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Ronja E. M. Wedegärtner

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Thesis for the degree of
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Ronja E. M. Wedegärtner

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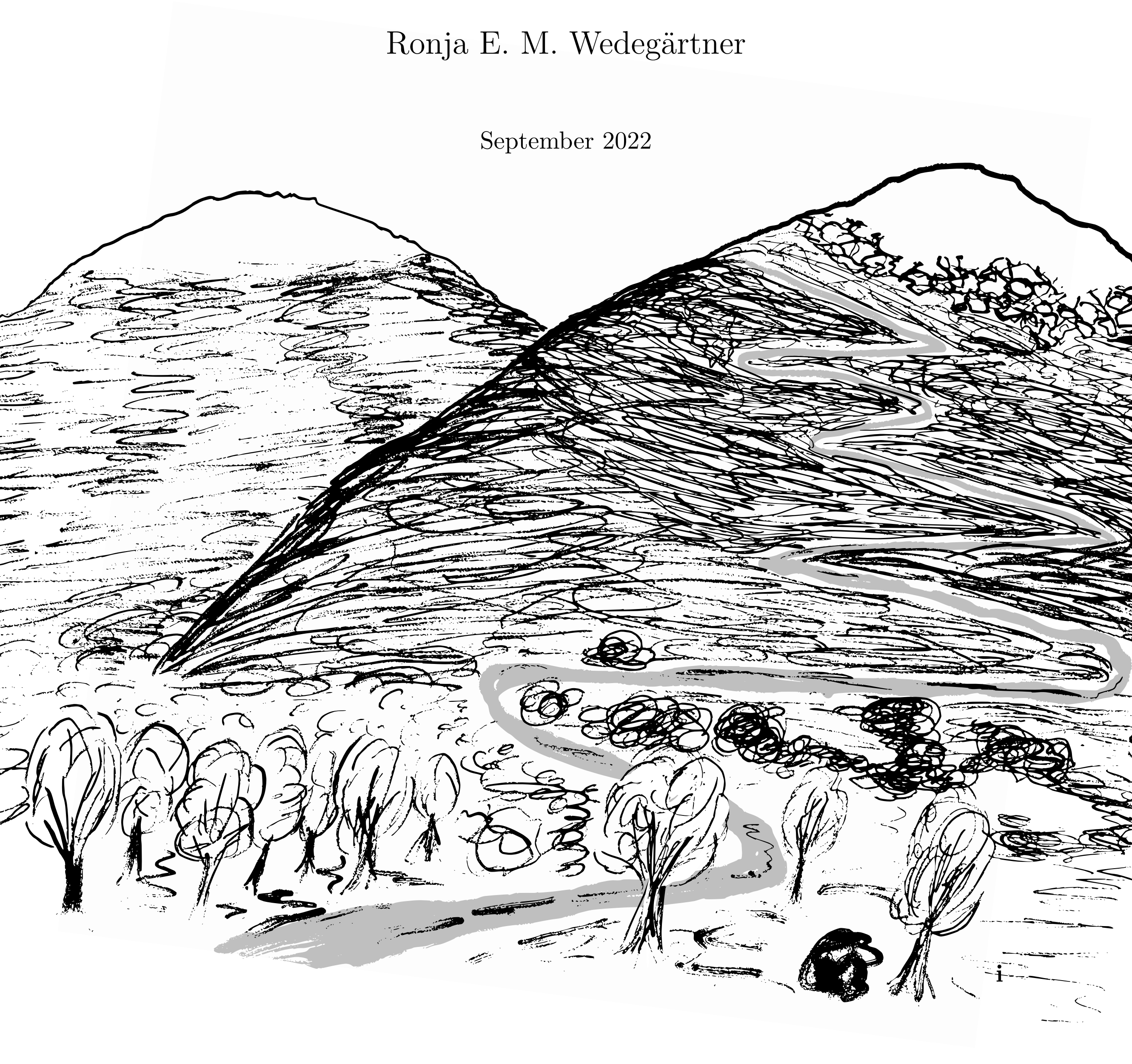

Abstract

To protect mountain ecosystems, their biodiversity, ecosystem services, and other contributions to people, it is necessary to understand how climate and disturbances affect them. Trails may change seed dispersal and disrupt biotic interactions between plants, thereby creating opportunities for recruitment in locations where seeds did not arrive or competition prevented establishment. This could change plant distributions in mountain areas. Colonization opportunities may also allow species that are non-native in a particular mountain ecosystem to establish. Such changes in species distributions can influence ecosystem functions, services, and benefits. The aim of this thesis is to improve our understanding of trails' impacts on species' distributions in the Scandinavian mountains, known as the Scandes and to improve knowledge on the impact of invasive species in mountain ranges as they are perceived by stakeholders.

I conducted systematic observational surveys along hiking trails in Norway and Sweden and examined the effect of hiking trails on seed rain, seed bank abundance, seedling recruitment, and species' realized climatic niches. For further insights in establishment and persistence of species, I investigated the importance of positive and negative neighbour interactions on different species and life stages in a field experiment manipulating environmental stress and distance to neighbouring vegetation. Using a global survey, I evaluated stakeholder perceptions of invasive species' impacts on ecosystem functions and services in mountains.

Seed rain, seed bank, and seedling recruitment were strongly elevated along trails and trail disturbances reached far into the vegetation. Along trails, alpine species shifted their warm climatic niche edges and optima towards warmer locations, leading to an increased overlap in species' climatic niches. This was reflected by a greater species richness in trailside vegetation than in the vegetation far from trails. Recipient community and distance to anthropogenic structures modulated this increase in species richness in trailsides.

Gap size influenced the microclimate within vegetation gaps. Increased seedling establishment in small gaps appeared to be a result of reduced competition for light, which masked the amelioration of climate by neighbouring vegetation that becomes apparent when including larger gaps sizes. Facilitation by neighbouring vegetation was important throughout the plants' life cycle under stressful conditions. Stress type mattered for the importance of facilitation, with seedlings more susceptible to acute stress.

Stakeholders across regions ranked impacts of invasive species on biodiversity and ecosystem functions predominantly negative, while the ranking of impacts on ecosystem functions and benefits also included positive perceptions. Stakeholder groups varied in their perception of impacts, with on-the-ground stakeholders more frequently reporting positive impacts. Conflicting views on impacts may be a reason for the large proportion of species that currently have no management plan.

This thesis illustrates that trailsides may provide temporary escape routes from strongly competitive lowland plants for pressed alpine species, and locally increase species richness in the Scandes. When examining biotic interactions, the spatial scales on which different stresses act and target species tolerances to them should be considered. Further research on changes in native and non-native species distributions should consider impacts beyond biodiversity.

Sammendrag

For å beskytte fjelløkosystemer, deres biologiske mangfold og andre økosystemtjenester, må vi også forstå hvordan de påvirkes av klima og forstyrrelser. Menneskeskapte stier finnes det mange av i fjellområder, og dette er forstyrrelser som kan bidra til frøspredning og endre biotiske interaksjoner mellom planter, og potensielt tilrettelegge for rekruttering på steder hvor frø tidligere ikke kom frem, eller hvor etablering var hindret av konkurranse. Slik kan stier være med på å endre utbredelsen av hjemlige planter og bidra til spredning av fremmedarter i fjellområder, som igjen vil kunne påvirke økosystemfunksjoner, -tjenester og -goder. Målet med denne avhandlingen er å øke vår forståelse av hvordan stier påvirker arters utbredelse i den skandinaviske fjellkjeden og å øke kunnskapen vår om hvordan ulike aktører oppfatter påvirkningen av invaderende arter i fjellet.

Jeg utførte systematiske observasjonsundersøkelser langs turstier i Norge og Sverige og undersøkte hvilken effekt stiene hadde på frøregn, frøbanksammensetning, rekruttering fra frø og arters realiserte klimatiske nisjer. For å finne ut enda mer om de ulike artenes evne til å etablere seg og overleve, undersøkte jeg positive og negative interaksjoner mellom arter i forskjellige livsstadier. Det gjorde jeg i et felteksperiment ved å manipulere miljøstress og plantenes avstand til nabovegetasjonen. For å evaluere ulike aktørers oppfatning av påvirkningen fremmede skadelige arter/invaderende arter har på økosystemtjenester og -funksjoner utførte jeg en global spørreundersøkelse.

Langs stiene var det både økt frøregn, større frøbank og flere frøplanter, og forstyrrelser fra stiene nådde langt inn i vegetasjonen. Langs stier skiftet alpine arter sine varme klimatiske nisjekanter og optima mot varmere steder, noe som førte til økt overlapping av artens klimatiske nisjer. Dette gjenspeiles i at artsrikdommen var større i vegetasjonen langs stiene enn i vegetasjonen langt fra stien. Hvor mye artsrikdommen økte var avhengig av vegetasjonstype og avstand til menneskeskapte strukturer. Størrelsen på forstyrrelsen påvirket mikroklimaet i de forstyrrede åpningene i vegetasjonen. Økt etablering i små forstyrrelser ser ut til å være et resultat av redusert konkurranse om lys, noe som maskerer klimaforbedring av nabovegetasjon som blir tydeligere når man inkluderer større forstyrrelser. Under stressende forhold var fasilitering fra nabovegetasjonen viktig gjennom hele livssyklusen. Hvor viktig denne fasiliteringen var, kom an på

type miljøstress. Spirer var mer utsatt for alvorlig stress enn voksne planter.

Aktører på tvers av regioner rangerte i hovedsak virkningene av invaderende arter/fremmede skadelige arter på biologisk mangfold og økosystemfunksjoner til å være negative, men det var også noen som rangerte virkningene på økosystemfunksjoner og -goder til å være positive. Aktørgruppene hadde ulik oppfatning av virkningene, og det var oftere rapporter om positve effekter fra aktører med en praktisk tilnærming. Motstridende syn på invaderende arters innvirkninger kan være grunnen til den store andelen av arter som i dag mangler en forvaltningsplan.

Denne avhandlingen viser at stikantvegetasjon kan fungere som midlertidige rømningsveier for fjellplanter fra konkurransedyktige lavlandsplanter, og at stier kan føre til lokalt høyere artsrikdom i den skandinaviske fjellkjeden. Avhandlingen understreker også viktigheten av å vurdere på hvilke skala ulikt miljøstress opererer, samt stresstoleranse hos fokusarten, når man undersøker biotiske interaksjoner. Videre forskning på endringer i utbredelsen av hjemlige og fremmede arter bør også ta hensyn til påvirkninger utover biologisk mangfold.

Zusammenfassung

Um Gebirgsökosysteme mit ihrer Artenvielfalt und ihren Ökosystemdienstleistungen zu schützen, ist es notwendig zu verstehen, wie Klima und Störungen diese beeinflussen. Eine häufige Störung in Gebirgen sind Wanderwege. Wanderwege können die Ausbreitung von Samen verändern und die biotischen Interaktionen zwischen Pflanzen stören. Dadurch können Samen an Orte gelangen, die sie sonst nicht erreichen würden und sich so Pflanzen an Orten etablieren, an denen die Konkurrenz dies sonst verhindert hätte. So können Wanderwege die Verbreitung von Pflanzen in Gebirgsregionen verändern. Durch Störungen können sich auch Arten etablieren, die in einem bestimmten Bergökosystem nicht heimisch sind. Veränderungen in der Artenverteilung können wiederum die Ökosystemfunktionen und -dienstleistungen verändern. Ziel dieser Arbeit ist es, die Auswirkungen von Wanderwegen auf die Verbreitung von Arten in den Skanden, dem Gebirge Norwegens und Schwedens, besser zu verstehen und das Wissen darüber, wie verschiedene Interessensgruppen die Auswirkungen invasiver Arten in Gebirgsregionen wahrnehmen zu verbessern.

Mit systematischen Vegetationserhebungen entlang von Wanderwegen in Norwegen und Schweden untersuchte ich die Auswirkungen von Wanderwegen auf die Samenverteilung, die Samenbank, die Rekrutierung von Keimlingen und die realisierten klimatischen Nischen der dort heimischen Arten. Um weitere Erkenntnisse über die Etablierung und das Überleben von Arten zu gewinnen, untersuchte ich die Bedeutung von Interaktionen mit benachbarter Vegetation für ausgewählte Zielarten in verschiedenen Lebensstadien in einem Feldexperiment. Hierzu manipulierte ich Umweltstress und die Entfernung zur benachbarten Vegetation. Mithilfe einer Umfrage unter Interessenvertretern erhob ich deren Wahrnehmung der Auswirkungen invasiver Arten auf Ökosystemfunktionen und -dienstleistungen.

Samenregen, Samenbank und Keimlingsrekrutierung waren entlang von Wegen stark erhöht, und die Störungen durch Wege reichten weit in die Vegetation hinein. Entlang von Wanderwegen konnten alpine Arten weiter unten vorkommen, ihre warmen klimatischen Nischenränder und Optima in wärmere Gebiete verschieben), was zu einer stärkeren Überlappung der klimatischen Nischen mit Flachlandarten führte. Dies spiegelte sich in einem größeren Artenreichtum an Wegrändern als in der Vegetation abseits der Wege wider. Die ursprünglichen

Planzengemeinschaft am Rande des Wanderwegs und die Entfernung zu anthropogenen Strukturen, wie Hütten, beeinflussten, wie stark der Artenreichtum an Wegrändern zunahm. Die Größe der Vegetationslücken beeinflusste ihr Mikroklima. Die verstärkte Ansiedlung von Keimlingen in kleinen Vegetationslücken scheint das Ergebnis einer geringeren Konkurrenz um Licht zu sein. Bei kleinen Vegetationslücken scheint das einen größeren Effekt zu haben als die Verbesserung des Klimas durch die benachbarte Vegetation, die bei größeren Lücken fehlt. Die positiven Klimaeffekte durch die benachbarte Vegetation sind unter Stressbedingungen während des gesamten Lebenszyklus wichtig, doch besonders Keimlinge sind anfällig für akuten Stress. Je nach Art des Stresses ist die Unterstützung durch benachbarte Vegetation wichtiger oder unwichtige. Die Umfrage hat ergeben, dass die Auswirkungen invasiver Arten auf die biologische Vielfalt und die Ökosystemfunktionen von den Interessengruppen in allen Regionen überwiegend als negativ eingestuft wurde. Die Auswirkungen auf die Ökosystemdienstleistungen und -vorteile wurden hingegen auch positiv wahrgenommen. Verschiedene Interessentengruppen nahmen die Auswirkungen unterschiedlich wahr, wobei die Interessentengruppen vor Ort, wie z.B.Bauern oder Förster häufiger von positiven Auswirkungen berichteten. Die widersprüchlichen Auffassungen über die Auswirkungen könnten ein Grund für den großen Anteil der invasiven Arten sein, für die derzeit kein Managementplan vorliegt.

Diese Arbeit veranschaulicht, dass Wegränder für bedrängte alpine Arten temporäre Fluchtwege vor konkurrenzstarken Flachlandpflanzen darstellen und den Artenreichtum in den Skanden lokal erhöhen können. Bei der Untersuchung biotischer Interaktionen sollten die räumlichen Skalen, auf denen die verschiedenen Umweltstressoren wirken, und die Toleranz der Zielarten gegenüber diesen Belastungen berücksichtigt werden. Weitere Forschungsarbeiten zu Veränderungen in der Verbreitung einheimischer und invasiver Arten sollten Auswirkungen berücksichtigen, die über die biologische Vielfalt hinausgehen.

List of Articles

Articles included in this thesis

I. A. Jolivet, A. C. MacDougald, B. J. Graae, K. Klanderud, and **R. E. M. Wedegärtner**,

Sticking to the trail: Seed rain, seed bank, and seedling density are elevated along hiking trails in the Scandes mountains,
Journal of Vegetation Science, **33**(4):1-14 (2022). DOI: 10.1111/jvs.13144.

II. **R. E. M. Wedegärtner**, J. J. Lembrechts, R. van der Wal, A. Barros, A. Chauvin, I. Janssens, and B. J. Graae,

Hiking trails shift plant species' realized climatic niches and locally increase species richness,

Diversity and Distributions **00**:1-14 (2022). DOI: 10.1111/ddi.13552.

