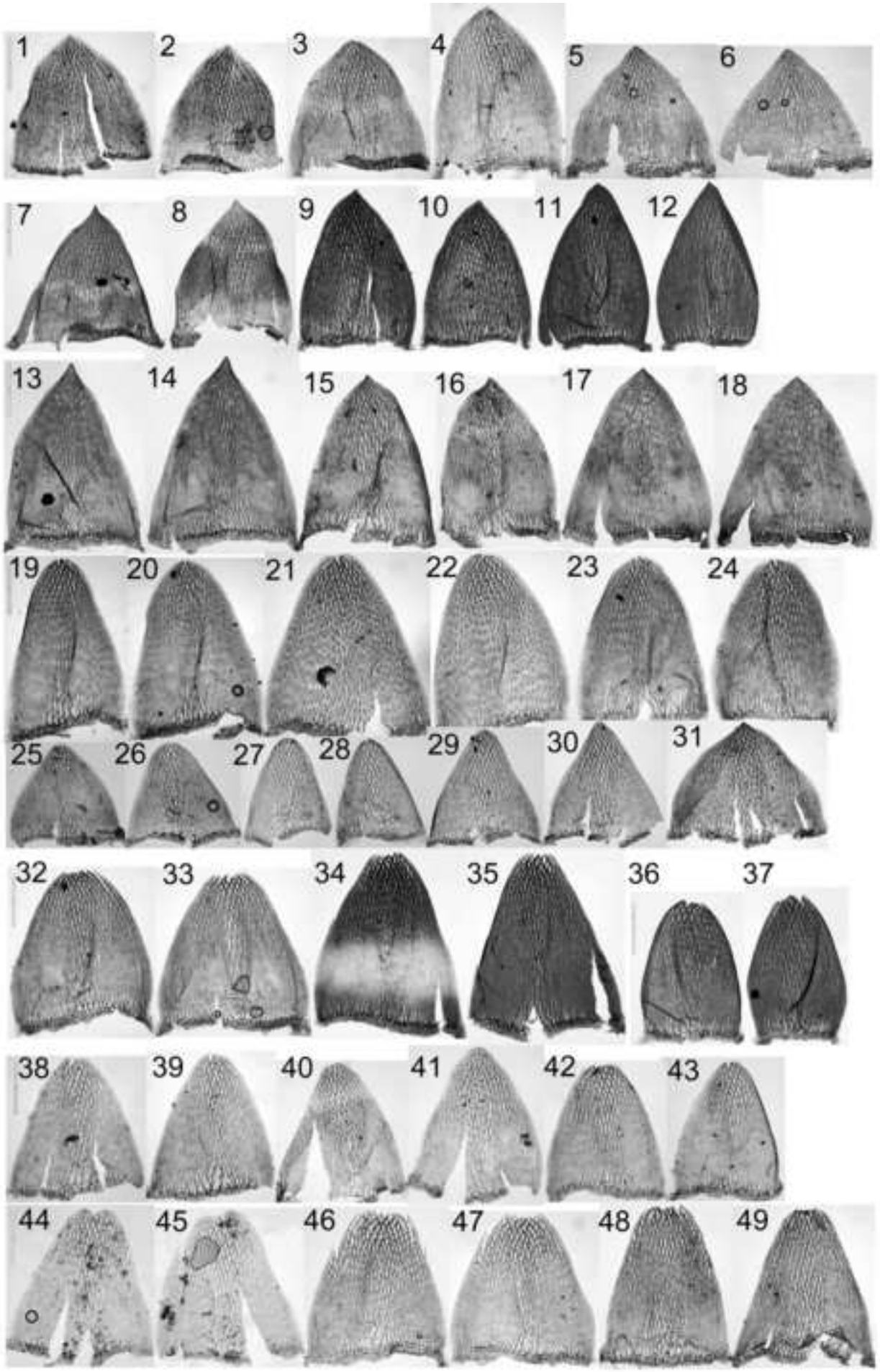

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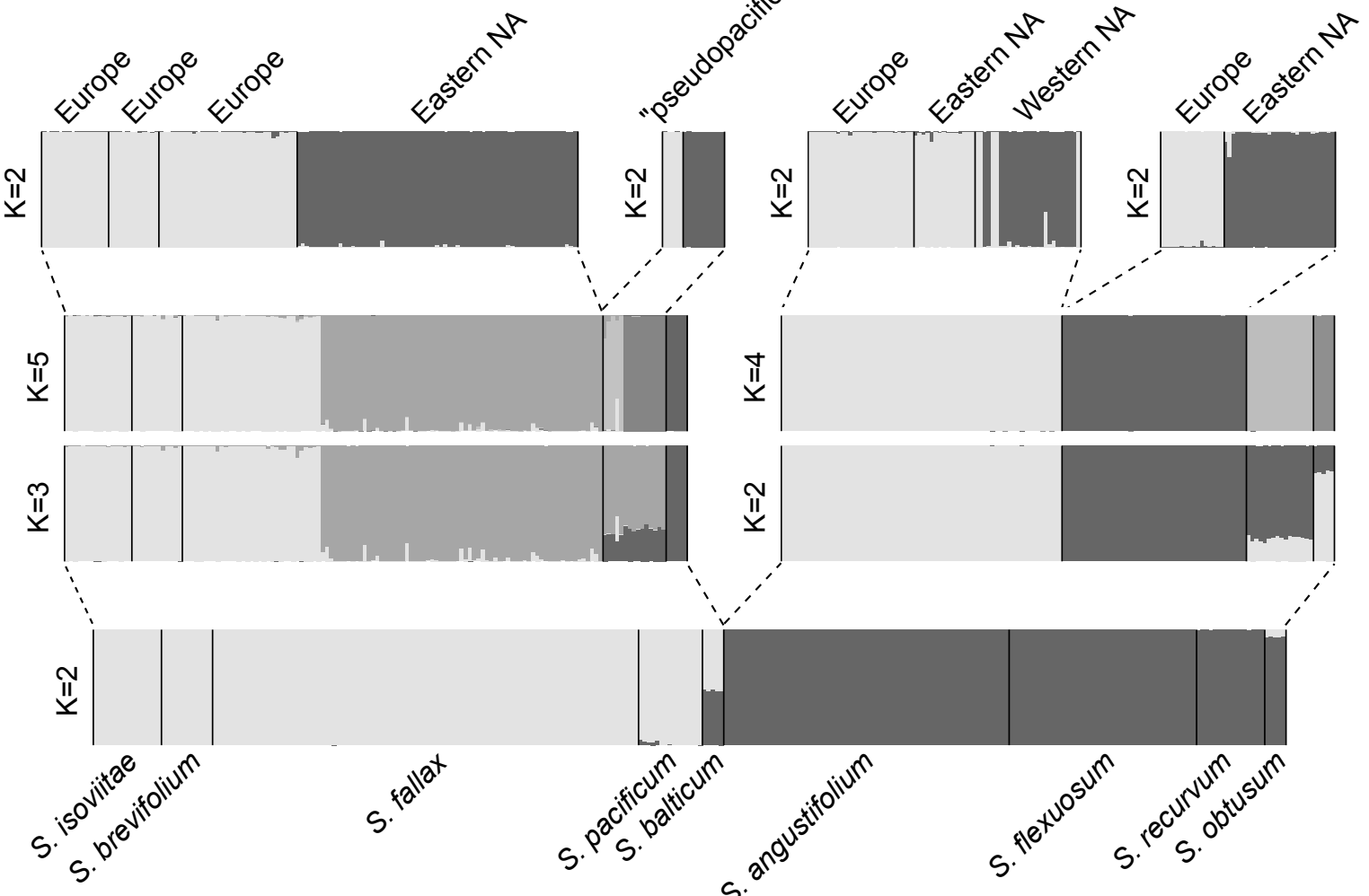

Table 1—Pairwise estimates of Nei's unbiased distance (above the diagonal) and Fst (below the diagonal) between species and leaf types in the *Sphagnum recurvum* complex.