III. **R. E. M. Wedegärtner**, J. J. Lembrechts, R. van der Wal, and B. J. Graae,

Closing the gap: facilitation is important but depends on life stage, stress type, and gap size in tundra vegetation,

In preparation for resubmission to Journal of Ecology.

IV. S. Geange*, A. D. Barraclough*, **R. E. M. Wedegärtner***, D. Urbach, L. A. Cavieres, C. Chisholm, J. J. Lembrechts, A. Pauchard, J. C. Pizarro, I. Rashid, T. Seipel, M. Snethlage, and V. Vandvik,
* Denotes co-lead authorship.

Global survey on invasive species impacts and management in mountains,

Manuscript.

Additional scientific contributions

1 M. A. Alvarez, A. Barros, D. P. Vázquez, L. de Jesús Bonjour, J. J. Lembrechts, **R. E. M. Wedegärtner**, and V. Aschero,

Hiking and livestock favor non-native plants in the high Andes,

Biological Invasions (2022). DOI: 10.1007/s10530-022-02851-1.

2 J. J. Lembrechts, J. van den Hogen, J. Aalto, M. B. Ashcroft, P. De Frenne, J. Kemppinen, . . . , **R. E. M. Wedegärtner**, . . . , and J. Lenoir,

Global maps of soil temperature,

Global Change Biology (2021). DOI: 10.1111/gcb.16060.

3 J. Bartlett, K. Bakke Westergaard, I. M. G. Paulsen, **R. E. M. Wedegärtner**, F. Wilken, and V. Ravolainen,

Moving out of town? The status of alien plants in high-Arctic Svalbard, and a method for monitoring of alien flora in high-risk, polar environments,

Ecological Solutions and Evidence (2021). DOI: 10.1002/2688-8319.12056.

4 M. Pareyn, A. Rutten, B. Merdekios, **R. E. M. Wedegärtner**, N. Girma, L. Regelbrugge, S. Shibru, and H. Leirs,

High-resolution habitat suitability model for Phlebotomus pedifer, the vector of cutaneous leishmaniasis in southwestern Ethiopia,

Parasites Vectors (2020). DOI: 10.1186/s13071-020-04336-3.

5 R. Liedtke, A. Barros, F. Essl, J. J. Lembrechts, **R. E. M. Wedegärtner**, A. Pauchard, and S. Dullinger,

Hiking trails as conduits for the spread of non-native species in mountain areas,

Biological Invasions (2020). DOI: 10.1007/s10530-019-02165-9.

Contribution to Articles

Article I: *Sticking to the trail: Seed rain, seed bank, and seedling density are elevated along hiking trails in the Scandes mountains*
A. Jolivet & A. C. MacDougald: Conceptualization (equal), investigation (equal), formal analysis (equal), writing - original draft (lead), writing - review & editing (supporting). B. Jessen Graae & K. Klanderud: Conceptualization (equal), writing - original draft (supporting), supervision (equal), writing - review & editing (supporting). **R. E. M. Wedegärtner**: Conceptualization (equal), investigation (equal), formal analysis (equal), supervision (equal), writing - original draft (lead), writing - review & editing (lead).

Article II: *Hiking trails shift plant species' realised climatic niches and locally increase species richness*
R. E. M. Wedegärtner: Conceptualization (equal), project administration (lead), investigation (lead), formal analysis (lead), writing – original draft (lead), writing – review and editing (lead). J. J. Lembrechts: Conceptualization (equal), project administration (supporting), investigation (supporting), formal analysis (supporting), writing – original draft (supporting), writing – review and editing (supporting, supervision (supporting). R. van der Wal: Conceptualization (equal), writing – original draft (supporting), writing – review and editing (supporting), supervision (supporting). A. Barros: Writing – original draft (supporting), writing – review and editing (supporting). A. Chauvin - Investigation (supporting), writing – original draft (supporting, writing – review and editing (supporting). I. Janssens: Investigation (supporting), writing – original draft (supporting), writing – review and editing (supporting). B. Jessen Graae: Conceptualization (equal), project administration (supporting), writing – original draft (supporting), writing – review and editing (supporting), supervision (lead).

Article III: *Closing the gap: facilitation is important but depends on life stage, stress type, and gap size in tundra vegetation*
R. E. M. Wedegärtner: Conceptualization (equal), project administration (lead), resources (lead), investigation (lead), formal analysis (lead), writing – original draft (lead). J. J. Lembrechts: Conceptualization (equal), resources (support-

ing), formal analysis (supporting), writing – original draft (supporting). R. van der Wal: Conceptualization (equal), investigation (supporting), writing – original draft (supporting). B. Jessen Graae: Conceptualization (equal), project administration (supporting), investigation (supporting), resources (supporting), writing – original (supporting).

Article IV: *Global survey on alien invasive species impacts and management in mountains*
S. R. Geange, Alicia Donnellan Barraclough, **R. E. M. Wedegärtner**: Conceptualization (equal), methodology (lead), data curation (lead), formal analysis (lead), visualization (lead), writing - original draft (lead). Vigdis Vandvik: Conceptualization (equal), methodology (lead), writing - original draft (lead). All other authors: Conceptualization (equal) , methodology (supporting), writing - original draft (supporting).

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Preface

This thesis is submitted to the Norwegian University of Science and Technology (NTNU) as a partial fulfillment of the requirements for the degree of Philosophiae Doctor.

Ronja Elisabeth Magdalene Wedegärtner
Trondheim, September 2022

List of Abbreviations

95%CI	95% Confidence intervals
IPBES	The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem S
NCP	Nature's Contributions to People, see Díaz et al. (2018)
MIREN	Mountain Invasion Research Network
SDM	Species Distribution Model
SEICAT	Socio-Economic Impact Classification for Alien Taxa
SGH	Stress Gradient Hypothesis
SLA	Specific Leaf Area

Contents

1 Introduction

> *"The world reveals itself to those who travel on foot"*
>
> Werner Herzog

Mountain trails

As one walks along a mountain trail, one retraces the steps of others, who before oneself have traversed this landscape and chosen to walk the same route. Trails as such are a manifestation of repeated use of a route, resulting in repeated trampling, on the way from one point of interest to another. Trampling removes biomass, making trails linear features of disturbance. As humans and animals move along trails they may carry with them propagules, depositing them in locations that would be out of reach without this dispersal. Together, disturbances and changes in dispersal may change resident plant communities by destruction of individuals with low trampling-tolerance, changes in biotic interactions, and creation of colonization opportunities. Colonization opportunities may also allow for the establishment of species that are non-native in a particular mountain ecosystem and have the potential to influence ecosystem functions and services. Still, in the Scandes mountains of Norway and Sweden, the role of trails in the distribution of propagules, creation of disturbances, interruption of biotic interactions, and the resulting effects on plant species' realized ranges and species richness remain uncharted. Furthermore, it remains unclear how impacts of rapidly colonizing species, native and non-native, are perceived by stakeholders, not only in the Scandes, but in mountain ranges around the globe. With this thesis I aim to contribute to a better understanding of the impacts of trails on vegetation in the Scandes and improve comprehension of the impacts of rapidly colonizing species in mountain ranges around the globe as they are perceived by stakeholders.

1.1 Drivers of changes in the distribution of species

To protect mountain ecosystems, their biodiversity and other contributions to people, it is necessary to understand how climate warming and human disturbances affect them (IPBES, 2019). Rising temperatures, especially in high latitudes (Post et al., 2009; Pepin et al., 2015), changes in land use such as increases in infrastructure associated with tourism (Körner et al., 2006; Debarbieux et al., 2014), recreation pressure (Leung et al., 2018), and invasions of non-native species (Pauchard et al., 2009) put pressure on mountain ecosystems. Northern Europe and the Arctic are more strongly affected by climate warming than other regions worldwide (Post et al., 2019; IPCC, 2021). Additionally, recreation pressure on nature through hiking is growing in both Norway and Sweden (Innovation Norway, 2017; Svenska Turistföreningen, 2017). While the Scandes mountains have a relatively low number of invasive[1], non-native species (McDougall et al., 2018), invasions along mountain roads into alpine habitats have been observed (Lembrechts et al., 2014).

Under which circumstances a species can exist is determined by its environmental niche, e.g. a species has certain requirements of temperature or nutrients that must be met, yet biotic interactions restrict this fundamental niche of tolerated environmental conditions to a realized niche (Hutchinson, 1957). The environmental tolerances of species influence their geographic distribution (Pulliam, 2000). Climate is considered the main determinant of species ranges at broad scales (Woodward, 1987) and under the assumption of niche-conservatism, shifts into previously unsuitable high elevation habitats are expected (Pearman et al., 2008). Alpine plant species are considered vulnerable to increased competition at their warmer rear range edges as competitive lowland species move in (Grabherr et al., 1994; Gottfried et al., 2012; Alexander et al., 2015) and in Scandinavia range losses for alpine species are projected (Niskanen et al., 2019). However, dispersal rates (Engler et al., 2009) and disturbances influence species' realized climatic niches and therefore their spatial distribution (e.g., Lenoir et al., 2010). To move into new locations, seeds must arrive there, and successfully germinate and establish (Cichini et al., 2011). Disturbances, such as trampling, can disrupt biotic interactions through the removal of biomass and promote establishment of native and non-native species in locations where competition with resident vegetation would otherwise prevent it (Nystuen et al., 2014; Lembrechts, Pauchard, et al., 2016). Trails may change dispersal patterns, disrupt biotic interactions and create opportunities for establishment, and thereby change plant distributions in mountain areas. In the following I will give a more detailed introduction into

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[1] Definitions of what makes a species *invasive* vary (Blackburn et al., 2011). In this thesis I am using the definition of the Convention on Biological Diversity, that species whose introduction and/or spread outside their natural past or present distribution threatens biological diversity are considered invasive (CBD, 2010). However, native range-expansive species can at times also be perceived as invasive (Rew et al., 2020; Valéry et al., 2009).

these trail effects, their implications, and research needs.

1.2 Trails as conduits for dispersal

Trails are functionally similar to roads, which promote colonization in mountain areas (Alexander et al., 2016), and are likely to act as corridors for dispersal of propagules (Suárez-Esteban et al., 2016; Liedtke et al., 2020) due to movement of humans and animals on them. Hikers may transport propagules attached to their boots (Ware et al., 2012) or clothing and other equipment (Mount and Pickering, 2009; Ansong and Pickering, 2014) along trails. While most propagules are detaching at the beginning of a hike (Wichmann et al., 2009) dispersal over long distances is possible, especially when combined with motorized transportation (Auffret and Cousins, 2013; Ansong and Pickering, 2014). Animals, especially livestock (Manzano and Malo, 2006), may disperse propagules over long distances through endozoochory, depositing propagules in scat after passage through the digestive tract, (Janzen, 1984) and epizoochory, transporting propagules attached to fur or hooves (Fischer et al., 1996; Graae, 2002). Additionally propagules can be transported along relatively smooth trail surfaces via wind and water, with vegetation in trailsides acting as a seed trap and accumulating propagules (Bullock and Moy, 2004; Isselin-Nondedeu and Bédécarrats, 2007). Often trailsides also harbour trampling resistant species with great propagule production such as grasses, which may locally increase input (Marchand and Roach, 1980). Trails should therefore allow for long-distance dispersal and increased seed deposition by humans and other animals, which has implications for community composition. Increased propagule deposition is frequently hypothesized to be an important contributor to increases in species richness of native and non-native species along trails (Suárez-Esteban et al., 2016). However, the changes in propagule deposition along trails in northern mountain ecosystems remain unclear.

1.3 Trails as linear features of disturbance

As trails typically connect points of interest, form a path of least resistance through landscapes (Ottesen, 2008), and may be attractions in themselves (Moore and Shafer, 2001), activity is concentrated around them (Monz et al., 2013). The creation and use of hiking trails causes mechanical disturbances leading to vegetation loss with a typical zonation (Bates, 1935). At low to medium use of hiking trails, more trampling by hikers result in wider trails (Cole, 1995) with some debate about the shape of this relationship (Monz et al., 2013). Impacts of trampling are not limited to the denuded trails surface, though, but extend also beyond (Barros et al., 2020). Trails are bordered by a diffuse boundary zone of transition to the surrounding vegetation, illustrating a gradient in disturbance (Bates, 1935). Trampling along trails results in reduced vegetation cover in trailsides (e.g., Bates, 1935; Cole, 1995; Barros et al., 2013) and already trampling by few hikers can reduce biomass in northern mountain tundra significantly (Emanuelsson, 1984). Trampling resistance of vegetation is influenced by growth form (e.g., Emanuelsson, 1984; Cole, 1995) and functional traits such as plant height and Specific Leaf Area (SLA) (Bernhardt-Römermann et al., 2011). Graminoids and forbs are generally more resistant to trampling than shrubs (Yorks et al., 1997; R. Hill and Pickering, 2009).

Hikers tend to deviate from the main trail where trails are wet and root or large rocks exposed (Evju et al., 2021). In open landscapes hikers also frequently veer off trail to access points of interest such as viewpoints or creeks (Dixon et al., 2004; Barros and Pickering, 2017). Where the vegetation surrounding the trail is low, hikers are more likely to leave the trail and walk abreast (Leung and Marion, 1996).

While research on trail effects tends to focus on the destructive effects of disturbance on vegetation, the creation of gaps may also pose an opportunity for establishment of new individuals for native (Graae et al., 2011) and non-native (Lembrechts, Pauchard, et al., 2016; Haider, Palm, et al., 2022) species in Scandinavian mountain ecosystems as tourism can facilitate invasions into new ecosystems (Williams et al., 2010). This is reflected by a greater diversity and abundance of non-native species adjacent to trails (e.g., Benninger-Truax et al., 1992; Barros and Pickering, 2014; Liedtke et al., 2020).

1.4 Trails reshuffling species niches?

By disrupting species interactions trails may facilitate the redistribution of plant species in mountains along climatic gradients. Their climatic tolerances and biotic interactions determine where along a climatic gradient species exist (Normand et al., 2009). Positive effects of neighbouring vegetation on growth, survival or reproduction of target plants are considered facilitation, while competition can broadly be summarized as negative effects on these parameters (Callaway, 2007). Facilitation may expand species' realized climatic niche through amelioration of environmental conditions, while competition may exclude them from a part of their fundamental climatic niche (Hutchinson, 1957; Bruno et al., 2003). The importance of interactions for a target plant depends on the surrounding environmental conditions and physiological tolerance of the target plant (Welden and Slauson, 1986). At the boundary of its physiological tolerance a small increase in performance through neighbouring vegetation may be crucial for survival, while under more benign conditions the same increase in performance may be of negligible importance (Welden and Slauson, 1986, see Figure 1.1). Along gradients of environmental stress the importance of interactions are therefore expected to change.

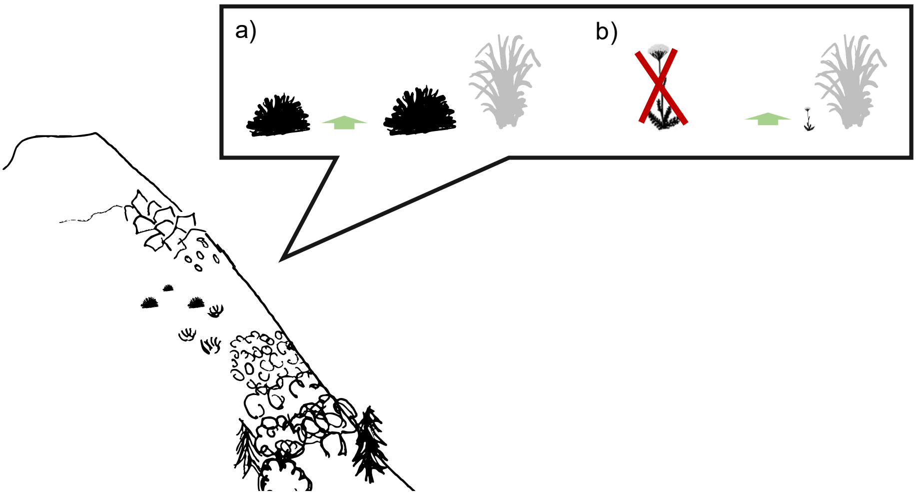

Figure 1.1: Illustration of the importance of facilitation. Both plants, a) and b) receive the same amount of facilitation when growing with a neighbour (in grey), symbolized by the green arrow. However, for a) the well-adapted cushion plant the facilitation is not as important as for b) the less adapted forb, which is not able to survive without it (as represented by the red cross).