	S. fallax	"pseudopacificum"	*S. pacificum*	*S. balticum*	*S. angustifolium*	*S. flexuosum*	*S. recurvum*	*S. obtusum*
S. fallax	0.000	0.017	0.024	0.084	0.103	0.119	0.123	0.137
"pseudopacificum"	0.041	0.000	0.035	0.080	0.105	0.121	0.129	0.135
S. pacificum	0.060	0.248	0.000	0.083	0.117	0.135	0.142	0.149
S. balticum	0.069	0.146	0.194	0.000	0.120	0.124	0.133	0.145
S. angustifolium	0.492	0.237	0.307	0.152	0.000	0.114	0.116	0.131
S. flexuosum	0.511	0.365	0.456	0.237	0.523	0.000	0.088	0.156
S. recurvum	0.250	0.157	0.283	-0.010	0.276	0.238	0.000	0.164
S. obtusum	0.115	0.318	0.381	0.045	0.128	0.220	0.010	0.000

Leaf type:

	Pointed	Rounded
Pointed	0	0.085
Rounded	0.336	0

Table 2—Genetic variability in species and leaf-types in the *Sphagnum recurvum* complex. N, number of individuals for each species or genetic cluster excluding clones and individuals showing >10% admixture between clusters; PPL, percent polymorphic loci; Na, mean alleles per locus; Ne, mean effective number of alleles per locus; PPr, percent private alleles; I, Shannon's information index.

	N	PPL	Na ±SE	Ne ±SE	PPr	I ±SE
Total	280	100.00	1.558 ±0.015	1.122 ±0.007		0.131 ±0.006
Pointed Leaf	148	41.24	1.418 ±0.021	1.082 ±0.009	23.76	0.091 ±0.007
S. fallax	128	29.51	1.300 ±0.023	1.070 ±0.010	13.33	0.073 ±0.008
"pseudopacificum"	5	7.73	1.077 ±0.013	1.049 ±0.009	1.09	0.044 ±0.007
S. pacificum	10	5.62	1.056 ±0.011	1.031 ±0.007	2.00	0.029 ±0.006
S. balticum	5	5.39	1.054 ±0.011	1.037 ±0.008	3.78	0.032 ±0.006
Rounded Leaf	132	68.38	1.699 ±0.020	1.163 ±0.012	36.40	0.171 ±0.009
S. angustifolium	67	27.40	1.274 ±0.022	1.076 ±0.010	14.89	0.079 ±0.008
S. flexuosum	44	16.63	1.169 ±0.018	1.056 ±0.009	10.42	0.058 ±0.008
S. recurvum	16	14.75	1.148 ±0.017	1.046 ±0.007	11.43	0.053 ±0.007
S. obtusum	5	7.73	1.077 ±0.013	1.052 ±0.009	8.70	0.045 ±0.008

AppendixS1

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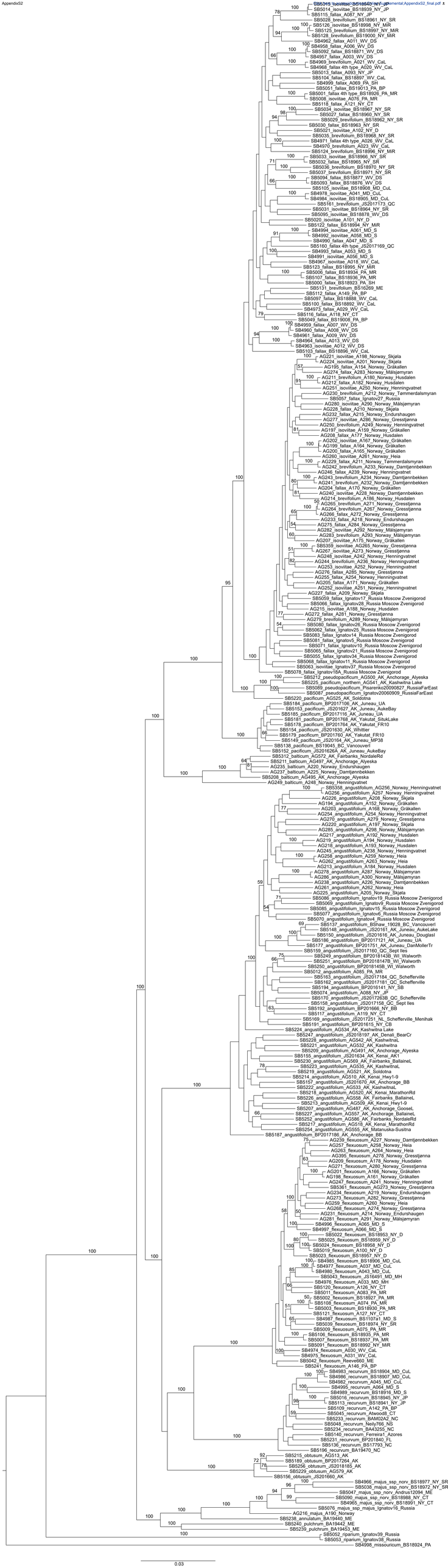
DNA isolate	plate	barcode	Sphagnum species	Collectors	Col. nr.	Country	State/Province	County/District	Collection Date	Locality short	Locality full	Loc abbr
AG194	1	GACTCGTT	angustifolium	A. Garrett	A152	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG195	1	AGTTAGTT	fallax	A. Garrett	A154	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG197	1	CAGATCTT	isovitae	A. Garrett	A159	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG198	1	CTATCCTT	flexuosum	A. Garrett	A161	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG199	1	GGTACCTT	fallax	A. Garrett	A164	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG200	1	TCCTACTT	fallax	A. Garrett	A165	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG201	1	AGAGTATT	flexuosum	A. Garrett	A166	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG202	1	GAGCGATT	isovitae	A. Garrett	A167	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG203	1	CCTCCATT	angustifolium	A. Garrett	A168	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG204	1	GTTGAATT	fallax	A. Garrett	A170	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG205	1	TGCTTGGT	fallax	A. Garrett	A171	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG207	1	GCAGTCGT	isovitae	A. Garrett	A175	Norway	Sør-Trøndelag	Trondheim	8/12/13	Gråkallen	Gråkallen	
AG208	1	AACCTCGT	fallax	A. Garrett	A177	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG209	1	TATAACGT	flexuosum	A. Garrett	A178	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG211	1	TCGATTCT	brevifolium	A. Garrett	A180	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG212	1	AGTCGTCT	fallax	A. Garrett	A182	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG213	1	GACGTACT	angustifolium	A. Garrett	A184	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG214	1	CGGAGACT	brevifolium	A. Garrett	A186	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG215	1	ACGCAACT	isovitae	A. Garrett	A188	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG216	1	TACGGTAT	majus	A. Garrett	A190	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG217	1	CTGCCTAT	angustifolium	A. Garrett	A192	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG218	1	ATAGATAT	angustifolium	A. Garrett	A193	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG219	1	CCAATGAT	angustifolium (toward flexuosum)	A. Garrett	A194	Norway	Sør-Trøndelag	Orkdal	8/13/13	Husdalen	Husdalen, series of mires around lake Husdalsvatnet	
AG220	1	TCTCGGAT	angustifolium	A. Garrett	A197	Norway	Sør-Trøndelag	Trondheim	8/14/13	Skjøla	Skjøla, mountain-side by parking lot	
AG221	1	AATACGAT	isovitae	A. Garrett	A198	Norway	Sør-Trøndelag	Trondheim	8/14/13	Skjøla	Skjøla. Vassfjellet Chapel	
AG224	1	AGCTCAAT	isovitae	A. Garrett	A201	Norway	Sør-Trøndelag	Trondheim	8/14/13	Skjøla	Skjøla. Vassfjellet Chapel	
AG225	1	ATAGGCTG	angustifolium	A. Garrett	A205	Norway	Sør-Trøndelag	Trondheim	8/14/13	Skjøla	Skjøla. Vassfjellet Chapel	
AG226	1	TGGAGCTG	angustifolium	A. Garrett	A208	Norway	Sør-Trøndelag	Trondheim	8/14/13	Skjøla	Skjøla. Vassfjellet Chapel	
AG227	1	GCCATATG	fallax	A. Garrett	A209	Norway	Sør-Trøndelag	Trondheim	8/14/13	Skjøla	Skjøla. Vassfjellet Chapel	
AG228	1	TGATAATG	fallax	A. Garrett	A210	Norway	Sør-Trøndelag	Trondheim	8/14/13	Skjøla	Skjøla. Vassfjellet Chapel	
AG229	1	CAAGATGG	fallax	A. Garrett	A211	Norway	Sør-Trøndelag	Klæbu	8/14/13	Tømmerdalsmyran	Tømmerdalsmyran mire	
AG230	1	TAGGTCGG	brevifolium	A. Garrett	A212	Norway	Sør-Trøndelag	Klæbu	8/14/13	Tømmerdalsmyran	Tømmerdalsmyran mire	
AG231	1	CCTGGCGG	flexuosum	A. Garrett	A214	Norway	Sør-Trøndelag	Melhus	8/14/13	Endurshaugen	Endurshaugen	
AG232	1	TCGCGAGG	fallax	A. Garrett	A215	Norway	Sør-Trøndelag	Melhus	8/14/13	Endurshaugen	Endurshaugen	
AG233	1	GATAGAGG	fallax	A. Garrett	A218	Norway	Sør-Trøndelag	Melhus	8/14/13	Endurshaugen	Endurshaugen	
AG234	1	ACCGAAGG	flexuosum	A. Garrett	A219	Norway	Sør-Trøndelag	Melhus	8/14/13	Endurshaugen	Endurshaugen	
AG235	1	CCTAATCG	balticum	A. Garrett	A220	Norway	Sør-Trøndelag	Melhus	8/14/13	Endurshaugen	Endurshaugen	
AG237	1	ATGATTAG	balticum	A. Garrett	A225	Norway	Sør-Trøndelag	Klæbu	8/14/13	Damtjønnbekken	Damtjønnbekken W Stream fen	
AG238	1	GTTCATAG	angustifolium	A. Garrett	A226	Norway	Sør-Trøndelag	Klæbu	8/14/13	Damtjønnbekken	Damtjønnbekken W Stream fen	
AG239	1	TTCTTCAG	flexuosum	A. Garrett	A227	Norway	Sør-Trøndelag	Klæbu	8/14/13	Damtjønnbekken	Damtjønnbekken W Stream fen	
AG240	1	ACTCTCAG	isovitae	A. Garrett	A228	Norway	Sør-Trøndelag	Klæbu	8/14/13	Damtjønnbekken	Damtjønnbekken W Stream fen	
AG241	1	TTAGCAAG	brevifolium	A. Garrett	A232	Norway	Sør-Trøndelag	Klæbu	8/14/13	Damtjønnbekken	Damtjønnbekken W Stream fen	
AG242	1	AACCGTTC	brevifolium	A. Garrett	A233	Norway	Sør-Trøndelag	Klæbu	8/14/13	Damtjønnbekken	Damtjønnbekken W Stream fen	
AG243	1	GGCTATTC	brevifolium	A. Garrett	A234	Norway	Sør-Trøndelag	Klæbu	8/14/13	Damtjønnbekken	Damtjønnbekken W Stream fen	
AG244	1	TTATGGTC	brevifolium	A. Garrett	A236	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG245	1	CGGCGGTC	angustifolium	A. Garrett	A238	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG246	1	TCGCTCTC	fallax	A. Garrett	A239	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG247	1	CTTATATC	flexuosum	A. Garrett	A241	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG248	1	AGCGCGGC	isovitae	A. Garrett	A242	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG249	1	TGGTCCGC	balticum	A. Garrett	A248	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG250	1	GGAATAGC	brevifolium	A. Garrett	A249	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG251	1	GCCTCAGC	isovitae	A. Garrett	A250	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG252	1	AATCAAGC	isovitae	A. Garrett	A251	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG253	1	GTAGTTCC	isovitae	A. Garrett	A252	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG254	1	CGCCTTCC	angustifolium	A. Garrett	A254	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG255	1	TTGCGTCC	fallax	A. Garrett	A254	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG256	1	ATCTCTCC	angustifolium	A. Garrett	A257	Norway	Nord-Trøndelag	Steinkjer	8/15/13	Henningvatnet	Henningvatnet	
AG257	1	CAGGCTCC	flexuosum	A. Garrett	A258	Norway	Nord-Trøndelag	Grong	8/15/13	Heia	Heia	
AG258	1	TGAACTCC	angustifolium	A. Garrett	A259	Norway	Nord-Trøndelag	Grong	8/15/13	Heia	Heia	
AG259	1	AGATTGCC	flexuosum	A. Garrett	A260	Norway	Nord-Trøndelag	Grong	8/15/13	Heia	Heia	
AG260	1	GGTAGGCC	isovitae	A. Garrett	A261	Norway	Nord-Trøndelag	Grong	8/15/13	Heia	Heia	
AG261	1	CTACCGCC	angustifolium	A. Garrett	A262	Norway	Nord-Trøndelag	Grong	8/15/13	Heia	Heia	
AG262	1	ACGACGCC	angustifolium	A. Garrett	A263	Norway	Nord-Trøndelag	Grong	8/15/13	Heia	Heia	
AG263	1	ATTGAGCC	flexuosum	A. Garrett	A264	Norway	Nord-Trøndelag	Grong	8/15/13	Heia	Heia	
AG264	1	CCGTTACC	brevifolium	A. Garrett	A267	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG265	1	TGCTGACC	brevifolium	A. Garrett	A271	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG266	1	ATAAGACC	fallax	A. Garrett	A272	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG267	1	CGAGAACC	isovitae	A. Garrett	A273	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG268	1	GTCCAACC	flexuosum	A. Garrett	A274	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG270	1	CCATCTAC	angustifolium	A. Garrett	A279	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG271	1	AGGCATAC	flexuosum	A. Garrett	A280	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG272	1	TAGAGGAC	fallax	A. Garrett	A281	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG273	1	GACGAGAC	flexuosum	A. Garrett	A282	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG274	1	GAACCAAC	fallax	A. Garrett	A283	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG275	1	TTGCAGTA	fallax	A. Garrett	A284	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG276	1	GACGGCTA	fallax	A. Garrett	A285	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG277	1	CTCGTTGA	isovitae	A. Garrett	A286	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
AG278	1	GTATCTGA	angustifolium	A. Garrett	A287	Norway	Sor-Trøndelag	Klæbu	8/17/13	Målsjømyran	Målsjømyran	
AG279	1	TCTACTGA	brevifolium	A. Garrett	A289	Norway	Sor-Trøndelag	Klæbu	8/17/13	Målsjømyran	Målsjømyran	
AG280	1	CGTAAGGA	isovitae	A. Garrett	A290	Norway	Sor-Trøndelag	Klæbu	8/17/13	Målsjømyran	Målsjømyran	
AG281	1	GGTCTCGA	flexuosum	A. Garrett	A291	Norway	Sor-Trøndelag	Klæbu	8/17/13	Målsjømyran	Målsjømyran	
AG282	1	AATTGCGA	isovitae	A. Garrett	A292	Norway	Sor-Trøndelag	Klæbu	8/17/13	Målsjømyran	Målsjømyran	
AG283	1	GCGTACGA	brevifolium	A. Garrett	A293	Norway	Sor-Trøndelag	Klæbu	8/17/13	Målsjømyran	Målsjømyran	
AG285	1	CCGCGCCA	angustifolium	A. Garrett	A298	Norway	Sor-Trøndelag	Klæbu	8/17/13	Målsjømyran	Målsjømyran	
AG286	1	ACTGGTAA	angustifolium	A. Garrett	A300	Norway	Sor-Trøndelag	Klæbu	8/17/13	Målsjømyran	Målsjømyran	
AG395	1	GCTTCGAA	flexuosum	A. Garrett	A278	Norway	Nord-Trøndelag	Høylandet	8/16/13	Gresstjønna	Gresstjønna lake and Latmyrbukta	
SB4957	2	GACTCGTT	fallax	A. Garrett	A003	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	0.3 mi E of Dolly Sods. Picnic Ground on FR19. Poor fen with smal	DS
SB4958	2	AGTTAGTT	fallax	A. Garrett	A006	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	0.3 mi E of Dolly Sods. Picnic Ground on FR19. Poor fen with smal	DS
SB4959	2	TAAGAGTT	fallax	A. Garrett	A007	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	0.3 mi E of Dolly Sods. Picnic Ground on FR19. Poor fen with smal	DS
SB4960	2	CAGATCTT	fallax	A. Garrett	A008	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	0.3 mi E of Dolly Sods. Picnic Ground on FR19. Poor fen with smal	DS
SB4961	2	CTATCCTT	fallax	A. Garrett	A009	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	0.3 mi E of Dolly Sods. Picnic Ground on FR19. Poor fen with smal	DS
SB4962	2	GGTACCTT	fallax	A. Garrett	A011	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	0.3 mi E of Dolly Sods. Picnic Ground on FR19. Poor fen with smal	DS
SB4963	2	TCCTACTT	isovitae	A. Garrett	A012	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	0.3 mi E of Dolly Sods. Picnic Ground on FR19. Poor fen with smal	DS
SB4964	2	AGAGTATT	fallax	A. Garrett	A013	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	0.3 mi E of Dolly Sods. Picnic Ground on FR19. Poor fen with smal	DS
SB4965	2	GAGCGATT	majus ssp. norvegicum	B. Shaw	18991	USA	New York	Warren Co.	24-Jun-13	Carl Turner	Along Carl Turner Rd. just E of I-87, S of Schroon Lake, 0.4 mi NE	CT
SB4966	2	CCTCCATT	majus ssp. norvegicum	B. Shaw	18977	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR
SB4967	2	GTTGAATT	isovitae	A. Garrett	A018	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	1.5 in on FR13. Wet drainage ditch around a field. Surrounding ar	CaL
SB4968	2	TGCTTGGT	fallax 4th type	A. Garrett	A020	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	1.5 in on FR13. Wet drainage ditch around a field. Surrounding ar	CaL
SB4969	2	GTTCCGGT	brevifolium	A. Garrett	A021	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	1.5 in on FR13. Wet drainage ditch around a field. Surrounding ar	CaL
SB4970	2	GCAGTCGT	brevifolium	A. Garrett	A023	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	3.0 mi in on FR13. Shrubby poor fent with Picea, Tsuga, Acer rubr	CaL
SB4971	2	AACCTCGT	fallax 4th type	A. Garrett	A026	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	3.0 mi in on FR13. Shrubby poor fent with Picea, Tsuga, Acer rubr	CaL
SB4973	2	TAATCAGT	fallax	A. Garrett	A029	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	3.0 mi in on FR13. Shrubby poor fent with Picea, Tsuga, Acer rubr	CaL
SB4974	2	TCGATTCT	flexuosum	A. Garrett	A030	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	3.0 mi in on FR13. Shrubby poor fent with Picea, Tsuga, Acer rubr	CaL
SB4975	2	AGTCGTCT	flexuosum	A. Garrett	A031	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	3.0 mi in on FR13. Shrubby poor fent with Picea, Tsuga, Acer rubr	CaL
SB4976	2	GACGTACT	flexuosum	A. Garrett	A033	USA	Maryland	Garrett Co.	20-Jun-13	McHenry	Mosser rd. E of junction with US219 in McHenry. Stream floodpla	MH
SB4977	2	CGGAGACT	flexuosum (toward angustifolium)	A. Garrett	A037	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	SW of Grantsville. SW of US 219 on 4H Camp rd. End of road at sr	CuL
SB4978	2	ACGCAACT	isovitae	A. Garrett	A041	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	SW of Grantsville. SW of US 219 on 4H Camp rd. End of road at sr	CuL
SB4980	2	CTGCCTAT	flexuosum	A. Garrett	A043	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	SW of Grantsville. SW of US 219 on 4H Camp rd. End of road at sr	CuL
SB4982	2	CCAATGAT	recurvum	A. Garrett	A045	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	SW of Grantsville. SW of US 219 on 4H Camp rd. End of road at sr	CuL
SB4983	2	TCTCGGAT	recurvum	B. Shaw	18904	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	Along NE shore of Cunningham Lake, S of 4-H Camp Rd., 0.85 mi	CuL
SB4984	2	AATACGAT	isovitae	B. Shaw	18905	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	Along NE shore of Cunningham Lake, S of 4-H Camp Rd., 0.85 mi	CuL
SB4985	2	CAGTAGAT	flexuosum	B. Shaw	18906	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	Along NE shore of Cunningham Lake, S of 4-H Camp Rd., 0.85 mi	CuL
SB4986	2	TCGGCCAT	recurvum	B. Shaw	18907	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	Along NE shore of Cunningham Lake, S of 4-H Camp Rd., 0.85 mi	CuL
SB4987	2	AGCTCAAT	flexuosum	B. Shaw	1107a/1	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4989	2	TGGAGCTG	recurvum	B. Shaw	18916	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4990	2	GCCATATG	fallax	A. Garrett	A047	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4991	2	TGATAATG	isovitae	A. Garrett	A056	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4992	2	CAAGATGG	isovitae	A. Garrett	A058	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4993	2	TAGGTCGG	fallax	A. Garrett	A053	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4994	2	CCTGGCGG	isovitae	A. Garrett	A061	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4995	2	TCGCGAGG	recurvum	A. Garrett	A064	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4996	2	GATAGAGG	flexuosum	A. Garrett	A065	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4997	2	ACCGAAGG	flexuosum	A. Garrett	A066	USA	Maryland	Garrett Co.	21-Jun-13	Salem Dr.	Wetland along E shore of dam S of Salem Dr., 0.35 mi W of jct. w	S
SB4998	2	CCTAATCG	missouricum	B. Shaw	18924	USA	Pennsylvania	Elk Co.	22-Jun-13	Stony Hill	Stony Hill Rd., between Market Rd. and Lime Kiln Rd., 0.8 mi S of	SH
SB4999	2	AACTACCG	fallax	A. Garrett	A069	USA	Pennsylvania	Elk Co.	22-Jun-13	Stony Hill	Stony Hill Rd., between Market Rd. and Lime Kiln Rd., 0.8 mi S of	SH
SB5000	2	ATGATTAG	fallax	B. Shaw	18923	USA	Pennsylvania	Elk Co.	22-Jun-13	Stony Hill	Stony Hill Rd., between Market Rd. and Lime Kiln Rd., 0.8 mi S of	SH
SB5001	2	GTTCATAG	fallax 4th type	B. Shaw	18926	USA	Pennsylvania	Elk Co.	22-Jun-13	Martin Run	Stony Hill Rd., between Market Rd. and Lime Kiln Rd., 0.8 mi S of	MR
SB5002	2	TTCTTCAG	flexuosum	B. Shaw	18927	USA	Pennsylvania	Elk Co.	22-Jun-13	Martin Run	Stony Hill Rd., between Market Rd. and Lime Kiln Rd., 0.8 mi S of	MR
SB5003	2	ACTCTCAG	flexuosum	B. Shaw	18930	USA	Pennsylvania	Elk Co.	22-Jun-13	Martin Run	Stony Hill Rd., between Market Rd. and Lime Kiln Rd., 0.8 mi S of	MR
SB5006	2	GGCTATTC	fallax	B. Shaw	18934	USA	Pennsylvania	Elk Co.	22-Jun-13	Martin Run	Stony Hill Rd., between Market Rd. and Lime Kiln Rd., 0.8 mi S of	MR
SB5007	2	TTATGGTC	flexuosum	B. Shaw	18937	USA	Pennsylvania	Elk Co.	22-Jun-13	Martin Run	Stony Hill Rd., between Market Rd. and Lime Kiln Rd., 0.8 mi S of	MR
SB5008	2	CGGCGGTC	isovitae	A. Garrett	A076	USA	Pennsylvania	McKean Co	22-Jun-13	Martin Run	Sergeant Twp., along Martin Run just N of Wilcox-Claremont Rd.	MR
SB5009	2	TCGCTCTC	flexuosum	A. Garrett	A075	USA	Pennsylvania	McKean Co	22-Jun-13	Martin Run	Sergeant Twp., along Martin Run just N of Wilcox-Claremont Rd.	MR
SB5011	2	AGCGCGGC	flexuosum	A. Garrett	A083	USA	Pennsylvania	McKean Co	22-Jun-13	Martin Run	Sergeant Twp., along Martin Run just N of Wilcox-Claremont Rd.	MR
SB5012	2	TGGTCCGC	angustifolium	A. Garrett	A085	USA	Pennsylvania	McKean Co	22-Jun-13	Martin Run	Sergeant Twp., along Martin Run just N of Wilcox-Claremont Rd.	MR
SB5013	2	GGAATAGC	fallax	A. Garrett	A093	USA	New York	Chenango Co.	22-Jun-13	Jam Pond	German Twp., Jam Pond Bog, N of county rd. 5 between Rabbit P	JP
SB5014	2	GCCTCAGC	isovitae	B. Shaw	18939	USA	New York	Chenango Co.	22-Jun-13	Jam Pond	German Twp., Jam Pond Bog, N of county rd. 5 between Rabbit P	JP
SB5015	2	AATCAAGC	isovitae	B. Shaw	18940	USA	New York	Chenango Co.	22-Jun-13	Jam Pond	German Twp., Jam Pond Bog, N of county rd. 5 between Rabbit P	JP
SB5016	2	GTAGTTCC	recurvum	B. Shaw	18945	USA	New York	Chenango Co.	22-Jun-13	Jam Pond	German Twp., Jam Pond Bog, N of county rd. 5 between Rabbit P	JP