1.4.1 The Stress Gradient Hypothesis

The Stress Gradient Hypothesis (SGH), formulated in response to observations of facilitative interactions in stressful environments, predicts that in stressful conditions facilitation is more important, while competition is especially important in benign and productive environments (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). Elevation gradients in mountains provide large scale gradients of macroclimate. In temperate regions climatic harshness broadly rises with elevations as average temperatures drop. According to the SGH a greater importance of facilitation is therefore expected at higher elevations corresponding to colder locations in mountains (e.g., Brooker and Callaghan, 1998; Choler et al., 2001). When considering species' realized niches along climatic gradients, facilitation is expected to be more important at the more stressful end of a given climatic gradient, while competition will be more important at more benign conditions (Normand et al., 2009; Paquette and Hargreaves, 2021).

1.4.2 Gaps disrupt biotic interactions

The removal of neighbouring vegetation is a classical approach to test for the outcomes of biotic interactions (Tansley, 1914; Clements et al., 1929; Aarsen and Epp, 1990) as it allows for the observation of target plant performance without or with limited neighbour interactions, depending on the removal approach (Silander, 1976; Margreiter et al., 2021). In this context gap size matters as well, since plants have specific *zones of influence* and temperature-, drought-, light-, and nutrient stress gradients interact within gaps (Goldberg and Werner, 1983; Lembrechts et al., 2015).

Currently, the evidence for the SGH in northern mountain ecosystem along elevation-, respectively temperature-gradients, is contradictory: while some studies lend support to the SGH (e.g., Eränen and Kozlov, 2008; Olsen and Klanderud, 2014) or support it partially (e.g., Carlsson and Callaghan, 1991; Klanderud, 2005), others find facilitation (Bråthen and Lortie, 2016) or competition (e.g., Moen, 1993; Graae et al., 2011; Lembrechts, Pauchard, et al., 2016) along the whole examined gradient of climatic harshness.

Reasons for such contradictory findings could be 1.) differences in the perception of stress between species (Auffret et al., 2010) and life stages (Schiffers and Tielbörger, 2006), resulting in not capturing the stress gradient at locations that are truly stressful for target plants (Liancourt et al., 2005), 2.) measuring plant performance parameters that show diverging responses to certain types of stress, 3.) counteracting stress gradients in experimental gaps (Lembrechts et al., 2015), and 4.) interpreting the raw change in plant performance along the gradient and disregarding the importance of biotic interactions relative to environmental stress (Brooker et al., 2005).

1.4.3 Trails, climatic niches, and species richness

Trails, as linear features of disturbance and focus point for trampling, may provide natural experiments of the SGH along climatic gradients in mountains. If competition is dominant at the more benign edge of species realized climatic niche, trampling along trails should lead to competitive release at such locations and an expansion of the realized niche towards more benign conditions. This has implications for the conservation of alpine species which are considered vulnerable to increased competition by lowland plants as climate warms (Alexander et al., 2015). Establishment in gaps close to the trail should be most common in more benign locations, where facilitation is less important, and less abundant at the stressful end of the climatic gradient. Expansion of species' climatic niches after disturbance should lead to a greater overlap in niches and therefore a greater species richness along trails.

There is some evidence for competitive release of alpine species at the benign edge of their climatic niche in the Rocky Mountains (Chardon et al., 2019) yet a community-wide examination and evidence from northern mountain ecosystems are lacking. A greater species richness along trails is documented in some ecosystems, but information from alpine ecosystems is scarce (Suárez-Esteban et al., 2016). Here, effects are either negative (Crisfield et al., 2012), neutral (Monz, 2002; Jägerbrand and Alatalo, 2015; Rawat et al., 2021), or depending on community type and soil moisture (Gremmen et al., 2003), trail type (W. Hill and

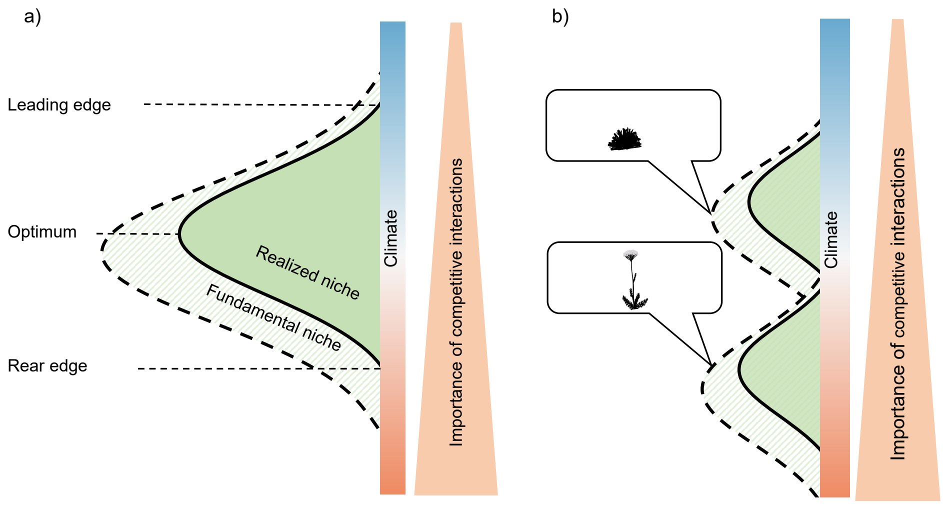

Figure 1.2: a) Illustration of the distribution of a species along a climatic gradient with its fundamental (hatched) and realized niche (green) shown. b) The fundamental and realized niches of an alpine and a lowland plant with the realized niche of the alpine plants restricted by competitive interactions at the rear edge of the niche. When these competitive interactions are disrupted, e.g., by trampling, niche overlap is expected.

Pickering, 2006; Nepal and Way, 2007) and use intensity (Benninger-Truax et al., 1992). The contradictory findings may to some extent be based in differences in resistance to colonization between communities (Graae et al., 2011; Milbau et al., 2013) and examining trails at different climatic harshness.

1.5 Trail research in northern mountain ecosystems

Research on the impact of trails in mountain areas has a geographical bias towards North-America and Oceania (Ballantyne and Pickering, 2015b). In northern European mountain ecosystems research on trail impacts had a short bloom in interest in the 1980s (Emanuelsson, 1984; Pounder, 1985; Gellatly et al., 1986) focusing on trampling resistance, while newer research is scarce and either extremely local (Arnesen, 1999; Jägerbrand and Alatalo, 2015; Rawat et al., 2021) or focused on trail degradation (Evju et al., 2021). Studies which quantify the effect of trails on seed dispersal at a landscape scale in northern mountain ecosystems are currently lacking and there is debate regarding the applicability of the SGH and consequences of improved establishment in small gaps (e.g., Graae et al., 2011). A better understanding of the importance of facilitation and competition along climatic gradients should give new insights into the ability of trails to promote the redistribution of species along climatic gradients.

1.6 Non-native plants in mountain ecosystems

1.6.1 Prevalence

Globally, records of invasive non-native species are increasing exponentially (Paulo et al., 2022) and while mountains are less invaded by non-native species than lowlands (Guo et al., 2018) they are not inherently resistant to invasions (e.g., Pauchard et al., 2009; Alexander et al., 2011; Lembrechts et al., 2014). With increasing warming (Dainese et al., 2017) and traffic (Alexander et al., 2016) increased rates of invasion in mountain areas are expected. The prevalence of invasive species in a mountain ecosystem is likely to be shaped by its inter-connectivity with surrounding lowland landscapes, its elevation extents and habitat complexity, the relative impact of global change drivers such as climate or land-use change, and pathways for accidental or intentional introductions from human activity (Brown and Sax, 2004; Pauchard et al., 2009; Petitpierre et al., 2016; Guo et al., 2018; Fuentes-Lillo et al., 2021). Research on invasions in mountain ecosystems is currently biased towards plants (Pauchard et al., 2009; McDougall et al., 2011). This may be a reflection of the focus of global research networks such as MIREN (the Mountain Invasion Research Network) working on plant invasions in mountains specifically (Haider, Lembrechts, et al., 2022). Research on invasive animals in mountain ecosystems is more localised and limited (e.g., Knapp et al., 2001; Nogueira-Filho et al., 2009; Driscoll et al., 2019) and knowledge on invasive microorganisms is relatively sparse (Pyšek et al., 2020).

1.6.2 Impacts on ecosystem functions, services, and benefits

Nature in mountain ecosystems contributes both positively and negatively to people's quality of life (Martín-López et al., 2019). These contributions can be see through different lenses e.g., as Nature's Contributions to People (NCP, Díaz et al., 2018) or as ecosystem functions, services, and their benefits to people[2] (Boyd and Banzhaf, 2007; Kadykalo et al., 2019).

Through their interactions with other species and direct impacts on ecosystems and physical properties of nature, invasive species influence ecosystem functions, services, and benefits such as biodiversity (Vilà et al., 2011), recreation and culture (García-Llorente et al., 2008), and human safety (De Neergaard et al., 2005). As negative impacts on native biodiversity are common (Crystal-Ornelas and Lockwood, 2020) the focus of invasive species research in mountains has often

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[2] In the context of this thesis ecosystem functions capture biodiversity, disturbance, pollination, soil stability, and water, while ecosystem services and benefits are represented by recreation and culture, resource provisioning, human health, and human safety (Boyd & Banzhaf, 2007).

been placed on negative effects (Goodenough, 2010). However, many invasive species have been purposefully introduced into ecosystems for agriculture, forestry, or pest control (Shackleton, Richardson, et al., 2019) and positive impacts on ecosystem functions, services, and benefits are possible (e.g., Charles and Dukes, 2007; Schlaepfer et al., 2011). Most assessment frameworks focus on negative impacts (but see: Kumschick et al., 2012; Martinez-Cillero et al., 2019) yet the development of frameworks which incorporate both negative and positive impacts could facilitate a better understanding of invasive species impacts.

A species may have divergent impacts on different ecosystem functions and services, and impacts frequently differ between stakeholder groups (Beever et al., 2019; Kourantidou et al., 2022). While one group may use a species to support their livelihood, it may be detrimental to that of others (Coates, 2007; Kannan et al., 2014; Kapitza et al., 2019). Together with their background, knowledge base, ethical and societal values, such economic considerations shape stakeholders' perception of invasive species (Shackleton, Adriaens, et al., 2019; Vimercati et al., 2020). Differences in burdens and benefits and the perception of an invasive species between stakeholder groups and regions can be a source of conflict regarding its management (Kourantidou et al., 2022) and lead to a lack of targeted management actions (Novoa et al., 2018), yet an overview from mountain ecosystems is lacking.

1.6.3 Management of invasive species

To avoid and limit negative effects of invasive species on mountain ecosystems and people, a prioritization of management is necessary. Depending on the phase of the invasion process, the perceived risk for spread, the species' impacts, and the vulnerability of the native ecosystem, different management approaches, spanning from prevention to containment, may be used (Blackburn et al., 2011; Larson et al., 2011). However, as described above, the ecological, economic, and social impacts of invasive species are highly complex and stakeholder-dependent. Currently, most frameworks exploring the impacts of invasive species in mountains focus upon biodiversity or broader ecosystem functions and do not take into account social and economic impacts nor differences between stakeholder groups (but see Bravo-Vargas et al., 2019). Considering the socio-ecological complexity explicitly and including meaningful participation and input from institutional and non-institutional stakeholder groups may improve invasive species management and aid the prioritization of resources (Shackleton, Adriaens, et al., 2019; Evans et al., 2008).

2 Aims and Questions

The overall aim of this thesis is to gain a better understanding of trails as redistributors of species in northern high latitude mountain ecosystems, with a special focus on the role of trails as conduits for dispersal and as linear gaps that can disrupt biotic interactions. Additionally, I explore the perception of the impacts of invasive species in mountains from a global perspective.

Specifically, I investigate:
1) How do hiking trails influence seed rain, seed bank, and natural seedling recruitment? (Article I)
2) How do trails change plant species' realized climatic niches, and how does this affect species richness along trails? (Article II)

To improve our understanding interactions of gap effects and climate on species establishment and persistence, I also ask:
3) How does the importance of facilitation vary along gradients of acute and persistent stress during seedling establishment and for adult plants of different species? (Article III)
4) Are there differences in the importance of facilitation between establishment and survival, and accumulation of biomass? (Article III)
5) How does gap size as a modulator of microclimate and distance to neighboring plants influence the importance of facilitation? (Article III)

Additionally I ask:
6) How are invasive species in mountain regions perceived by stakeholder groups in different regions and what guides management practices? (Article IV)

3 Methods

General approaches

This thesis combines observational surveys, experimental manipulations, and a stakeholder survey. First, we surveyed seed rain, seed bank abundance, and seedling recruitment (Article I), species composition and cover, and disturbances (Article II) at different distances from hiking trails along climatic gradients. Second, we investigated the importance of positive and negative neighbour interactions in a field experiment that manipulated environmental stress and distance to neighbouring vegetation (Article III). Finally, we surveyed stakeholders on their perceptions of invasive alien species in mountain areas (Article IV).

Field work was carried out in June to September 2018 (Article II), 2019 (Article I-III), 2020 and 2021 (Article III) and the survey was open for answers March to September 2020.

Study sites

Our study sites (Figure 3.1) are located in the Scandes mountains in Dovrefjell (62.2°N; 9.5°E), Norway (Article I and III), and Dovrefjell and Abisko (68.3°N; 18.8°E), Sweden (Article II). Both are popular destinations for hiking tourism and are accessible by road and rail. The growing season is short, and average temperatures are low in both areas. Vegetation is dominated by mountain birch (*Betula pubescens*) at the tree line and below. Low-alpine plateaus host dwarf shrub communities and lichen heaths dominated by *Empetrum nigrum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Betula nana* and *Arctostaphylos uva-ursi*, lichens and bryophytes, with considerably denser and more widespread lichen heath in Dovrefjell than in Abisko. Vegetation at higher elevation is a mosaic of dry heath, meadow vegetation, snow beds, and sparsely vegetated boulder and scree fields (Sjögersten et al., 2003; De Wit et al., 2014) with graminoids such as *Carex bigelowii* and *Juncus trifidus* and small statue forbs such as *Omalotheca supina.* The elevation gradients surveyed in the Abisko area span from 400 m to 1490 m, and from 683 m to 1726 m in Dovrefjell.

The study site for the experiment (Article III) is located in Dovrefjell on the slopes of Hjerkinnhøe mountain at 62.243°N, 9.595°E between 1092 m and 1263 m. The vegetation at this site is dominated by lichen heath with low *Betula nana* and *Salix sp.* shrubs. A more in-depth description of the study sites can be found in Articles I–III.

The studies

Observational study of trail effects on dispersal, disturbance, and vegetation (Article I and II)

We surveyed the vegetation along 16 hiking trails, eight in Dovrefjell, and eight in Abisko, following the trail survey protocol from the Mountain Invasion Research Network (MIREN) as described in Liedtke et al. (2020) (Article II) and investigated seed rain, seed bank abundance, and seedling recruitment along four of the trails in Dovrefjell (Article I). The trails lead from trailheads close to major transportation corridors uphill towards points of interest such as mountain peaks and were spanning large macroclimatic gradients.