SB5019	2	ATCTCTCC	flexuosum	A. Garrett	A100	USA	New York	St. Lawrence Co.	23-Jun-13	Dubuar	Adirondacks region, N of NY-3 just W of James Dubuar Memorial	D
SB5020	2	CAGGCTCC	isovitae	A. Garrett	A101	USA	New York	St. Lawrence Co.	23-Jun-13	Dubuar	Adirondacks region, N of NY-3 just W of James Dubuar Memorial	D
SB5021	2	TGAACTCC	isovitae	A. Garrett	A102	USA	New York	St. Lawrence Co.	23-Jun-13	Dubuar	Adirondacks region, N of NY-3 just W of James Dubuar Memorial	D
SB5022	2	AGATTGCC	flexuosum	B. Shaw	18953	USA	New York	St. Lawrence Co.	23-Jun-13	Dubuar	Adirondacks region, N of NY-3 just W of James Dubuar Memorial	D
SB5023	2	GGTAGGCC	flexuosum	B. Shaw	18957	USA	New York	St. Lawrence Co.	23-Jun-13	Dubuar	Adirondacks region, N of NY-3 just W of James Dubuar Memorial	D
SB5024	2	CTACCGCC	flexuosum	B. Shaw	18958	USA	New York	St. Lawrence Co.	23-Jun-13	Dubuar	Adirondacks region, N of NY-3 just W of James Dubuar Memorial	D
SB5025	2	ACGACGCC	flexuosum	B. Shaw	18959	USA	New York	St. Lawrence Co.	23-Jun-13	Dubuar	Adirondacks region, N of NY-3 just W of James Dubuar Memorial	D
SB5027	2	CCGTTACC	fallax	B. Shaw	18960	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR
SB5028	2	TGCTGACC	brevifolium	B. Shaw	18961	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR
SB5029	2	ATAAGACC	brevifolium	B. Shaw	18962	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR
SB5030	2	CGAGAACC	fallax	B. Shaw	18963	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR
SB5031	2	GTCCAACC	isovitae	B. Shaw	18964	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR
SB5032	2	CTCAGTAC	fallax	B. Shaw	18965	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR
SB5033	2	CCATCTAC	isovitae	B. Shaw	18966	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR

SBS034	2	AGGCATAC	isoviitae	B. Shaw	18967	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR	
SBS035	2	TAGAGGAC	brevifolium	B. Shaw	18968	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR	
SBS036	2	GACGAGAC	brevifolium	B. Shaw	18970	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR	
SBS037	2	GAACCAAC	brevifolium	B. Shaw	18971	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR	
SBS038	2	TTGCAGTA	majus ssp. norvegicum	B. Shaw	18972	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR	
SBS039	2	GACGGCTA	flexuosum	B. Shaw	18974	USA	New York	Franklin Co	23-Jun-13	St. Regis Lake	Adirondacks region, E side of Lower St. Regis Lake N of Tupper La	SR	
SBS042	2	TCTACTGA	flexuosum	M. Reeve	660	USA	ME	Waldo Co.	10-Nov-10	Belfast	Belfast. Just NE of the beginning of the "Little River Nature Trail"		
SBS043	2	CGTAAGGA	flexuosum	J. Shaw	16491	USA	Maryland	Garrett Co.	20-Jun-13	McHenry	The Glades, 4.2 mi E of McHenry	MH	
SBS045	2	AATTGCGA	recurvum	J. Atwood	8	USA	Connecticut	New London Co.	28-Jul-02	Voluntown, Pachaug State Forest	Town of Voluntown, Pachaug State Forest, W of CT 49, immediately N of Herman Hauptman and Chapman Management Area		
SBS047	2	CAAGTCCA	majus ssp. norvegicum	R.E. Andrus	12094	USA	ME	Penobscot Co.	11-Aug-09	Marble Fen	Marble Fen		
SBS048	2	CCGCGCCA	recurvum	T. Neily	766	Canada	Nova Scotia	Yarmouth Co.	22-Aug-12	Long Lake	Long Lake		
SBS049	2	ACTGGTAA	fallax	B. Shaw	19008	USA	Pennsylvania	Pike Co.	25-Jun-13	Billings Pond	Billings Pond, N of Co. rd. 4004 (Blooming Grove Rd.), 1.1 mi W of	BP	
SBS051	2	GCTTCGAA	fallax	B. Shaw	19013	USA	Pennsylvania	Pike Co.	25-Jun-13	Billings Pond	Billings Pond, N of Co. rd. 4004 (Blooming Grove Rd.), 1.1 mi W of	BP	
SBS052	3	ATCAGGTT	riparium	M. Ignatov & E. Ignatova	2015-39	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS053	3	GACTCGTT	riparium	M. Ignatov & E. Ignatova	2015-38	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS055	3	TAAGAGTT	fallax	M. Ignatov & E. Ignatova	2015-34	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS057	3	CTATCCTT	fallax	M. Ignatov & E. Ignatova	2015-27	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS059	3	TCCTACTT	fallax	M. Ignatov & E. Ignatova	2015-17	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS062	3	CCTCCATT	fallax	M. Ignatov & E. Ignatova	2015-25	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS063	3	TGCTTGGT	isoviitae	M. Ignatov & E. Ignatova	2015-37	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS065	3	GTTCCGGT	fallax	M. Ignatov & E. Ignatova	2015-21	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS066	3	GCAGTCGT	fallax (macroscopically angustifolium-like)	M. Ignatov & E. Ignatova	2015-28 (loc 36)	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS068	3	TATAACGT	fallax	M. Ignatov & E. Ignatova	2015-11	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS069	3	TAATCAGT	angustifolium	M. Ignatov & E. Ignatova	2015-9	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS070	3	TCGATTCT	angustifolium (homophyllous plants)	M. Ignatov & E. Ignatova	2015-4	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS071	3	AGTCGTCT	fallax	M. Ignatov & E. Ignatova	2015-10	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS074	3	ACGCAACT	angustifolium	A. Garrett	A088	USA	New York	Chenango Co.	22-Jun-13	Jam Pond	German Twp., Jam Pond Bog, N of county rd. 5 between Rabbit P	JP	
SBS076	3	CTGCCTAT	majus ssp. majus	M. Ignatov & E. Ignatova	2015-16	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS077	3	ATAGATAT	angustifolium	M. Ignatov & E. Ignatova	2015-6	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS078	3	CCAATGAT	fallax	M. Ignatov & E. Ignatova	2015-18A	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS080	3	AATACGAT	fallax	M. Ignatov & E. Ignatova	2015-26	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS081	3	CAGTAGAT	fallax	M. Ignatov & E. Ignatova	2015-5	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS083	3	AGCTCAAT	fallax s.l.	M. Ignatov & E. Ignatova	2015-14	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS085	3	TGGAGCTG	angustifolium	M. Ignatov & E. Ignatova	2015-15	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS086	3	GCCATATG	angustifolium	M. Ignatov & E. Ignatova	2015-19	Russia	Moscow Province	Odinzovo Distr.	2015	Zvenigorod	Zvenigorod Biological Station of Moscow State University	RU	
SBS087	3	TGATAATG	pseudopacificum	M. Ignatov	9.9.2006	Russia			9-Sep-06	RU2		RU2	
SBS089	3	TAGGTCGG	pseudopacificum	Pisarenko	27.8.2009	Russia			27-Aug-09	RU4		RU4	