Along each trail, we placed ten T-shaped transects at intervals of equal elevation from the trailhead to the highest occurrence of vascular plant species along the trail, or the highest point of the trail feasible if this occurred below the limit of vascular vegetation (Article II). Each so-called T-transect consisted of three 2 × 10 m plots, with the trailside (T) plot directly adjacent to the trail and parallel to its edge forming the short side of the T. Perpendicular to this, the midplot (M) and farthest away the interior vegetation plot (F) form the long side of the T (see Figure 3.2). We therefore captured a gradient from strongly trail-influenced vegetation (T) to interior vegetation that was not visibly influenced by the trail (F). For each plot, we determined the presence of vascular plant species and estimated their cover alongside that of total vascular vegetation, herbs and forbs, shrubs, dwarf shrubs, bryophytes, rocks and bare soil. We measured the visible extent of mechanical disturbance from trampling exceeding the trail edges and surveyed the number of gaps in the vegetation with exposed soil encountered along a line transect crossing the middle of the plot.

For our survey of seed rain, seed bank abundance, and seedling recruitment (Article I), we selected four of the hiking trails surveyed in Dovrefjell and recorded these parameters in our T-transects at four elevations per trail. Transects were placed at fixed intervals corresponding to 1.) the trailhead elevation, 2.) 40 % of the elevation up the trail from trailhead to highest plot, 3.) 70 % up the trail, and 4.) where the trail becomes indistinguishable from surrounding terrain.

In each of these T-transects we placed four 15 × 15 cm Astroturf® seed traps in each plot (T, M, F) to capture the seed rain. Seed traps were installed 0.5 m from the trail in the first plot (T), 7 m (M), and 17 m from the trail edge(F). To investigate the soil seed bank, four soil cores with a diameter of 7.5 cm and 5 cm depth were collected in each plot, one underneath each seed trap. In total, 192 seed traps were deployed and 192 soil cores sampled. In each plot natural seedling recruitment was recorded in a 0.5×0.5 m quadrat.

We related seed rain, seed bank abundance, and seedling recruitment to distance to the trail, climatic harshness and covariates (Article I). Based on our vegetation surveys we investigated how distance to the trail affected species richness in our plots and related these changes to disturbances and characteristics of the resident vegetation. By linking species occurrences and abundances with high-resolution down-scaled climate data derived from CHELSA (Karger et al., 2017) we calculated species' climatic niches and optima. We then linked shifts in niches and optima between the interior vegetation and trailsides to species' optima in the interior vegetation (Article II).

More detailed descriptions of our methods can be found in Article I and II.

Experimental investigation of biotic interactions (Article III)

To improve our understanding of the importance of facilitation in mountain tundra ecosystems and its changes along interacting gradients of stress, we set up a field experiment split into one part investigating the establishment phase (sowing experiment) and one part investigating the persistence of adult plants (transplant experiment). We placed 20 plots along microclimatic gradients, ten sheltered by shrubs and ten exposed. In each plot we established five gap sizes, spanning a diameter from 0 cm (control) to 60 cm. We transplanted the lowland species *Achillea millefolium* and the highland species *Solidago virgaurea*, and sowed these species, three more lowland-highland species pairs, and an alpine cushion plant, into the gaps of the respective sub-experiment (Figure 3.3).

We monitored seedling germination, survival, and establishment of seedlings, and transplant survival and establishment of transplants and measured shoot, root, and total weight of *A. millefolium* and *S. virgaurea* seedlings and transplants. Based on these performance measurements we calculated the importance of facilitation using the Neighbour-effect Importance index, $\mathrm{NImp}_{\mathrm{A}}$ (Díaz-Sierra et al., 2017).

We measured persistent stress — growing degree days (GDD), and acute stress — maximum soil temperature — at the plot level in undisturbed vegetation and in all gap sizes. For our models of facilitation we used plot level measurements due to a high failure rate of gap-level temperature loggers. We investigated how life stage, species identity, acute and persistent stress and gap size influenced the importance of facilitation in our experiment.

For a more in-depth description of the experimental set-up and analyses please refer to Article III.

Survey of stakeholder perceptions of invasive species (Article IV)

To better understand the stakeholder perceptions of invasive species' impacts on nature and society, we developed a survey with the Mountain Invasion Research Network group (MIREN). We tested a draft version of the survey with invasion biologists and social scientists associated with MIREN and integrated feedback. Ethics approval for the survey was gained through an agreement with the Norwegian data protection society (NSD; Meldeskjema 131841). The survey was distributed in ten languages with the aim to collect responses globally and was distributed through mailing lists, social media, and print-outs in spring 2020.

We asked respondents to rate impacts of global change drivers and to identify which organism groups were invasive in their mountain region. Furthermore, we inquired what guides the management of invasive species in the mountain region, whether there is support for management, and who is responsible for management. For the most prominent invasive species in their mountain range, stakeholders were asked to rate impacts on five ecosystem functions, and four ecosystem services and benefits. Species' impacts were recorded on a scale based on the Socio-Economic Impact Classification of Alien Taxa (SEICAT), capturing negative and positive impacts, and data deficient cases (Bacher et al., 2018.)

See Article IV for a more detailed description of the methods.

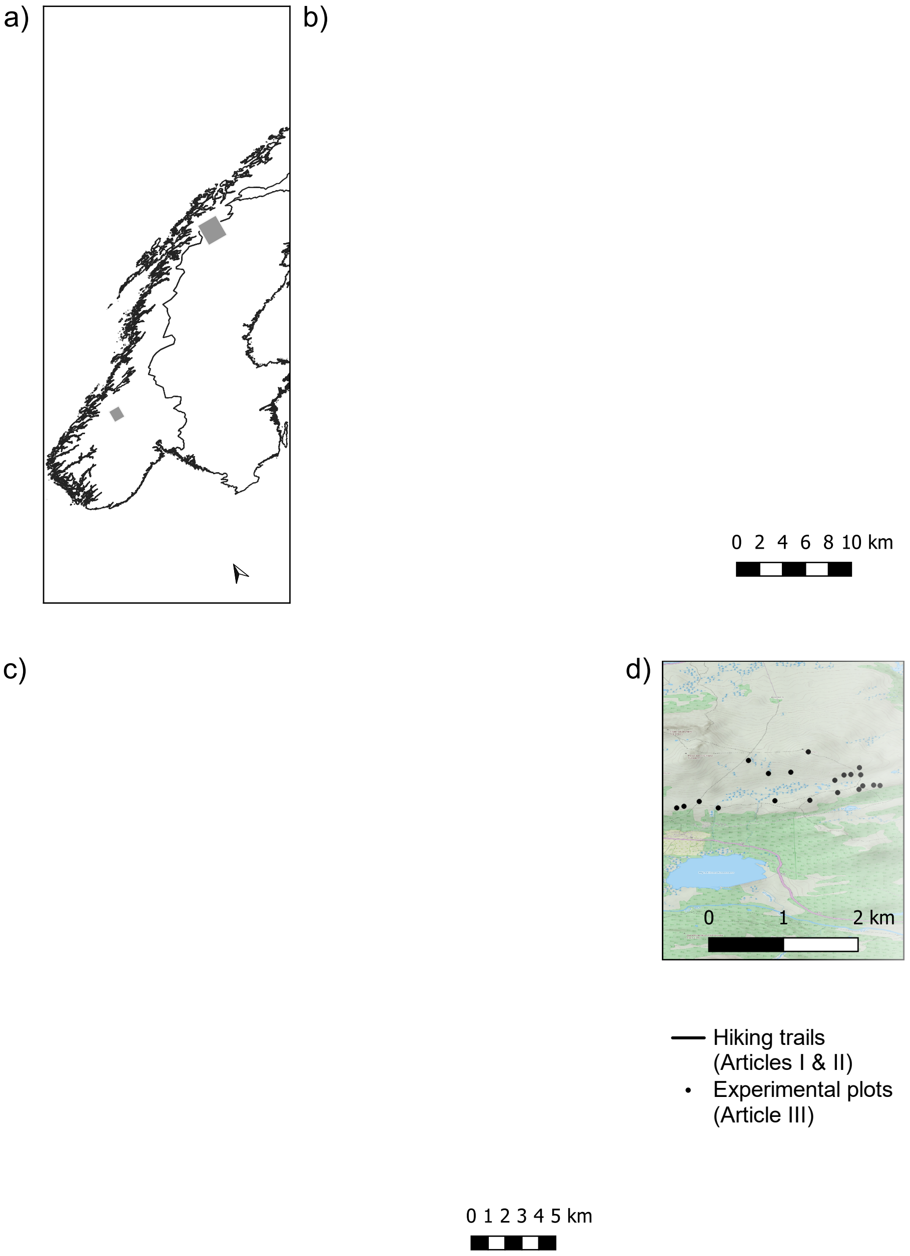

Figure 3.1: a) Overview of the study sites within Scandinavia, with Abisko in the north and Dovrefjell in the south marked by grey inlays. b) The Abisko and c) the Dovrefjell study site with surveyed trails. The inlay shows the location of the experimental site. d) The experimental site on Hjerkinnhøe with 20 experimental plots.

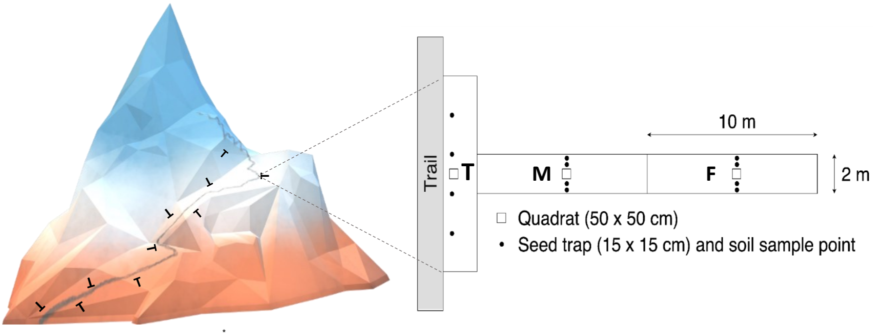

Figure 3.2: Illustration of T-transects placed along a hiking trail with zoom-in providing a detailed overview about the layout of a T-transect. Trailside- (T), mid- (M), and the interior vegetation plot (F) farthest away from the trail are shown and the placement of seed traps, soil sampling points, and quadrats for seedling censuses are illustrated. (Article I & II)

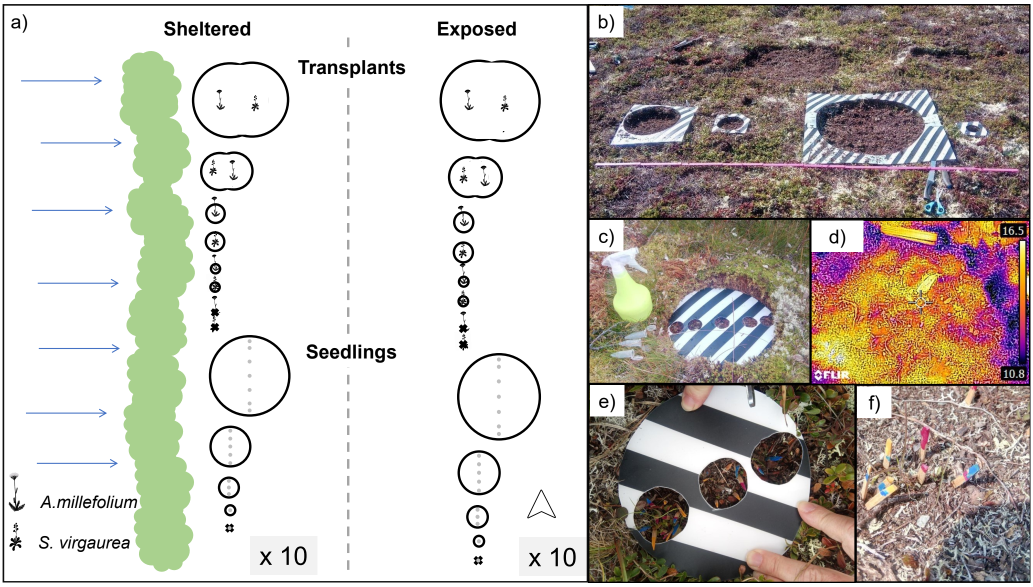

Figure 3.3: a) Experimental set-up of sheltered and exposed gaps with gap sizes from 0 cm to 60 cm, shelter created by a row of shrubs blocking the prevailing winds. b) Exposed plot in the field with gap templates that allowed for precise gap sizes; c) seed sowing template with fixed sowing positions. d) Temperature gradient in a 60 cm gap during mid-day with shaded gap edges. Panel e) and f) show seedlings marked with color-coded toothpicks in their sowing positions. (Article III)

4 Main Results and Discussion

Close to trails, seed rain, seed bank, and seedling recruitment were elevated, yet this was modulated by climate (Article I).

Gap creation by trails reached far into the natural vegetation and increased the number of vegetation gaps. Disturbances along trails allowed alpine species to shift their rear edges and optima towards warmer locations, leading to an increased overlap in species' climatic niches. This was reflected by a greater species richness in trailsides than in the interior vegetation. Recipient community and distance to anthropogenic structures modulated by how much species richness in trailsides increased (Article II).

Gap size altered within vegetation gap microclimate, and increased seedling establishment in small gaps appeared to be a result of reduced competition for light, which masks the amelioration of climate by neighbouring vegetation that becomes apparent when including larger gaps sizes. Facilitation by neighbouring vegetation is important throughout the life cycle under stressful conditions and the SGH is supported more clearly when examining the effects of stress on growth. Stress type matters for the importance of facilitation, with seedlings more susceptible to acute stress (Article III).

Stakeholders across regions ranked impacts of invasive species on biodiversity and ecosystem functions predominantly negative, while the ranking of impacts on ecosystem services and benefits also included positive perceptions. Stakeholder groups varied in their perception of impacts, with on-the-ground stakeholders more frequently reporting positive impacts. Conflicting views on impacts may be a reason for the large proportion of species that currently have no management plan (Article IV).

4.1 Sticking to the trail: more propagules in trailsides

Our study of seed rain, and seed banks along hiking trails in (Article I) provided the first quantitative estimates of the dispersal effect of trails in the Scandes mountains. While seed rain was generally low, it was predicted to be on average 3.4 times higher in trailside plots than in those 17 m away (Figure 4.1 a) and declined with colder climate at all distances from trails. Seed bank abundance in trailsides at the warmest location was eight times higher than in plots at 17 m distance, while there was no significant difference at colder locations (Figure 4.1 b).

These findings support our hypothesis that seed deposition along trails is higher and corroborate previous evidence that trails may act as dispersal corridors, facilitating colonization (Liedtke et al., 2020). As trails often access areas of special ecological value and remote locations (Ballantyne and Pickering, 2015a; Liedtke et al., 2020), such increased influx of propagules may be negative for biodiversity, when invasive species are able to spread from trails into the ecosystem (Barros et al., 2020). However, it may also be positive, when trails support the maintenance a collection of rare local populations occupying discrete habitat patches, i.e. a meta-population (Hanski, 1998) by increasing functional connectivity *sensu* Auffret et al. (2017). Trails may therefore preserve dispersal-maintained local diversity and facilitate the establishment of new species into dispersal-limited locations.

Compared to the steady increase in seed rain close to the trail along the climatic gradient, seed bank abundance in cold locations was not significantly higher in trailsides than in the interior vegetation. This could be due to a lower arrival of deposited seeds in the seed bank, or a lower likelihood of germination after dormancy in cold locations, and corroborates observations by Thompson, 1978 of larger seed banks in climatically benign disturbed locations. As we only examined the germinable seed bank, our observation may be influenced by insufficient dormancy-breaking of high-elevation species (Cavieres and Sierra-Almeida, 2018), as well as germination strategies adapted to unpredictable environments, spreading germination through multiple years (Jaganathan et al., 2015). Long-term studies of seed banks along trails are therefore warranted.

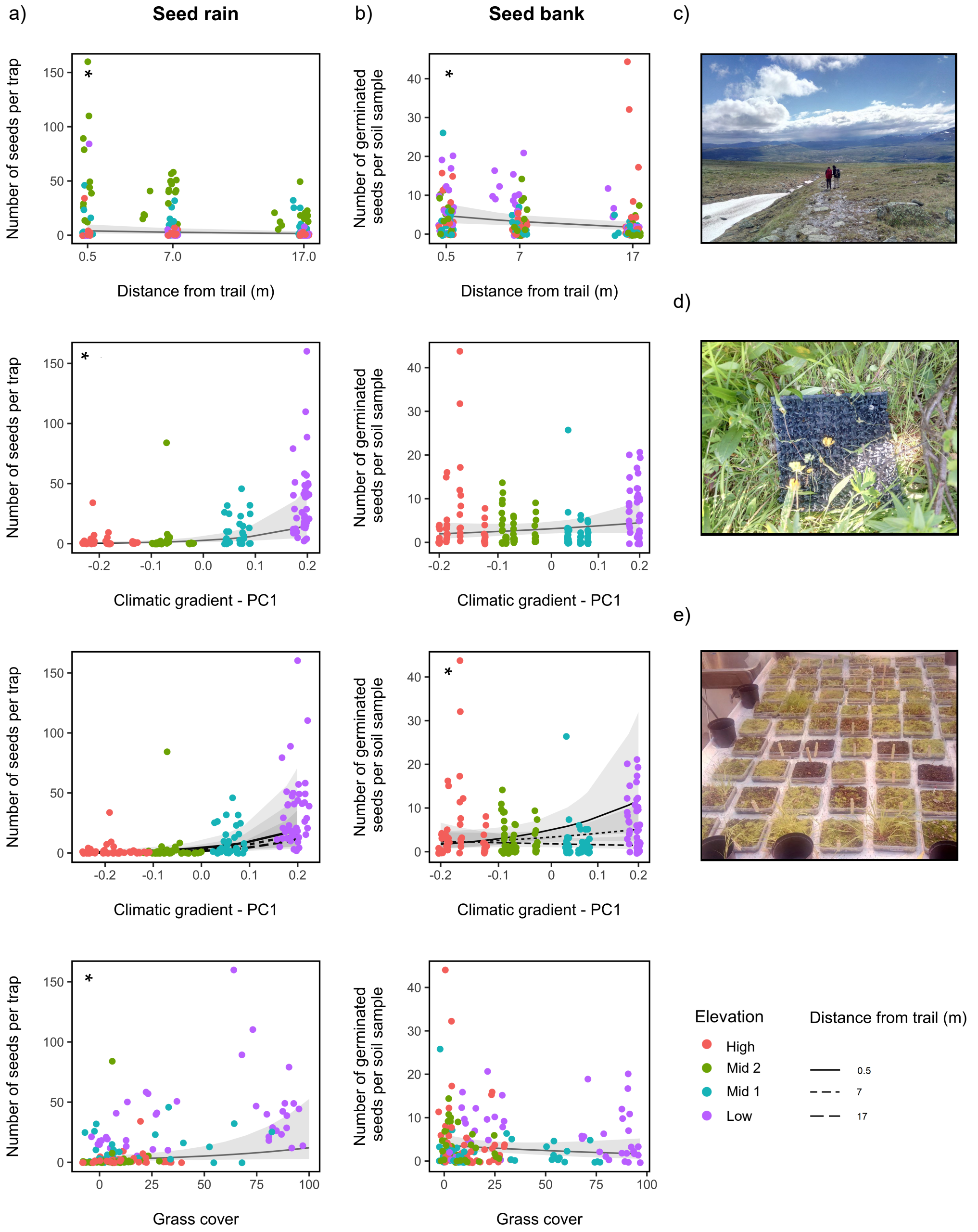

Figure 4.1: Graphical representation of the best models for a) seed rain, and b) seed bank abundance, against distance from the trail, the climatic gradient (negative values denote harsher conditions), their interaction, and grass cover, where it was retained in the best model. Gray shading indicates 95 % confidence intervals. Stars denote significance at the $p < 0.05$ level. Raw data is displayed as dots. c) Trail along which seed traps, shown in panel d) were placed. e) Determination of seed bank abundance in the greenhouse. (Article I)

4.2 Disturbing trails

In our study of hiking trails in Abisko and Dovrefjell (Article II) we measured a mean trail width of 2.5 m, and a mean visible disturbance extent from the trail verge of 0.4 m with a range from 0 m to 4.3 m. Trails in both hiking areas are predominantly informal, without marked trail boundaries, and trampling beyond the bare soil surface of the trail resulted in a significantly higher number of gaps and a greater area covered by gaps in trailside plots than in the interior vegetation (Appendix S1, Figure 4.2). Even though off-trail hiking may be rare, mountain tundra is susceptible to trampling, with 50 passes resulting in a loss of up to 80 % of cover (Emanuelsson, 1984). This accentuates that disturbance effect of trails are not limited to the denuded trail surface, but extend into the vegetation beyond.

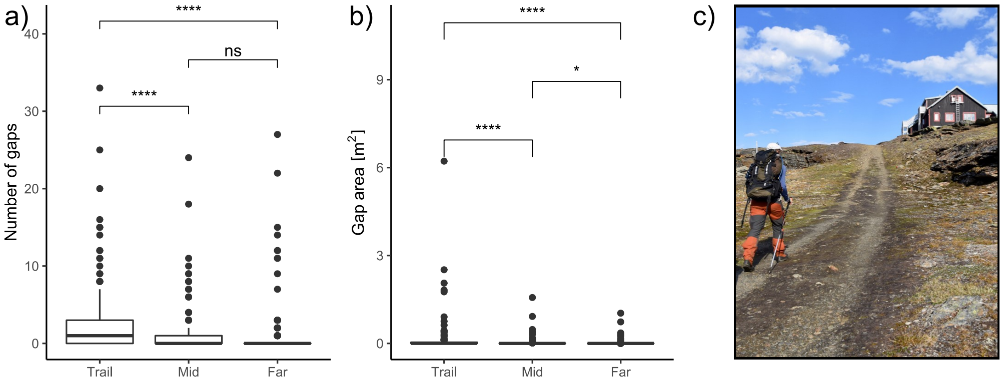

Figure 4.2: a) Number of gaps along a 10 m transect in plots located in trailside, and at mid- and far-distance. b) Gap area based the number of gaps along the transect and the size of five random gaps of those counted, with one outlier removed for better visibility. c) Trampling gaps extend from the trailside into the vegetation. Picture: J. Lembrechts.

The role of trails as linear channels for disturbances in mountains is relevant not only in so far as trampling may damage vegetation including individuals of rare species, but also as gaps can provide suitable microsites for germination and establishment (Graae et al., 2011). Successful seed recruitment has major implications for population dynamics, community turnover and species' range dynamics (Meineri et al., 2019). If species are to track the warming climate, establishment at newly suitable locations is necessary (Graae et al., 2018). In accordance with the SGH the creation of gaps should result in competitive release in benign locations, while in climatically extreme, stressful locations, disturbances should disrupt facilitation and result in lower recruitment. However, even in harsh alpine tundra gap creation benefits establishment, suggesting a continued importance of competitive interactions (Graae et al., 2011; Milbau et al., 2013; Klanderud et al., 2017; Alexander et al., 2016). Based on our data, we see that trails create many opportunities for establishment in the form of vegetation gaps.

4.3 Seedling establishment along hiking trails

In our survey of natural seedling recruitment along trails seedling occurrence was predicted to be 3.5 times higher in trailsides than in the interior vegetation away from trails along the whole climatic gradient (Figure 4.3, Article I). This relatively large increase in seedling number close to hiking trails highlights that future research on species ability to track climate change in mountain ecosystems should include distance to trails as a proxy for dispersal and disturbance, both of which may facilitate establishment (Lembrechts, Alexander, et al., 2016). The increased recruitment in disturbed trailsides underscores the importance that small gap might have for tracking a shifting climate, but also as a potential opportunity for the establishment of non-native species. Increased seedling recruitment close to trails, even at climatically harsh points, plots towards a continued importance of competition under stressful conditions, concurring observations of disturbance being crucial for establishment in mountain tundra (e.g. Graae et al., 2011). This discrepancy between predicted importance of facilitation and observed importance of competition motivated our experimental study of species interactions along a climatic gradient, since we hypothesized that it could be a result of gap size-effects and varying stress tolerance between species and life stages.

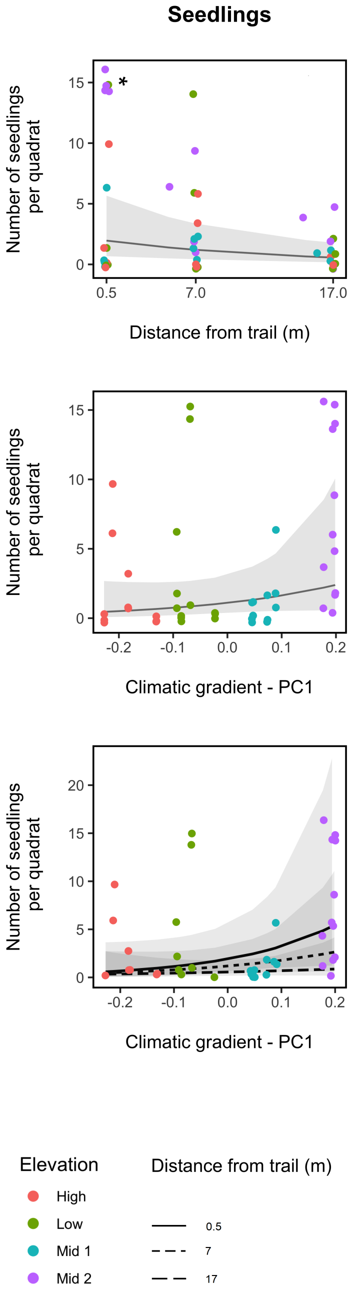

Figure 4.3: Graphical representation of the best model for a) seedling emergence in the field, against distance from the trail, the climatic gradient (negative values denote harsher conditions), and their interaction. Gray shading indicates 95 % confidence intervals. Stars denote significance at the $p < 0.05$ level. Raw data is displayed as dots, with red denoting plots located at high, green at medium high, blue at medium low, and purple at low elevations. (Article I)

4.4 Facilitation matters: Stressors, stress tolerances, and gap sizes

Most research on the SGH in cold mountain ecosystems comes from experiments with relatively small gap sizes (e.g., Milbau et al., 2013, but see Lembrechts, Pauchard, et al., 2016). In our experiment with gap sizes ranging from 0 to 60 cm (Article III) we found an increasing growing season length, but also higher maximum soil temperatures, lower minimum soil temperatures, and a greater number of frost occurrences during spring with increasing gap size.

Facilitation continued to be important even under climatically stressful conditions, for most vital rates and the accumulation of above-ground biomass of seedlings and transplants. Changes in the importance of facilitation for seedling were best explained by acute stress in the form of maximum soil temperatures. This corroborates expectations of susceptibility to heat damage (Marcante et al., 2014) and observations of a lower seedling establishment under warming in mountain tundra (Graae et al., 2009; Milbau et al., 2017) and might be correlated with surface drought conditions, an important driver of mortality in alpine and Arctic ecosystems (Bell & Bliss, 1980). The change in importance of facilitation along stress gradients was species-specific, corroborating other observations from climate gradients in Norway (Klanderud et al., 2017). Contrary to our expectations we did not find an increase in the importance of competition from seedlings to adults. However, observations of this pattern mostly come from arid ecosystems (e.g., Schiffers and Tielbörger, 2006) where there may be a strong and limiting competition for water as individuals grow. Our observation that the SGH was supported more clearly when considering growth than survival parameters corroborates meta-analysis results for alpine regions (He et al., 2013). We speculate that this may reflect a stronger influence of change event on survival, especially of young life stages, than on growth.

The influence of gap size on climatic stress was exemplified by its influence on the importance of interactions when considering the accumulation of above-ground biomass. In large gaps the importance of facilitation rose even though the growing season in the undisturbed vegetation was longer and therefore less stressful. Based on our climate measurements, the maximum soil temperature rose sharply with gap size. That we found a continued importance of facilitation at stressful locations, contrasting observations of e.g. Graae et al. (2011) and Milbau et al. (2013) may therefore be a result of the gap size effect. The small gap size commonly employed in other experiments may thus release from light competition while still providing microclimatic shelter (Lembrechts et al., 2015; Klanderud et al., 2021). This underlines the need for better understanding at under which circumstances and at which spatial scales neighbours influence different stresses to allow for a targeted experimental approach (Dormann & Brooker, 2002).

4.5 Highways up the mountain?

Using occurrence data from our vegetation surveys along hiking trails and high resolution climate data we were able to investigate how trails influence plant species' climatic niches, and linked niche shifts to their climatic preferences (Article II). As predicted, trails influenced plant species' realized climatic niches. In trailsides alpine species' rear edges and optima were more likely to shift towards warmer locations. This implies competitive release through trampling in more benign climates, corroborating observations from the Rocky Mountains (Chardon et al., 2019) and expands them to a community perspective. Trailsides and their disturbances may provide an temporary *escape route down the mountain* for pressed alpine species, allowing them to avoid competition in the trampling gaps. Grazing by sheep, another process causing disturbances in northern mountain ecosystems, can help counteract shifts to locations that have newly become climatically suitable (Speed et al., 2012), reinforcing the importance of disturbances for the persistence of alpine species. However, the zone of influence of trails appears much smaller than that of grazing with freely roaming animals.

In the European Alps lowland species had a greater tendency to fail tracking their ranges in a warming climate, which might be rooted in a relatively high resistance to colonization by new species (Alexander et al., 2018; Rumpf et al., 2019). We had therefore expected that disturbance by trails might help lowland species overcome establishment lags and improve range tracking with rising temperatures, proving a *highway up the mountain*. However, we did not find a significant shift of lowland species' leading edges towards colder locations (Figure 4.4). This stands in contrast to observations along mountain roads (Lembrechts, Alexander, et al., 2016) and implies that these species either do not benefit from disturbances equally much as alpine species (Le Roux et al., 2013), already had leading edge at the limit of their physiological tolerance, might not be able to tolerate other stresses of the alpine zone such as drought and wind, or the disturbance exerted by trails was too low to break down limiting biotic resistance of the recipient community (Milbau et al., 2013)). Lowland species optima did move towards colder locations though, indicating a greater cover in trailsides at colder locations than in the interior vegetation. This hints at some extent of competitive release in locations where species are not at their climatic tolerance limit yet. Due to the changes in species' realized niches in trailsides (Figure 4.5 a) we found indications for a greater overlap in species' climatic niches in trailsides (Figure 4.5 b). This greater overlap in climatic niches may, in conjunction with a small scale heterogeneity lead to greater species richness in trailsides (Opedal et al., 2015).