SBS090	3	CCTGGCGG	majus ssp. norvegicum	B. Shaw	18988	USA	New York	Warren Co.	24-Jun-13	Carl Turner	Along Carl Turner Rd. just E of I-87, S of Schroon Lake, 0.4 mi NE	CT	
SBS091	3	TCGCGAGG	flexuosum	B. Shaw	18992	USA	New York	Rensselaer Co.	24-Jun-13	Miller Rd.	Sandlake Twp. E of Albany, along Miller Rd. 0.8 mi S of jct. with N	MR	
SBS092	3	GATAGAGG	fallax	B. Shaw	18871	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	Along FR-19 (Dolly Sods Rd.), 0.2 mi NE of Dolly Sods Picnic Grou	DS	
SBS093	3	ACCGAAGG	fallax	B. Shaw	18876	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	Along FR-19 (Dolly Sods Rd.), 0.2 mi NE of Dolly Sods Picnic Grou	DS	
SBS094	3	CCTAATCG	fallax	B. Shaw	18877	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	Along FR-19 (Dolly Sods Rd.), 0.2 mi NE of Dolly Sods Picnic Grou	DS	
SBS095	3	AACTACCG	isoviitae	B. Shaw	18878	USA	West Virginia	Grant Co.	20-Jun-13	Dolly Sods	Along FR-19 (Dolly Sods Rd.), 0.2 mi NE of Dolly Sods Picnic Grou	DS	
SBS097	3	GTTCATAG	fallax	B. Shaw	18888	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	Canaan Valley area, along FR-13 (Canaan Loop Rd.), 3.0 mi SW of	CaL	
SBS100	3	TTAGCAAG	fallax	B. Shaw	18892	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	Canaan Valley area, along FR-13 (Canaan Loop Rd.), 3.0 mi SW of	CaL	
SBS103	3	TTATGGTC	fallax	B. Shaw	18896	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	Canaan Valley area, along FR-13 (Canaan Loop Rd.), 3.0 mi SW of	CaL	
SBS104	3	CGGCGGTC	fallax	B. Shaw	18897	USA	West Virginia	Grant Co.	20-Jun-13	Canaan Loop Rd.	Canaan Valley area, along FR-13 (Canaan Loop Rd.), 3.0 mi SW of	CaL	
SBS105	3	TCGCTCTC	isoviitae	B. Shaw	18908	USA	Maryland	Garrett Co.	21-Jun-13	Cunningham Lake	Along NE shore of Cunningham Lake, S of 4-H Camp Rd., 0.85 mi	CuL	
SBS106	3	CTTATATC	flexuosum	B. Shaw	18935	USA	Pennsylvania	McKean Co	22-Jun-13	Martin Run	Sergeant Twp., along Martin Run just N of Wilcox-Claremont Rd.	MR	
SBS107	3	AGCGCGGC	fallax	B. Shaw	18936	USA	Pennsylvania	McKean Co	22-Jun-13	Martin Run	Sergeant Twp., along Martin Run just N of Wilcox-Claremont Rd.	MR	
SBS108	3	TGGTCCGC	flexuosum (rubroflexuosum topotype)	A. Garrett	A074	USA	Pennsylvania	McKean Co	22-Jun-13	Martin Run	Sergeant Twp., along Martin Run just N of Wilcox-Claremont Rd.	MR	
SBS109	3	GGAATAGC	recurvum	A. Garrett	A142	USA	Pennsylvania	Pike Co.	25-Jun-13	Billings Pond	Billings Pond, N of Co. rd. 4004 (Blooming Grove Rd.), 1.1 mi W of	BP	
SBS112	3	GTAGTTCC	fallax	A. Garrett	A149	USA	Pennsylvania	Pike Co.	25-Jun-13	Billings Pond	Billings Pond, N of Co. rd. 4004 (Blooming Grove Rd.), 1.1 mi W of	BP	
SBS113	3	CGCCTTCC	recurvum	B. Shaw	18941	USA	New York	Chenango Co.	22-Jun-13	Jam Pond	German Twp., Jam Pond Bog, N of county rd. 5 between Rabbit P	JP	
SBS115	3	ATCTCTCC	fallax	A. Garrett	A087	USA	New York	Chenango Co.	22-Jun-13	Jam Pond	German Twp., Jam Pond Bog, N of county rd. 5 between Rabbit P	JP	
SBS116	3	CAGGCTCC	fallax	A. Garrett	A118	USA	New York	Warren Co.	24-Jun-13	Carl Turner	Along Carl Turner Rd. just E of I-87, S of Schroon Lake, 0.4 mi NE	CT	
SBS117	3	TGAACTCC	angustifolium	A. Garrett	A119	USA	New York	Warren Co.	24-Jun-13	Carl Turner	Along Carl Turner Rd. just E of I-87, S of Schroon Lake, 0.4 mi NE	CT	
SBS118	3	AGATTGCC	fallax	A. Garrett	A121	USA	New York	Warren Co.	24-Jun-13	Carl Turner	Along Carl Turner Rd. just E of I-87, S of Schroon Lake, 0.4 mi NE	CT	
SBS120	3	CTACCGCC	flexuosum	A. Garrett	A126	USA	New York	Warren Co.	24-Jun-13	Carl Turner	Along Carl Turner Rd. just E of I-87, S of Schroon Lake, 0.4 mi NE	CT	
SBS121	3	ACGACGCC	flexuosum	A. Garrett	A127	USA	New York	Warren Co.	24-Jun-13	Carl Turner	Along Carl Turner Rd. just E of I-87, S of Schroon Lake, 0.4 mi NE	CT	
SBS122	3	ATTGAGCC	fallax	B. Shaw	18994	USA	New York	Rensselaer Co.	24-Jun-13	Miller Rd.	Sandlake Twp. E of Albany, along Miller Rd. 0.8 mi S of jct. with N	MR	
SBS123	3	CCGTTACC	isoviitae	B. Shaw	18995	USA	New York	Rensselaer Co.	24-Jun-13	Miller Rd.	Sandlake Twp. E of Albany, along Miller Rd. 0.8 mi S of jct. with N	MR	
SBS124	3	TGCTGACC	brevifolium	B. Shaw	18996	USA	New York	Rensselaer Co.	24-Jun-13	Miller Rd.	Sandlake Twp. E of Albany, along Miller Rd. 0.8 mi S of jct. with N	MR	
SBS125	3	ATAAGACC	brevifolium	B. Shaw	18997	USA	New York	Rensselaer Co.	24-Jun-13	Miller Rd.	Sandlake Twp. E of Albany, along Miller Rd. 0.8 mi S of jct. with N	MR	
SBS126	3	CGAGAACC	isoviitae	B. Shaw	18998	USA	New York	Rensselaer Co.	24-Jun-13	Miller Rd.	Sandlake Twp. E of Albany, along Miller Rd. 0.8 mi S of jct. with N	MR	
SBS128	3	CTCAGTAC	brevifolium	B. Shaw	19000	USA	New York	Rensselaer Co.	24-Jun-13	Miller Rd.	Sandlake Twp. E of Albany, along Miller Rd. 0.8 mi S of jct. with N	MR	
SBS131	3	TAGAGGAC	brevifolium	B. Shaw	16269	USA	ME	Hancock Co.	3-Jul-12	Winter Harbor	Schoodic Peninsula, Winter Harbor Township. Between Winter H	ME	
SBS136	3	CTCGTTGA	recurvum	B. Shaw	17793	USA	North Carolina	Dare Co.	9-Dec-13	NC Dare co.	On mainland, on Milltail Rd., 0.41 mi NE from Milltail Creek cross	NC	
SBS137	3	GTATCTGA	angustifolium	B. Shaw	19028	Canada	British Columbia	Vancouver I.	12-Jul-10	San Juan Ridge			
SBS138	3	TCTACTGA	pacificum	B. Shaw	19045	Canada	British Columbia	Vancouver I.	12-Jul-10	San Juan Ridge			
SBS140	3	GGTCTCGA	recurvum	Ferreira M.	1	Portugal	Azores	Terceira	4-Jul-08	Azores	Central Plateau, near Lagoa do Negro		
SBS148	4	ATCAGGTT	angustifolium	J. Shaw	2016-1	USA	Alaska	Juneau	4-Jul-16	AukeLake	Alaska. Juneau area, along trail around Auke Lake, UAS campus		
SBS149	4	GACTCGTT	pacificum	J. Shaw	2016-4	USA	Alaska	Juneau	6-Jul-16	MP38	NW of Juneau on the Glacier Hwy, at mile post 38		
SBS150	4	AGTTAGTT	angustifolium	J. Shaw	2016-16	USA	Alaska	Juneau	10-Jul-16	Douglasl	Alaska. Douglas Island, west of Juneau. N end of Douglas Hwy., s		
SBS152	4	CAGATCTT	pacificum	J. Shaw	2016-26A	USA	Alaska	Juneau	13-Jul-16	AukeBay	Alaska. Juneau area, Pinus contorta muskeg, Spaulding Meadows		
SBS153	4	CTATCCTT	pacificum	J. Shaw	2016-27	USA	Alaska	Juneau	13-Jul-16	AukeBay	Alaska. Juneau area, Pinus contorta muskeg, Spaulding Meadows		
SBS154	4	GGTACCTT	pacificum	J. Shaw	2016-30	USA	Alaska	Valdez-Cordova	20-Jul-16	Whittier	Alaska. Whittier area, along Shotgun Cove Trail, ENE of Whittier.		