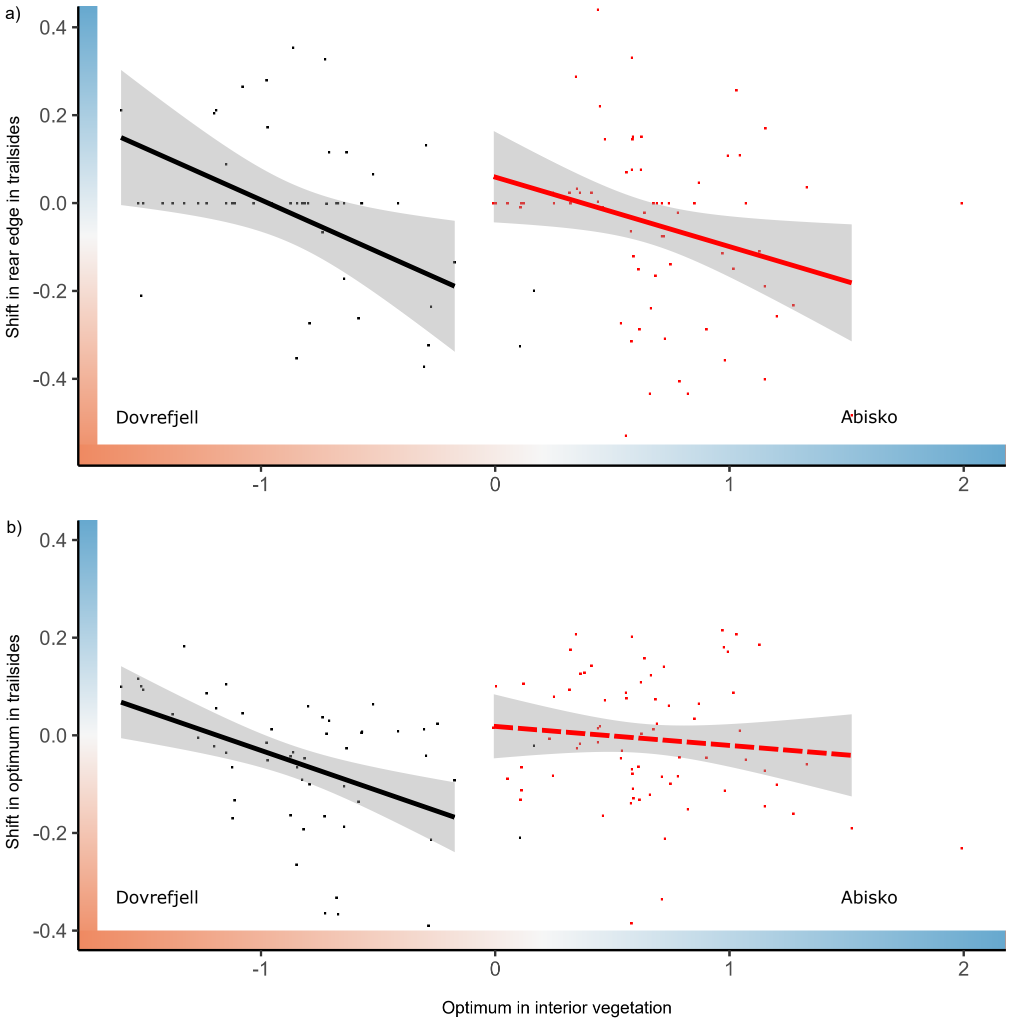

Figure 4.4: We compared how species' climatic niche edges and optima differed between trailsides and the interior vegetation and related shifts to species optima in the natural vegetation, shown on the x-axis (Article II). Predicted shifts between interior vegetation and trailsides (with 95 % confidence intervals) in a) rear edges and b) optimum of species plotted against each species' optimum in the interior vegetation along the climatic gradient studied in the Dovrefjell ($n = 52$, black) and Abisko ($n = 72$, red) areas. Solid lines denote significance at $p < 0.05$. The colour gradient on the axes illustrates climatic gradient from warmer (red) to colder (blue). Positive values on the x-axis correspond to harsher climate and species with a more alpine distribution. Positive values on the y-axis represent shifts towards colder locations in trailsides. (Article II)

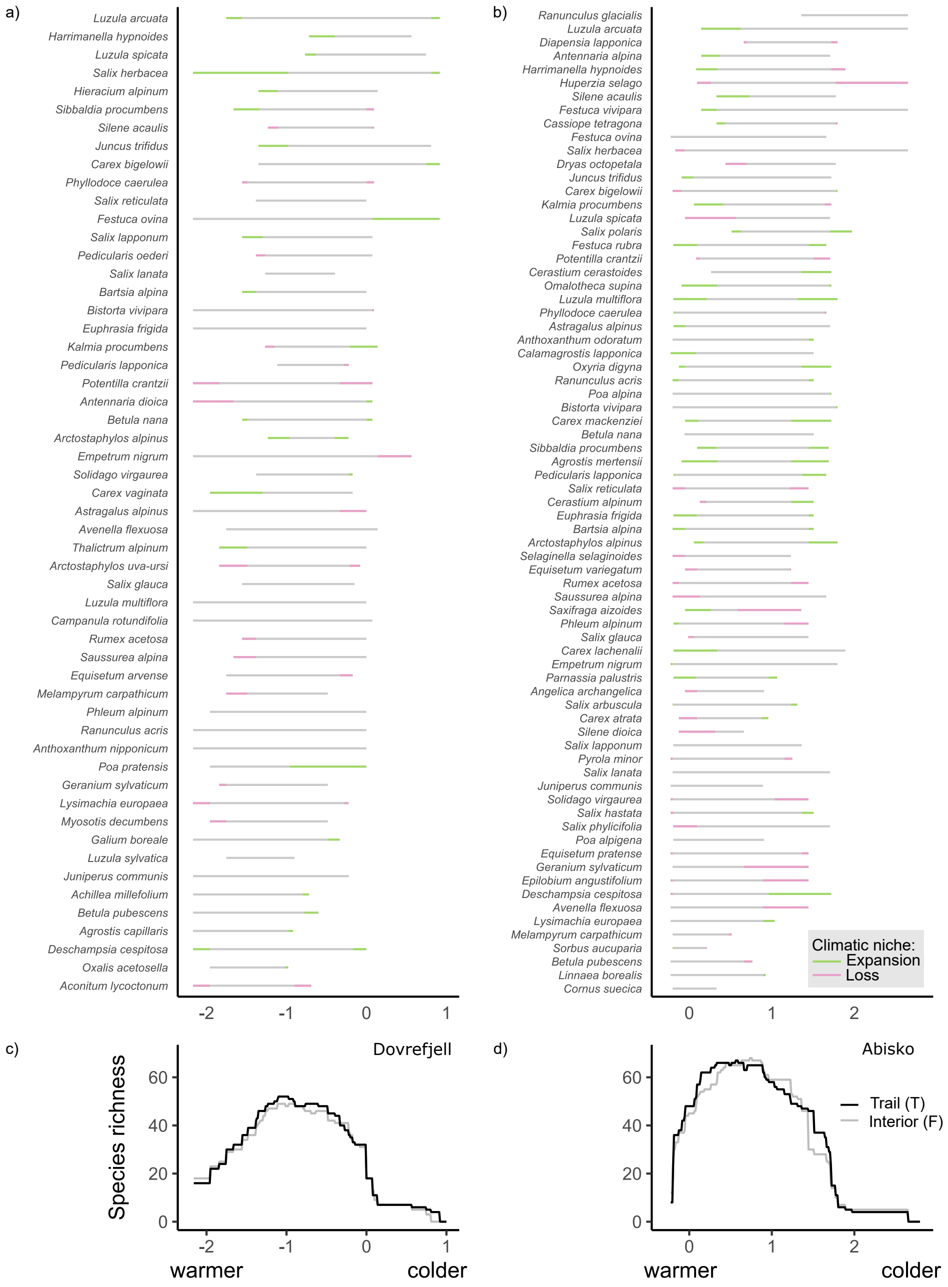

Figure 4.5: Species range changes along trails in comparison to the interior vegetation, with pink parts of the bar denoting a loss of range along trails, green range expansion along trails, and grey ranges occupied both along the trails and in the interior vegetation in a) Dovrefjell and b) Abisko area. Species are ordered according to their optimum in the interior vegetation, with those found at the coldest locations on the top. Cumulative number of species ranges overlapping at any given point along the climatic gradient in the interior vegetation (grey) and in trailsides (black) are shown in c) Dovrefjell and d) Abisko. (Article II)

4.6 Greater species richness in trailsides

We found that seedling emergence in the field is larger close to hiking trails (Article I) and that hiking trails shifted species' climatic niches (Article II). Together, these observation resulted in an increased species richness along hiking trails in Abisko and Dovrefjell. On average, trailside plots harboured 24 % more species than plots placed 12–22 m away from trails, which corresponds to a median of four species. Trampling-resistant grasses and low-stature forbs were most frequently gained in trailsides (Figure 4.6 a). Distance from trail accounted for 9 % of variation explained by our model of species richness, while climatic harshness captured 55 %. Richness was lower in colder locations (Figure 4.6 b). While our findings contradict other studies finding no or negative effects of trails on richness in cold ecosystems (Monz, 2002; Gremmen et al., 2003; Crisfield et al., 2012; Jägerbrand and Alatalo, 2015), they concur with observations of increased species richness and expansion of alpine species' ranges towards lower elevations along mountain roads close to Abisko (Lembrechts et al., 2014). Furthermore, our observations are based on surveys along 16 trails, extending for a total of more than 100 km and capturing the impact of trails on mountain ecosystems at a far larger scales than previous studies.

Trail effects on richness varied between communities, and greater cover of herbaceous vegetation was associated with a larger increase in species richness, while with increasing cover of dwarf shrubs richness in trailsides increased less. Meadow and willow-shrub communities dominated by herbaceous vegetation are considered more invasible than dwarf shrub heaths (Graae et al., 2011; Milbau et al., 2013; Opedal et al., 2021) and our findings corroborate these observations. Greater resistance of dwarf shrub dominated communities to colonization may be due to allelopathy of *Empetrum nigrum* (Wardle et al., 1998). Proximity to potential sites of propagule introduction such as trailheads and railway tracks also led to a greater increase in trailsides' richness, concurring with observations of mountain invasions close to human infrastructure in other ecoregions (Pickering et al., 2007; Fuentes-Lillo et al., 2021). Positive effects of mountain trails on species richness may also point towards a greater chance for non-native species to establish in these locations if they arrive and have the needed climatic tolerance.

While species richness itself is considered an insurance variable for ecosystem stability (IPBES, 2019), trampling does lead to a loss of biomass and may destroy rare species and vulnerable communities (Gundersen et al., 2012). Potential increases in richness along trails must therefore be balanced with potential losses of species that are only growing in few and specific locations.

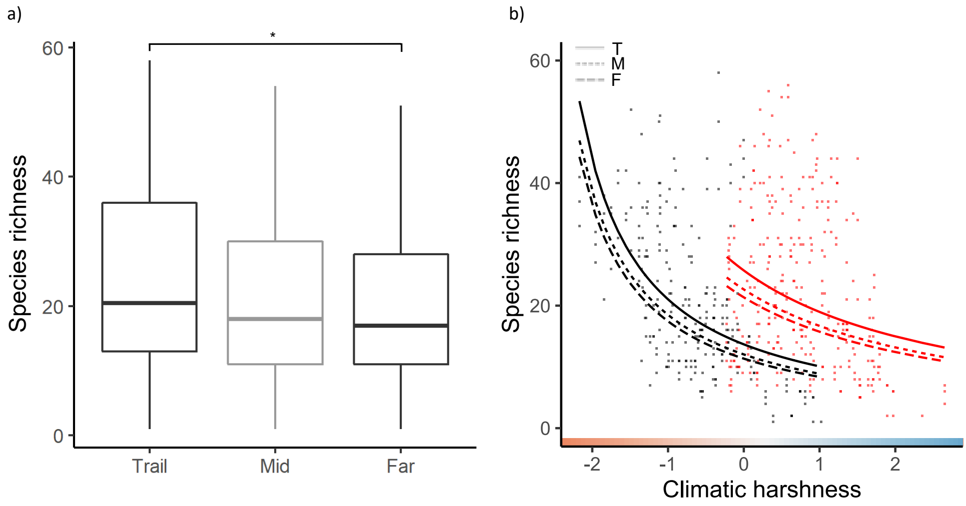

Figure 4.6: a) Species richness per plot at different distances to the surveyed hiking trails. b) Predicted species richness as a function of climatic harshness and distance from the trail for Dovrefjell (black lines) and Abisko (red lines). Raw data from Dovrefjell (black dots) and Abisko (red dots) are plotted as is, to show the variability among recorded plots. The coloured bar at the bottom illustrates the climatic harshness gradient from warmer (red) to colder (blue). (Article II)

Figure 4.7: *Achillea millefolium*, a non-native species was found predominantly close to trails or human infrastructure, such as this hiking cabin.

4.7 Trails as pathways for non-native species

While we did not explicitly examine the influence of hiking trails on the distribution of non-native species in Scandinavia, we did find some species that were locally non-native in the vicinity of the trails (e.g., *Achillea millefolium* and *Trifolium repens*). Most non-native species (with exception of *A. millefolium*, Figure 4.7) were only found in the trailside plots and predominantly at low elevations. This corroborates observations of increased occurrence along trails in other mountain ecosystems (Benninger-Truax et al., 1992; Barros and Pickering, 2014; Liedtke et al., 2020). Due to the extremely low overall incidence of non-native species, even in trailside plots, we were not able to further investigate if there were differences between the climatic niches in non-native and native plants as (Lembrechts, Alexander, et al., 2016) found along mountain roads.

As distance to anthropogenic introduction sources such as roads or skilifts were important determinants for increases in overall species richness in trailsides (Article II) we expect that non-native occurrences in our ecosystem would also cluster around such sources. A great importance of distance to the nearest human settlement for non-native species occurrence was also found in the Chilean mountains. (Fuentes-Lillo et al., 2021).

4.8 Perspective matters - invasive species impacts in mountain ecosystems

Our globally distributed survey of stakeholder perception of invasive species impacts in mountains (Article IV) yielded more than 600 responses. Overall, introduced invasive species were present in most mountain regions, yet also native species were considered as invasive by stakeholders. That native species were also considered invasive points towards the need to understand rapidly range-expanding species' impacts on alpine ecosystems (Alexander et al., 2016). Many of the most prominent of invasive species identified by respondents have documented detrimental impacts on ecosystems, as reflected by their inclusion on their list of the world's 100 worst invasive species (Global Invasive Species Database, 2022).

We found diverging perspectives regarding the impact of the most prominent invasive species on ecosystem functions, services, and benefits. Both negative and positive impacts were identified, reinforcing the need to include the option to report both burdens and benefits (Kumschick et al., 2012). Respondents ranked biodiversity as most negatively impacted, and effects on ecosystem functions and benefits more consistently and negatively across regions. Decreases in native biodiversity (Vilà et al., 2011) and higher extinction probability (Pyšek et al., 2012) are commonly observed impact of invasions. However, the lower variation in perception of impacts on ecosystem function may also reflect that research and communication focus on negative effects of invasive species on ecosystem functions (Pyšek & Richardson, 2010). Considering impacts on ecosystem services and benefits we found a divergence in perceived impacts between stakeholder groups, with e.g. government officials being consistently more concerned than local farmers and fishermen, that we consider "on-the-ground" stakeholders. Government officials may approach invasions with perspective aimed at larger scales and be involved in developing guidelines for the management of invasive species, when there is only limited knowledge about specific species' effects, leading to a general approach of precaution (Larson et al., 2011; Kapitza et al., 2019). "On-the-ground" stakeholder groups may also derive direct benefits from invasive species such as pigs or goats, e.g., through resource provisioning (Coates, 2007). Differences in utilization (Coates, 2007;Kannan et al., 2014; Kapitza et al., 2019) but also in societal and personal values (Shackleton, Richardson, et al., 2019; Vimercati et al., 2020) may be the reason for such differences in perception. Diverging perception of impacts may complicate management (Kourantidou et al., 2022). Our framework capturing negative and positive impacts on ecosystem functions and ecosystem services and benefits enables the identification of species of high priority with negative impacts on all dimensions, species with contrasting impacts, and those of least concern. Overall, almost a third of the most prominent invasive species did not have management plans identified, and the high number of species with contrasting impacts may contribute to conflicting management approaches or the lack of management plans (Novoa et al., 2018). Involving stakeholders into the development of management options for invasive species may improve management outcomes (Evans et al., 2008), and while our survey is only a first step towards more holistic assessments the large variation in perceived impacts between stakeholders, but also between regions, corroborates the need to involve stakeholders in management on a local level (Shackleton, Adriaens, et al., 2019). Using a survey approach and collaborating with social scientists allowed us to move beyond impacts of invasive species on biodiversity and ecosystem functions towards a more integrated perspective (Martín-López et al., 2019).

5 Synthesis and Perspectives

The aim of this thesis was to gain a better understanding of trails as redistributors of species in northern high latitude mountain ecosystems, with a special focus on their role as conduits for dispersal and as linear gaps that can disrupt biotic interactions. Additionally, I explored the perception of invasive species' impacts in mountains around the world from a stakeholder perspective.

Research often focuses on the negative effects that trails may have on the surrounding ecosystem, but our findings suggest that, in northern mountain ecosystems, they may also have positive impacts on vegetation and ecosystem resilience in a warming climate. Increased connectivity and seed deposition along trails may improve the exchange of genetic information and individuals between metapopulations (Hanski, 1998) and may support the persistence of dispersal- maintained and establishment of dispersal-limited species in mountain ecosystems (Vandvik & Goldberg, 2005). Dispersal is a major contributor to species diversity in sub-alpine grasslands in Norway (Vandvik & Goldberg, 2006), which has intrinsic conservation value and is associated with the maintenance of options in the NCP framework (Díaz et al., 2015; Díaz et al., 2018). Additionally, trails may increase alpine species ability to locally persist in a warming climate and with new neighbours, though the zone of influence of trails is relatively small compared to the extent of the ecosystem.

Potential negative effects of trails should not be disregarded in planning and management, though. When trails cross vulnerable communities such as mountain wetlands (Evju et al., 2021) or the habitat of rare species, that are susceptible to trampling (Gundersen, Hagen, et al., 2019), alternative routes or infrastructure such as walkways that canalize use and limit disturbances may be required (Miljødirektoratet, 2021). Additionally, trails may act as pathways for the introduction of non-native species in currently relatively unaffected areas and this thesis shows increased seedling recruitment close to trails. Establishment of source populations at trailheads and close to infrastructure, especially of cold-tolerant species, should be avoided to prevent such spread (Pauchard et al., 2015; Fuentes-Lillo et al., 2021). While this thesis focuses on vegetation effects, trails and associated presence of humans can have negative impacts on threatened wildlife such as wild reindeer, *Rangifer tarandus*, in the Scandes mountains (Gundersen, Vistad, et al., 2019) that must be accounted for.

In the context of predicted range losses for alpine species in Scandinavia in a warming climate (Niskanen et al., 2019), integrating the effects of trails into Species Distribution Models (SDMs) may aid the understanding of vulnerabilities and management for the conservation of threatened species. We showed that trails influence the realized climatic niches of species and that disturbances modify biotic interactions. The inclusion of disturbances and biotic interactions in SDMs can improve their explanatory power and predictions (Brooker et al., 2007; Le Roux et al., 2013; Mod et al., 2016). However, already small disturbances may change biotic interactions and allow for seedling establishment (Milbau et al., 2013) and even satellite imagery with the highest available resolution (currently a pixel size of 46 cm using Worldview-2, Cerrejón et al., 2021) may fail to capture disturbances at such scales. Distance to the trail has proven useful to model the distribution of non-native species sub-Antarctic islands (Bazzichetto et al., 2021), and we therefore expect that the integration of trails as linear features of disturbance and potential dispersal corridors into SDMs has the potential to improve model predictions of vegetation shifts in a changing climate.

Plant communities and their biodiversity in mountain ecosystems contribute to people's lives in various ways, through material, non-material, and regulating NCPs (Martín-López et al., 2019). Changes in species distributions, e.g., through range shifts or establishment in non-native ecosystems, will not only have ecological consequences, but may influence ecosystem services and benefits (Bonebrake et al., 2017). We explicitly considered stakeholder perspectives on the impacts that invasive species in mountains have on these factors in our survey and found positive and negative perceptions, which differed between stakeholder groups. However, in the research on range shifts of native species in mountain areas explanatory ecological approaches continue to prevail. While non-native species can e.g. influence the perceived recreation value in a landscape (Eiswerth et al., 2005; García-Llorente et al., 2008), the same perspective has to our knowledge not yet been explored with regards to changes in recreation value as a consequence of species' range shifts. Range shifts with climate, especially of woody species, may also change landscape appearance and may influence the perceived recreation value, and increased interest conflicts between recreation and and biodiversity conservation at high elevation climatic refugia are expected (Brambilla et al., 2016). Expanding research of range shift effects towards a more holistic approach, taking into account more dimensions of NCPs and perceptions of different stakeholder groups may help to avoid management conflicts in mountain areas. This is in line with the research direction outlined by Bonebrake at al. (2018) and Rew et al. (2020) who stipulate a greater involvement of local communities and stakeholders to facilitate proactive conservation management and discussions about the role of shifting native species.

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6 Appendix S1

6.1 Trails channel disturbances

We compared the number of gaps along a 10 m transect through each plot for 174 T-transects (described in 3) and the gap area based on the number of gaps and the size of five random gaps along the transect where trailside, mid- and interior-plot data on gaps existed using paired Wilcox tests. Both the number of gaps (Table 6.1) and the gap area (Table 6.2) were highest in trailside plots and declined towards the interior vegetation.

Table 6.1: Estimate, confidence intervals, W, significance and Bonferroni-adjusted significance of a paired Wilcox test of gap numbers as a function of plot distance (N, M, F, see Figure 3.2) to trails.

Est.	Conf.low	Conf.high	Gr. 1	Gr. 2	n	W	p	p.adj
0.000007	0.00001	0.000002	N	M	174	18297	< 0.01	< 0.01
0.00002	0.000019	1.00	N	F	174	19666	< 0.01	< 0.01
0.0000702	-0.00	0.00004	M	F	174	16510	0.05	0.15

Table 6.2: Estimate, confidence intervals, W, significance and Bonferroni-adjusted significance of a paired Wilcox test of gap area as a function of plot distance (N, M, F, see Figure 3.2) to trails.

Est.	Conf.low	Conf.high	Gr. 1	Gr. 2	n	W	p	p.adj
0.00005	0.00005	13.20	N	M	174	18572	< 0.01	< 0.01
0.00004	0.00005	21.99	N	F	174	19596	< 0.01	< 0.01
0.000006	-0.00	0.00004	M	F	174	16295	0.07	0.22

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Articles

Article I

A. Jolivet, A. C. MacDougald, B. J. Graae, K. Klanderud, and R. E. M. Wedegärtner

Sticking to the trail: Seed rain, seed bank, and seedling density are elevated along hiking trails in the Scandes mountains,

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RESEARCH ARTICLE

Sticking to the trail: Seed rain, seed bank and seedling density are elevated along hiking trails in the Scandes mountains

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Abstract

Aims: Plant species' distribution ranges are expected to shift towards previously uncolonized locations in response to climate warming. Mountain trails, which often access to areas of special ecological value as well as remote and climatically extreme locations, could influence such shifts through changes in dispersal and disturbance. Trails may facilitate the dispersal of propagules to new locations, influence the seed bank by changing propagule input and persistence and change establishment success through the creation of gaps and disruption of biotic interactions. However, knowledge regarding the influence of mountain trails on seed rain, seed bank abundance and seedling emergence in alpine ecosystems is lacking. In this study, we examine the influence of hiking trails on dispersal patterns in mountain ecosystems.

Location: Dovrefjell, Scandes mountains, Norway.

Methods: We surveyed seed rain, seed bank abundance and seedling emergence along four hiking trails spanning climate gradients with a mean 2.5°C difference between warmest and coldest location at four elevations per trail and at 0.5, 7 and 17 m from the trail (48 plots, in 16 transects).

Results: Seed rain was 3.4 times higher in trailside plots than in those 17 m away and declined with colder climate at all distances from trails. Seed bank abundance on trailsides at the warmest location was eight times higher than in plots at 17 m distance, while there was no significant difference at colder locations. Seedling establishment was disturbance-driven along the whole climate gradient, with 3.5 times more seedlings on trailsides than at 17 m distance.

Conclusion: Mountain trails have the potential to facilitate vegetation shifts by capturing more seed rain and creating opportunities for seedling establishment. Our findings highlight the importance of including trail effects in studies of vegetation shifts.

KEYWORDS
alpine vegetation, climate, dispersal, disturbance, elevation gradients, mountain, plant, range shifts, recreation, temperature, trampling

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1 | INTRODUCTION

The effects of climate change vary among regions (IPCC, 2019); northern alpine ecosystems will be especially vulnerable as the rate of warming is enhanced with elevation and latitude (Hock et al., 2019; Pepin et al., 2015). As sessile organisms, plants can only survive a changing climate by tolerating new conditions or by dispersing to more favourable sites (Graae et al., 2018). In alpine regions with steep climatic gradients, upslope migration has the potential to fast-sort species into suitable microclimatic niches in response to climate warming (Graae et al., 2018; Körner, 2003). However, such upslope migration requires good colonisation capacity by seeds and hence efficient seed dispersal and seedling recruitment of the colonizers (Cichini et al., 2011). Although vegetative reproduction is important in cold environments, especially for alpine plants (Billings & Mooney, 1968; Jónsdóttir et al., 1996; Morris & Doak, 1998), reproduction from seeds is the most common form of recruitment following many types of disturbance in alpine habitats (Chambers, 1995). The movement of seeds along trails could thus play a significant role in assisting lowland and alpine species in reaching new habitats in mountain areas. In addition, local and transported seeds accumulated in seed banks represent a potential long-term source of individuals, with consequences for population persistence and expansion (K. Fenner & Thompson, 2005; Vandvik et al., 2016). As the local seed bank represents the possibility to disperse through time, differential inputs and outputs in seed banks along trails could influence local vegetation shifts in the medium to long term. However, seed banks in the arctic and alpine tundra are often neglected (Molau & Larsson, 2000).

Due to their functional similarity with roads, hiking trails may act as seed dispersal corridors (Liedtke et al., 2020; Potito & Beatty, 2005; Suárez-Esteban et al., 2016). Roads have been demonstrated to facilitate colonization in mountain areas, especially at low and mid-elevations (Alexander et al., 2016; Fuentes et al., 2010), with consequences for species' ranges (Lembrechts et al., 2017). Increased species richness and abundance of plants along trails has been documented in some ecosystems, though information from alpine ecosystems is lacking (Suárez-Esteban et al., 2016). Additionally, past research of hiking trails has mostly focused on their role for the spread of non-native species (e.g., Liedtke et al., 2020, but see Klug et al., 2002). There is thus a lack of knowledge of how hiking trails function as dispersal corridors, especially for native species, and how trails influence seed deposition, seed banks and the establishment of seedlings. This knowledge gap is particularly dire as nature-based tourism and hiking activities continue to increase in popularity in Northern Europe and beyond (Bell et al., 2009), implying increases in the impacts of hiking trails on ecosystems.

Increased input of seeds at the verges of disturbances such as trails is expected due to the movement of humans and animals along these features, especially within dense surrounding vegetation (Suárez-Esteban et al., 2016). Hikers and bikers may transport propagules trapped on footwear, clothes, or equipment (Auffret & Cousins, 2013; Bullock et al., 2020; Mount & Pickering, 2009; Ware et al., 2012). Animals – especially livestock – can transport propagules over long distances (Laughlin, 2003; Manzano & Malo, 2006) through epizoochory (Fischer et al., 1996; Graae, 2002; Laughlin, 2003) and endozoochory (Janzen, 1984; Karimi et al., 2018). As such, hiking trails hypothetically allow long-distance dispersal and increased deposition of seeds by humans and animals, with potential implications for plant community composition (Liedtke et al., 2020). As trailsides experience high levels of disturbance, grasses may benefit, as they are generally considered to be more resistant to trampling than other functional plant types (Forbes, 1993; Jägerbrand & Alatalo, 2015) Grasses appear to be well adapted to early colonization of disturbed sites, producing large numbers of seeds (Marchand & Roach, 1980). Additionally, vegetation at trail verges can trap seeds transported along the relatively smooth trail surface by wind and water, resulting in a higher propagule input on trailsides (Bullock & Moy, 2004; Isselin-Nondedeu & Bédécarrats, 2007). While an increased deposition of propagules along trails is frequently hypothesized to be a main reason for increases in the richness of non-native and native plant species along trails, to our knowledge there have been no studies which quantified changes in propagules along trails in alpine habitats.

High plant diversity observed along linear structures in the landscape, such as roads or trails, compared to their surrounding habitats, could be due to both dispersal (higher seed rain and seed retention) and post-dispersal mechanisms, such as germination and seedling establishment (Suárez-Esteban et al., 2016). A higher deposition of seeds near hiking trails likely increases the seed bank. In addition, trails cause disturbances, with consequences on seed bank abundance and composition (Chambers, 1993; Ma et al., 2010; Zabinski et al., 2000). For instance, disturbances following campsite activity decreased subalpine seed bank density and species richness due to the removal of surface organic matter (Zabinski et al., 2000). On the other hand, Klug et al. (2002) found evidence of larger seed banks near trails, as grass species resistant to trampling that produce large amounts of diaspores were more dominant in disturbed than in intact vegetation.

Seedling recruitment has major implications for population dynamics, community turnover and species range dynamics (Meineri et al., 2020), and, in alpine tundra, is controlled primarily by disturbance (Graae et al., 2011; Lembrechts et al., 2016; Milbau et al., 2013) and biotic characteristics such as vegetation density (Meineri et al., 2020). The stress-gradient hypothesis postulates that competition is the dominant plant–plant interaction in productive (i.e., lowland) sites (Bertness & Callaway, 1994). At those sites, community invasibility and seedling recruitment may increase following small-scale disturbances, such as trampling by humans or livestock, which promotes open gaps and competitive release by increasing light and space (Klanderud et al., 2017; Milbau et al., 2013). At higher elevations where abiotic stress is more pronounced, facilitation is predicted to be more common (Choler et al., 2001). However, the creation of gaps benefits seedling establishment even in harsh alpine sites (Alexander et al., 2016; Graae et al., 2011; Klanderud et al., 2017; Milbau et al., 2013), suggesting that competitive interactions can be important also at these sites (Lembrechts et al., 2015). On the other hand, trampling and disturbance could have negative effects on seedling emergence and establishment due to soil compaction (Bassett et al., 2005) and seedling removal. Insights on seedling emergence close to hiking trails should yield a better understanding of plant community dynamics along gradients of climatic stress and disturbance.

In this study, we examine how seed rain, local seed banks and seedling recruitment vary with distance to trails and climate along four hiking trails following elevation gradients in the mountains of Dovrefjell, central Norway.

We expect seed rain and seed bank abundance to decrease with decreasing temperatures towards higher elevations because clonal growth and slower life cycles are more common than sexual reproduction in colder climates. We also expect seed rain and seed bank to be richer close to trails, because of higher seed deposition and seed retention in vegetation in trail verges and high seed production by species resistant to disturbance, such as grasses. In particular, a positive correlation between seed numbers and herbivore pellet counts should indicate the effect of propagule input by herbivores. Similarly, a positive correlation between seed numbers and grass cover should suggest an increased propagule input by trampling-resistant grasses. We predict higher seedling density close to trails in warmer, low-elevation sites, due to gap creation through trampling. At sites with harsher climatic conditions, we expect a more uniform seedling density across different distances from the trail as competitive interactions, and thus gap creation, become less important, in accordance with the stress-gradient hypothesis.

2 | METHODS

2.1 | Study region

The study area is located in the vicinity of Hjerkinn, Norway (62°13′ N, 9°33′ E). The region is characterized by mountainous terrain with elevation ranging from 900–1000 m at valley bottoms to 1500–1700 m at the highest mountain peaks. Much of the local terrain belongs to the Dovre and Dovre-Sunndalsfjella National Parks, popular tourist destinations with numerous hiking trails. Data for 1990–2019 from a weather station at Fokstugu (62°06′ N, 9°17′ E, 979 m) indicate a continental climate characterized by a mean annual temperature of 0.8°C and precipitation of 438 mm (Norsk Klimaservicesenter, 2020). Dovrefjell is known for its rich alpine plant diversity, mainly due to the calcareous bedrock, but also the climatically varied landscape and high-elevational peaks with presence of plants that survived the last Ice Age on nunataks — refuges for plant life above the level of glaciation (Sonstebo, 2003). The treeline, situated at approximately 1050–1100 m (Paus et al., 2011), consists of mountain birch (*Betula pubescens*), while low-alpine areas are dominated by meadow vegetation (e.g. *Festuca* spp., *Poa* spp., *Silene acaulis*, *Viola* spp.), dwarf shrubs (e.g. *Betula nana*, *Empetrum nigrum*, *Salix* spp., *Vaccinium* spp.) and lichen heaths. Higher-elevation areas are covered by sparsely vegetated heaths, boulder fields and scree (de Wit et al., 2014). The high species richness, particularly among forbs, has given the area its reputation as northern Europe's most diverse region for alpine plants (Stiftelsen iNasjonalparker, 2013). Numerous sheep and cattle were observed on and adjacent to trails, and the Dovre region is also home to wild reindeer and musk ox, potentially affecting dispersal dynamics and vegetative cover through grazing, trampling and deposition of dung.