SBS155	4	TCCTACTT	angustifolium	J. Shaw	2016-34	USA	Alaska	Kenai Peninsula	20-Jul-16	AK1	Alaska. Peatland E of the Seward Hwy (AK. 1), 15.4 mi. S of Hope		
SBS156	4	AGAGTATT	obtusum	J. Shaw	2016-60	USA	Alaska	Anchorage	28-Jul-16	Baxter Bog	Alaska, Anchorage, Anchorage, University of Alaska campus, Mos		
SBS157	4	GAGCGATT	angustifolium	J. Shaw	2016-70	USA	Alaska	Anchorage	31-Jul-16	Baxter Bog	Alaska, Anchorage, City of Anchorage, Baxter Bog Park between E		
SBS158	4	CCTCCATT	angustifolium	J. Shaw	2017-158	Canada	Quebec	Sept Iles	20-Sep-17	Boulevard Laure	Sept Iles area, W of Sept Iles along Hwy. 138 (Boulevard Laure), a		
SBS160	4	TGCTTGGT	fallax 4th type	J. Shaw	2017-169	Canada	Quebec	Sept Iles	20-Sep-17	Boulevard Laure	Sept Iles area, W of Sept Iles along Hwy. 138 (Boulevard Laure), a		
SBS159	4	GTTGAATT	angustifolium	J. Shaw	2017-160	Canada	Quebec	Sept Iles	20-Sep-17	Boulevard Laure	Sept Iles area, W of Sept Iles along Hwy. 138 (Boulevard Laure), a		
SBS161	4	GTTCCGGT	brevifolium	J. Shaw	2017-173	Canada	Quebec	Sept Iles	20-Sep-17	Boulevard Laure	Sept Iles area, W of Sept Iles along Hwy. 138 (Boulevard Laure), a		
SBS162	4	GCAGTCGT	angustifolium	J. Shaw	2017-181	Canada	Quebec	Schefferville	22-Sep-17	Lac Juin	Just WNW of Schefferville Airport along margin of Lac Juin		
SBS163	4	AACCTCGT	angustifolium	J. Shaw	2017-184	Canada	Quebec	Schefferville	22-Sep-17	Airport	Just WNW of Schefferville Airport along roadside	SCH-1	
SBS359	4	TCGATTCT	isoviitae	A. Garrett	A271	Norway	Nord-Trøndelag	Høylandet	16-Aug-13	Gresstjønna	Gresstjønna lake and Latmyrbukta		
SBS358	4	AGTCGTCT	angustifolium	A. Garrett	A257	Norway	Nord-Trøndelag	Steinkjer	15-Aug-13	Henningsvatnet	Henningsvatnet		
SBS361	4	GACGTACT	flexuosum	A. Garrett	A282	Norway	Nord-Trøndelag	Høylandet	16-Aug-13	Gresstjønna	Gresstjønna lake and Latmyrbukta		
SBS169	4	CGGAGACT	angustifolium	J. Shaw	2017-251	Canada	Labrador	Schefferville	24-Sep-17	to Menihak	N side of road (right side going out) between Schefferville and M	SCH-11	
SBS170	4	ACGCAACT	angustifolium	J. Shaw	2017-263B	Canada	Quebec	Schefferville	25-Sep-17	Avenue de la Gare	3.5 km W of Schefferville train station on Avenue de la Gare. Sma	SCH-13	
SBS177	4	CAGTAGAT	angustifolium	B. Piatkowski	2017-51	USA	Alaska	Juneau	28-May-17	DanMollerTr	Douglas Island: Dan Moller Trail		
SBS178	4	TCGGCCAT	pacificum	B. Piatkowski	2017-64	USA	Alaska	Yakutat	29-May-17	FR10	Tongass National Park; along Forest Road 10		
SBS179	4	AGCTCAAT	pacificum	B. Piatkowski	2017-60	USA	Alaska	Yakutat	29-May-17	FR10	Tongass National Park; along Forest Road 10		
SBS181	4	TGGAGCTG	pacificum	B. Piatkowski	2017-68	USA	Alaska	Yakutat	29-May-17	Situk Lake Tr	Tongass National Park; along Situk Lake Trail		
SBS184	4	CAAGATGG	pacificum	B. Piatkowski	2017-106	USA	Alaska	Juneau	1-Jun-17	UA	University of Alaska Southeast campus; bog behind housing comp		
SBS185	4	TAGGTCGG	pacificum	B. Piatkowski	2017-116	USA	Alaska	Juneau	3-Jun-17	UA	University of Alaska Southeast campus; Trailhead on University D		
SBS186	4	CCTGGCGG	angustifolium	B. Piatkowski	2017-121	USA	Alaska	Juneau	3-Jun-17	UA	University of Alaska Southeast campus; Trailhead on University D		
SBS187	4	TCGCGAGG	angustifolium	B. Piatkowski	2017-186	USA	Alaska	Anchorage	16-Jun-17	Baxter Bog	Baxter Bog		
SBS189	4	ACCGAAGG	obtusum	B. Piatkowski	2017-264	USA	Alaska	Anchorage	27-Jun-17	Goose Lake	Goose Lake		
SBS191	4	AACTACCG	angustifolium	B. Piatkowski	2016-15	USA	New York	Burlington Co.	17-Jul-16	Cranberry Bog	Greenwoods Conservancy, Cranberry Bog		
SBS192	4	ATGATTAG	angustifolium	B. Piatkowski	2016-66	USA	New York	Franklin Co.	18-Jul-16	Bloomingdale Bog	Bloomingdale Bog, Saranac Lakes Wild Forest		
SBS194	4	TTCTTCAG	angustifolium	B. Piatkowski	2016-141	USA	New York	Franklin Co.	10-Aug-16	Spitfire Bog	Spitfire Bog; towards the south of Upper St. Regis Lake		
SBS196	4	TTAGCAAG	recurvum	B. Aguero	19470	USA	North Carolina	Dare Co.	17-Apr-18	Milltail Rd	Alligator River NWR, along W side of Milltail Rd., 0.41 mi NE from		
SBS312	4	CGGCGGTC	balticum	A. Garrett	AG572	USA	Alaska	Fairbanks North Star	11-Aug-14	Nordale Rd	NE of Fairbanks town center along Nordale Rd. just S of Chena H		
SBS207	4	AATCAAGC	angustifolium	A. Garrett	AG487	USA	Alaska	Anchorage	07-Aug-14	Goose Lake	Goose Lake, trail around the lake accessed from Goose Lake Park		
SBS208	4	GTAGTTCC	balticum	A. Garrett	AG495	USA	Alaska	Anchorage	07-Aug-14	Alyeska	SE of Anchorage at Alyeska Ski area. Moose Meadow Park, trailh		
SBS209	4	CGCCTTCC	angustifolium	A. Garrett	AG491	USA	Alaska	Anchorage	07-Aug-14	Alyeska	SE of Anchorage at Alyeska Ski area. Moose Meadow Park, trailh		
SBS211	4	ATCTCTCC	balticum	A. Garrett	AG497	USA	Alaska	Anchorage	07-Aug-14	Alyeska	SE of Anchorage at Alyeska Ski area. Moose Meadow Park, trailh		
SBS212	4	CAGGCTCC	balticum (pseudopacificum clade)	A. Garrett	AG500	USA	Alaska	Anchorage	07-Aug-14	Alyeska	SE of Anchorage at Alyeska Ski area. Moose Meadow Park, trailh		
SBS213	4	TGAACTCC	angustifolium (toward pacificum)	A. Garrett	AG509	USA	Alaska	Kenai Penninsula	07-Aug-14	Hwy1-9	Downhill roadside sedge-y rich fen, 4.2 km north of the Highway		
SBS214	4	AGATTGCC	angustifolium	A. Garrett	AG510	USA	Alaska	Kenai Penninsula	07-Aug-14	Hwy1-10	Downhill roadside sedge-y rich fen, 4.2 km north of the Highway		
SBS215	4	GGTAGGCC	obtusum	A. Garrett	AG513	USA	Alaska	Kenai Penninsula	07-Aug-14	Hwy1-11	Downhill roadside sedge-y rich fen, 4.2 km north of the Highway		
SBS217	4	ACGACGCC	angustifolium	A. Garrett	AG518	USA	Alaska	Kenai Penninsula	07-Aug-14	MarathonRd	Soldotna-Kenai area, ca. 5 km N of Kenai on Marathon Rd. Flat, es		
SBS218	4	ATTGAGCC	angustifolium	A. Garrett	AG520	USA	Alaska	Kenai Penninsula	07-Aug-14	MarathonRd	Soldotna-Kenai area, ca. 5 km N of Kenai on Marathon Rd. Flat, es		
SBS219	4	CCGTTACC	angustifolium	A. Garrett	AG521	USA	Alaska	Kenai Penninsula	08-Aug-14	Soldotna	N of Soldotna, along Swanson River Rd. N of Sterling at the trailhe		
SBS220	4	TGCTGACC	pacificum (pseudopacificum clade)	A. Garrett	AG525	USA	Alaska	Kenai Penninsula	08-Aug-14	Soldotna	N of Soldotna along Swanson River Rd. N of Sterling. Small pond s		
SBS221	4	ATAAGACC	angustifolium	A. Garrett	AG532	USA	Alaska	Matanuska-Susitna	08-Aug-14	KashwitnaL	N of Wasilla, ca. along AK 3 (George Parks Hwy.) 0.5 mi S of Kashv		
SBS222	4	CGAGAACC	angustifolium	A. Garrett	AG533	USA	Alaska	Matanuska-Susitna	08-Aug-14	KashwitnaL	N of Wasilla, ca. along AK 3 (George Parks Hwy.) 0.5 mi S of Kashv		
SBS223	4	GTCCAACC	angustifolium	A. Garrett	AG535	USA	Alaska	Matanuska-Susitna	09-Aug-14	KashwitnaL	N of Wasilla, ca. along AK 3 (George Parks Hwy.) 0.5 mi S of Kashv		
SBS224	4	CTCAGTAC	angustifolium	A. Garrett	AG534	USA	Alaska	Matanuska-Susitna	09-Aug-14	KashwitnaL	N of Wasilla, ca. along AK 3 (George Parks Hwy.) 0.5 mi S of Kashv		
SBS225	4	CCATCTAC	pacificum (northern, pseudopacificum clade)	A. Garrett	AG541	USA	Alaska	Matanuska-Susitna	09-Aug-14	KashwitnaL	N of Wasilla, ca. along AK 3 (George Parks Hwy.) 0.5 mi S of Kashv		
SBS226	4	AGGCATAC	angustifolium	A. Garrett	AG558	USA	Alaska	Fairbanks North Star	09-Aug-14	BallaineL	Ballaine Lake, Fairbanks, off Farmers Loop Rd.		
SBS227	4	TAGAGGAC	angustifolium	A. Garrett	AG557	USA	Alaska	Fairbanks North Star	09-Aug-14	BallaineL	Ballaine Lake, Fairbanks, off Farmers Loop Rd.		
SBS228	4	GACGAGAC	angustifolium	A. Garrett	AG542	USA	Alaska	Matanuska-Susitna	09-Aug-14	KashwitnaL	N of Wasilla, ca. along AK 3 (George Parks Hwy.) 0.5 mi S of Kashv		
SBS229	4	GAACCAAC	obtusum	A. Garrett	AG579	USA	Alaska	Fairbanks North Star	11-Aug-14	Nordale Rd	Fairbanks, fen further south down Nordale Rd., 590 m N of Andrc		
SBS230	4	TTGCAGTA	angustifolium	A. Garrett	AG569	USA	Alaska	Fairbanks North Star	10-Aug-14	BallaineL	Ballaine Lake, Fairbanks, off Farmers Loop Rd.		
SBS231	4	GACGGCTA	recurvum	B. Piatkowski	2018-40	USA	Florida	Franklin	17-May-18	Wright Lake	Apalachicola National Forest; near Wright Lake		
SBS233	4	GTATCTGA	recurvum	B. Aguero	M02A/2	USA	North Carolina	Transylvania Co.	01-May-18	Pink Beds	Pisgah NF, along Pink Beds Trail Loop		
SBS234	4	TCTACTGA	recurvum	B. Aguero	19605	USA	North Carolina	Brunswick Co.	04-Jun-18	Green Swamp	Green Swamp		
SBS238	4	GCGTACGA	anullatum	B. Aguero	19440	USA	Maine	Penobscot Co.	24-Jun-17	Marble Fen	Marble Fen		
SBS239	4	CAAGTCCA	pulchrum	B. Aguero	19453	USA	Maine	Hancock Co.	25-Jun-17	Winter Harbor	Between Winter Harbor and Birch Harbor on ME 186		
SBS240	4	CCGCGCCA	pulchrum	B. Aguero	19442	USA	Maine	Penobscot Co.	24-Jun-17	Marble Fen	Marble Fen		
SBS241	4	ACTGGTAA	flexuosum	A. Garrett	A146	USA	Pennsylvania	Pike Co.	25-Jun-13	Billings Pond	Billings Pond, N of Co. rd. 4004 (Blooming Grove Rd.), 1.1 mi W of	BP	
SBS247	4	CCAATGAT	angustifolium	J. Shaw	2018-197	USA	Alaska	Denali Borough	26-Jun-18	Bear creek	Anderson area. W side of Hwy. 3, 14 mi. S of Anderson, 0.9 mi N		
SBS249	4	CCTAATCG	angustifolium	B. Piatkowski	2018-143B	USA	Wisconsin	Walworth	23-Jun-18	Beulah Bog	Beulah Bog State Natural Area	BB	
SBS250	4	ACTCTCAG	angustifolium	B. Piatkowski	2018-145B	USA	Wisconsin	Walworth	23-Jun-18	Beulah Bog	Beulah Bog State Natural Area	BB	
SBS251	4	AACCGTTC	angustifolium	B. Piatkowski	2018-147B	USA	Wisconsin	Walworth	23-Jun-18	Beulah Bog	Beulah Bog State Natural Area	BB	
SBS252	4	TGGTCCGC	angustifolium	A. Garrett	AG586	USA	Alaska	Fairbanks North Star	08-Nov-14	NordaleRd	NE of Fairbanks town center along Nordale Rd. just S of Chena H		
SBS254	4	TTGCGTCC	angustifolium	A. Garrett	AG555	USA	Alaska	Matanuska-Susitna	08-Sep-14	Matanuska-Susitna	14.7 miles S of intersection of AK 8 (Denali Hwy.) on AK 3 (George		
SBS256	4	GGTCTCGA	obtusum	J. Shaw	2018-185	USA	Alaska	North Slope Borough	21-Jun-18	Barrow	Barrow area, 1.0- 1.4 mi S of the junction Nunavak & Imaqsaun R		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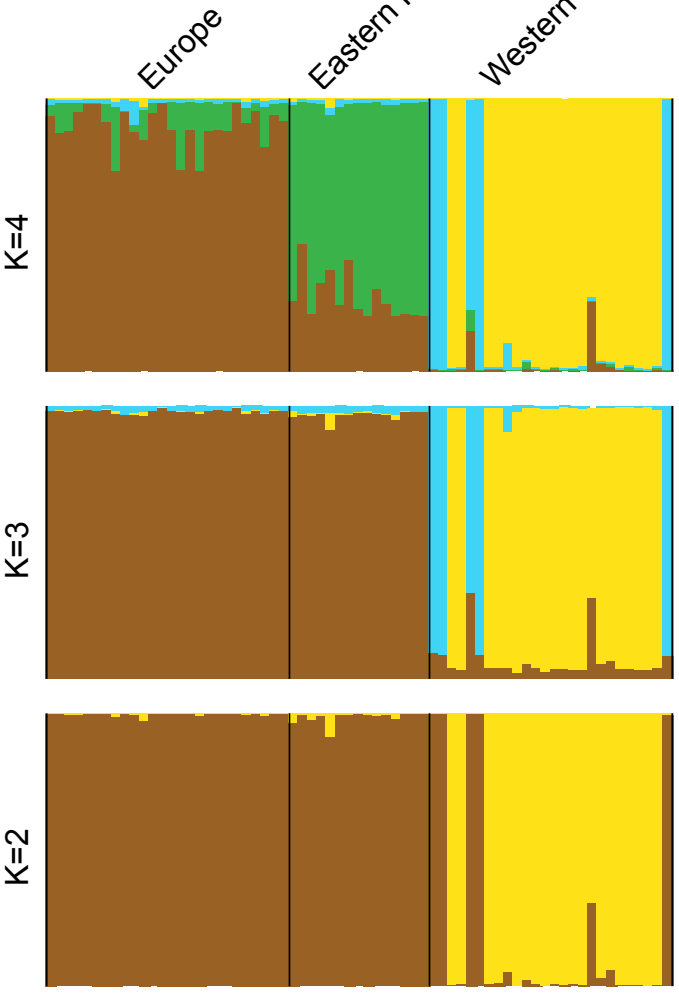
AppendixS3



AppendixS4

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