2.2 | Sampling design

We selected four trails with sustained levels of usage as determined by Strava heat maps (Figure 1). Trails A and B are popular day-hike trails (in particular A) used for tourists who wish to see musk ox, and a nearby visitor counter logged ca. 10,000 passes per summer (Gundersen et al., 2012). Trail C, with its trailhead being approximately two kilometres from the nearest publicly accessible road, is much less used. Trail D forms the northern end of a popular hiking route leading to Rondane national park. All four trails begin near major transportation corridors, facilitating access for hikers and span an elevational range of approximately 900–1400 m a.s.l.

Four T-shaped transects per trail were used to record seed rain, seed bank abundance, seedling density and vegetation cover (Figure 2). Transects were placed at fixed intervals corresponding to: (1) the trailhead elevation; (2) 40% of the elevation up the trail from trailhead to highest plot; (3) 70% up the trail; and (4) where the trail becomes indistinguishable from surrounding terrain. A coin toss determined at which side of the trail the transect was placed, unless scree, rocky outcrops, streams or cliffs made only one side feasible for the study. Placement was determined by registering elevation data with a handheld GPS.

Each transect consisted of three plots of 2 m × 10 m (Figure 2). The first plot was placed lengthwise parallel to the trail side. The two remaining plots were placed perpendicular to the trail from the middle of the trailside plot, covering a distance of 2–12 m and 12–22 m from the trail, respectively (following the trail survey protocol of the Mountain Invasion Research Network [MIREN]; see Liedtke et al., 2020). Four 15 cm × 15 cm seed traps were placed 0.5 m from the trail in the first plot. Here, the two innermost and two outer traps were placed 1 m and 3 m from the centre of the plot, respectively. Four more traps were placed in the second plot, 7 m from the trail edge and in the third plot, 17 m from the trail, with traps 0.5 m and 1 m from the centre of the plot (Figure 2). Four soil cores with a diameter of 7.5 cm and 5 cm depth were collected in each plot, underneath each seed trap. In total, 192 seed traps were deployed and 192 soil cores sampled. If rocks or shrubs inhibited the placement of traps or the collection of soil samples, the nearest available spot closer to the trail was chosen.

One 50 cm × 50 cm quadrat for seedling survey was placed in the middle of each plot at the same distance from the trail as seed traps (Figure 2).

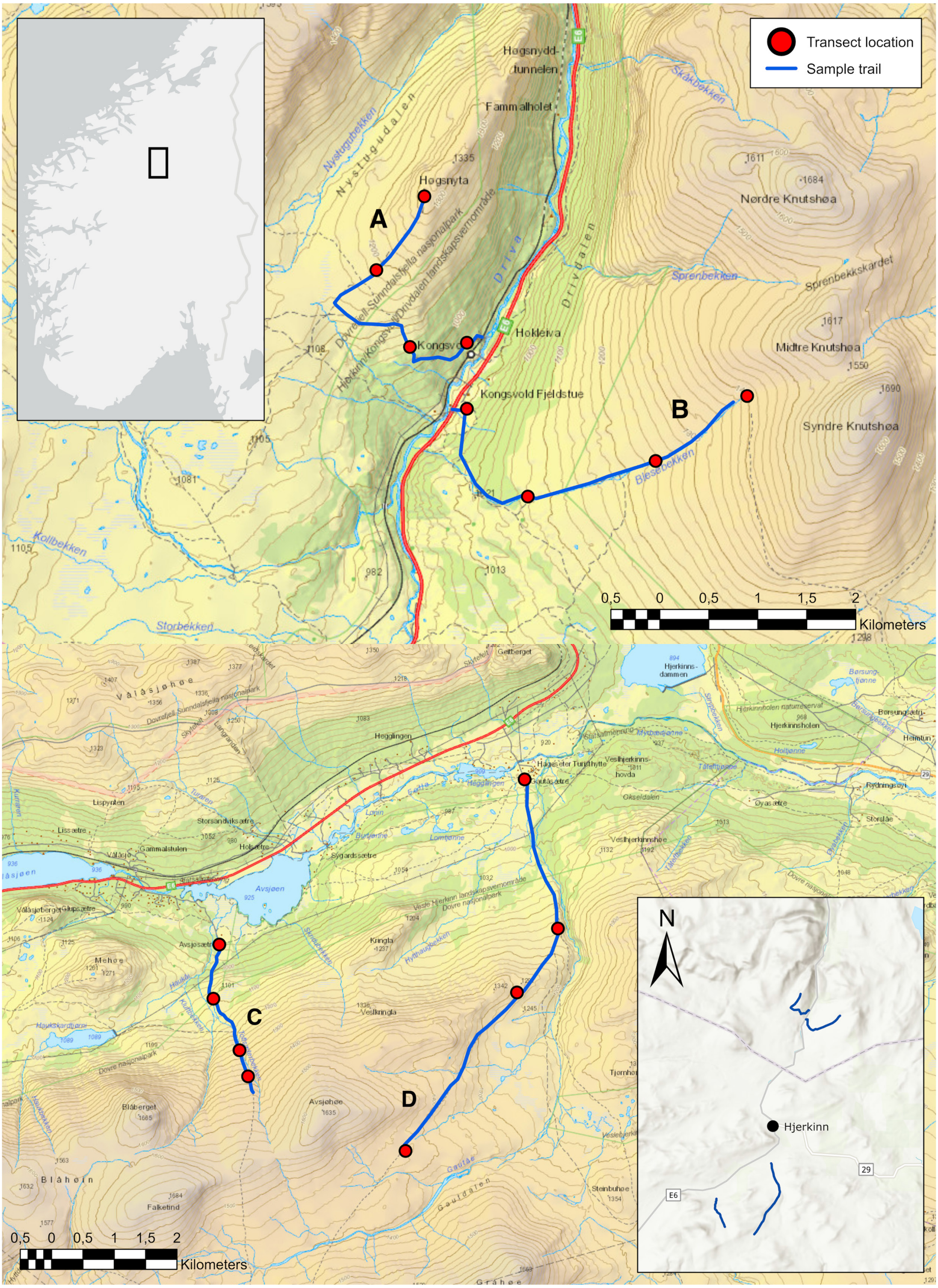

FIGURE 1 Location of the study area in the Dovre region of the Scandes mountains, Central Norway

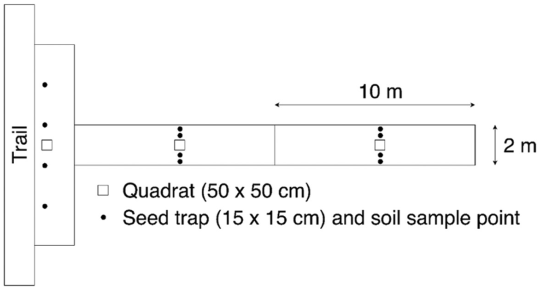

FIGURE 2 Schematic representation of the T-transect design placed along hiking trails that was used to measure seed rain in seed traps, collect soil samples to analyse the seed bank and survey seedling emergence in quadrats

2.3 | Seed rain survey

Astroturf© (Dalton, US) doormat-style seed traps were placed along the sampled trails in July 2019. These simulate vegetation cover and have proven useful to trap seeds in similar studies (Molau & Larsson, 2000). All traps were fastened to the ground with nails and, if necessary, levelled with rocks to minimize seed loss from runoff during rainfall. All traps were left in the field until collection in September 2019, when they were placed in resealable plastic bags and transported for processing. We registered 27 traps that were either found displaced or not found at all as not available (NA) during data analysis. The final number of analysed seed traps was thus 165.

Traps were emptied into a basin by knocking on the base of each trap. Remaining material was extracted with a scalpel and seeds were subsequently detected by naked eye, and by use of a microscope or stereomicroscope. Seeds were counted and identified to species level if possible, but in some cases to genus, or a functional group. Identification was conducted through comparison with the online databases Digital Plant Atlas 2006 and USDA Plants Database 2019, a reference collection at the Norwegian University of Science and Technology and help from botanists with special seed knowledge. The term seed as used in this paper includes *Bistorta vivipara* bulbils.

2.4 | Seed bank survey

At each seed trap location, a soil core of 7.5 cm diameter and 5 cm depth was collected in July 2019 and stored in a sealed plastic bag in a cold room at 4°C for five months. Soil samples were then kept in a freezer at −5°C for five weeks for cold stratification and acclimatized in the cold room again for one week. The majority of seeds in grasslands and heath seed banks can be found in the top 2–5 cm (Ma et al., 2010, 2011; Pywell et al., 1997) and we therefore limited sampling to this depth.

Each soil sample was weighed and loosened by hand when compacted. Soil from each sample was then spread on top of 2 cm of sterilized potting soil in plastic trays (18 cm × 18 cm × 4.5 cm). If the sample contained lichens or other vegetation, these were spread on top of the soil, in order to replicate more natural conditions. The trays were arranged randomly on three tables in the greenhouse and shuffled four weeks after the start of the germination survey. They were exposed to permanent light (complemented by artificial light in winter) and a temperature regime of 10°C for 8 h and 20°C for 16 h, to simulate optimal conditions for germination (Baskin & Baskin, 2014; Reinhardt & Leon, 2018), and watered every 2–4 days. The tables were covered with a fleece sheet to prevent exogenous seeds from landing on the trays. Trays were checked for germinants every four days during 11 weeks and seedlings were identified by comparison with online databases, a flora (Lid & Lid, 1994) and help from botanists from the Norwegian University of Science and Technology. As the trays were checked frequently and the soil samples had a relatively small depth, the number of germinated seedlings in the greenhouse was considered equivalent to the number of germinable seeds that can be identified using the germinable seedbank method (Reinhardt & Leon, 2018).

2.5 | Seedling emergence surveys

Seedlings were recorded from one 50 cm × 50 cm quadrat per plot in each transect in mid-August 2019. If no seedlings were found after searching a quadrat, it was moved so that its new placement was adjacent to the previous location. This process was repeated up to three times, until at least one seedling was found. For the purposes of this study, a seedling is defined as a sporophyte with one or two cotyledons and up to two leaves. Seedlings were identified to species when possible, to genus, or to unknown forb or graminoid. Identification was carried out in the field with reference photos and by expert knowledge.

2.6 | Vegetation and pellet count surveys

Vascular vegetation coverage and number of animal dung pellets were determined by conducting surveys of all 2 m × 10 m plots from July to August 2019. Coverage was assessed visually and each species present was given a percentage cover value per plot. Pellet count surveys were conducted in each plot to estimate the abundance of large herbivores. This was done by walking lengthwise back and forth and counting each pellet individually, by species.

2.7 | Climate data

We used high-resolution topographic layers to downscale CHELSA bioclimatic layers (Karger et al., 2016, 2017) with a 30 arcsecond (~1 km) resolution to produce microclimate at 30 m resolution using a Geographically Weighted Regression (GWR) approach (Lu et al., 2011) as described by Lenoir et al. (2017). Down-scaling was based on elevation, slope, northness, eastness, distance from the ocean and potential solar radiation. These predictor variables have shown good results for predicting temperature in previous studies (Ashcroft et al., 2012; Buytaert et al., 2006; Fridley, 2009; Lenoir et al., 2017). The down-scaling process is described in Appendix S1.

We used high-resolution mean annual temperature, maximum temperature of the warmest month and minimum temperature of the coldest month and applied a principal components analysis (PCA) on the scaled variables to capture the maximum variation in climate within all our plots, as those temperatures were highly correlated (Appendix S2). The first principal component captured 99.8% of the variation in the climate data and was strongly and positively correlated with mean annual temperature (0.999), minimum temperature of the coldest month (0.998) and maximum temperature of the warmest month (0.998). Using this principal component, a climatic gradient value describing the climatic harshness was determined for each plot.

2.8 | Statistical analyses

All statistical analyses were performed in R versions 4.0.2 and 3.6.2 (R Core Team, 2019, 2020) using RStudio versions 1.3.959 and 1.2.5033 (RStudio Team, 2020). Generalized linear mixed models (GLMM) with negative binomial error function and a log-link function were used to determine the effects of: (1) climate (first axis of the PCA run on the three temperature variables), distance from trail, their interaction, pellet count and grass cover on the seed rain and germinable seed bank; and (2) climate, distance from trail, their interaction and pellet count on seedling abundance.

Number of seeds per trap, number of germinated seedlings per soil sample and number of seedlings per quadrat were used as response variables. Seed bank studies often use seed bank density in their analyses (seeds per square metre) (e.g. Cooper et al., 2004; Venn & Morgan, 2010), but this approach can lead to heterogeneity or negative fitted values when the volumes differ between samples (Zuur et al., 2009). We thus chose to use seed bank abundance (number of germinated seeds per sample) and to add the logarithm of fresh weight of the sample (g) as an offset in the seed bank model. Soil seed bank density data are available in Appendix S3.

Full models were first obtained, with distance from trail, climate, their interaction and herbivore pellet count as predictor variables. Models for seed rain and seed bank additionally included grass cover as a predictor variable. For all three models, fixed predictor variables were scaled to a mean of zero and a standard deviation of one. In each case, the most parsimonious model was selected through backward selection from the full model using the function ‘stepAIC’ in the *MASS* package (Venables & Ripley, 2002). To avoid pseudoreplication, we used nested random effects for trail and transect identity in the seed rain and seedling emergence models, and transect and plot identity in the seed bank model. The optimal nested random effect structure was selected by comparing Akaike Information Criteria (AIC) values for models differing in their random effects starting from full nested random structure (i.e., trail, transect, plot and sample identity), and comparing to random structures with fewer levels of nestedness (e.g., trail and transect identity). Final model formulas for the (a) seed rain, (b) seed bank and (c) seedling models are:

a. Number of seeds per seed trap ~ distance to trail × climate + grass cover + pellet count + (1|trail/transect)
b. Number of germinable seeds from the soil bank per sample ~ distance to trail × climate + grass cover + pellet count + offset [log(dry weight)] + (1|transect/plot)
c. Number of seedlings per quadrat ~ distance to trail × climate + pellet count + (1|trail/transect)

Models were run with the *glmmTMB* package (Brooks et al., 2017) to account for zero inflation of the seed rain, seed bank and seedling emergence data, and over-dispersion in the seed rain data. For all models, we checked the magnitude of multicollinearity of the predictors by calculating the variance inflation factors using the *performance* package (Lüdecke et al., 2021). Model assumptions were verified with diagnostic plots and tests for over-/underdispersion and zero inflation were done with the *DHARMa* package (Hartig, 2021). No significant collinearity, over−/underdispersion or zero inflation were detected. One plot in the seedling data set was noticeably different from others at similar elevation and had a strong influence on model results. We therefore ran the seedling model excluding this outlier, but additionally report model results including these data in Appendix S4. Model predictions were extracted using the *ggeffects* package based on the final models (Lüdecke, 2018). Model estimates were back-transformed using the ‘inverse link’ function of the GLMMs.

3 | RESULTS

Seed rain, germinable seed bank and field seedling density varied with elevation and among trails (Figure 3). A detailed description and lists of all the species recorded in the three surveys with their growth form and their total abundances and densities per transect level can be found in Appendix S3.

3.1 | What drives patterns in seed rain, germinable seed bank and seedling emergence?

The seed number in seed traps, the germinable seed bank and seedling density significantly decreased with distance from the trail (Table 1, Figure 4).

Overall, seed rain was 3.4 times higher in the seed traps at 0.5 m distance to the trail in comparison to those 17 m away (see Appendix S5). At the same time, a plot at the warmest end of the gradient received 21.4 times more seed rain than those at the coldest end with all other parameters held constant, as seed rain increased with higher temperatures and larger cover of graminoid species in the most parsimonious GLMM (Table 1, Appendix S5).

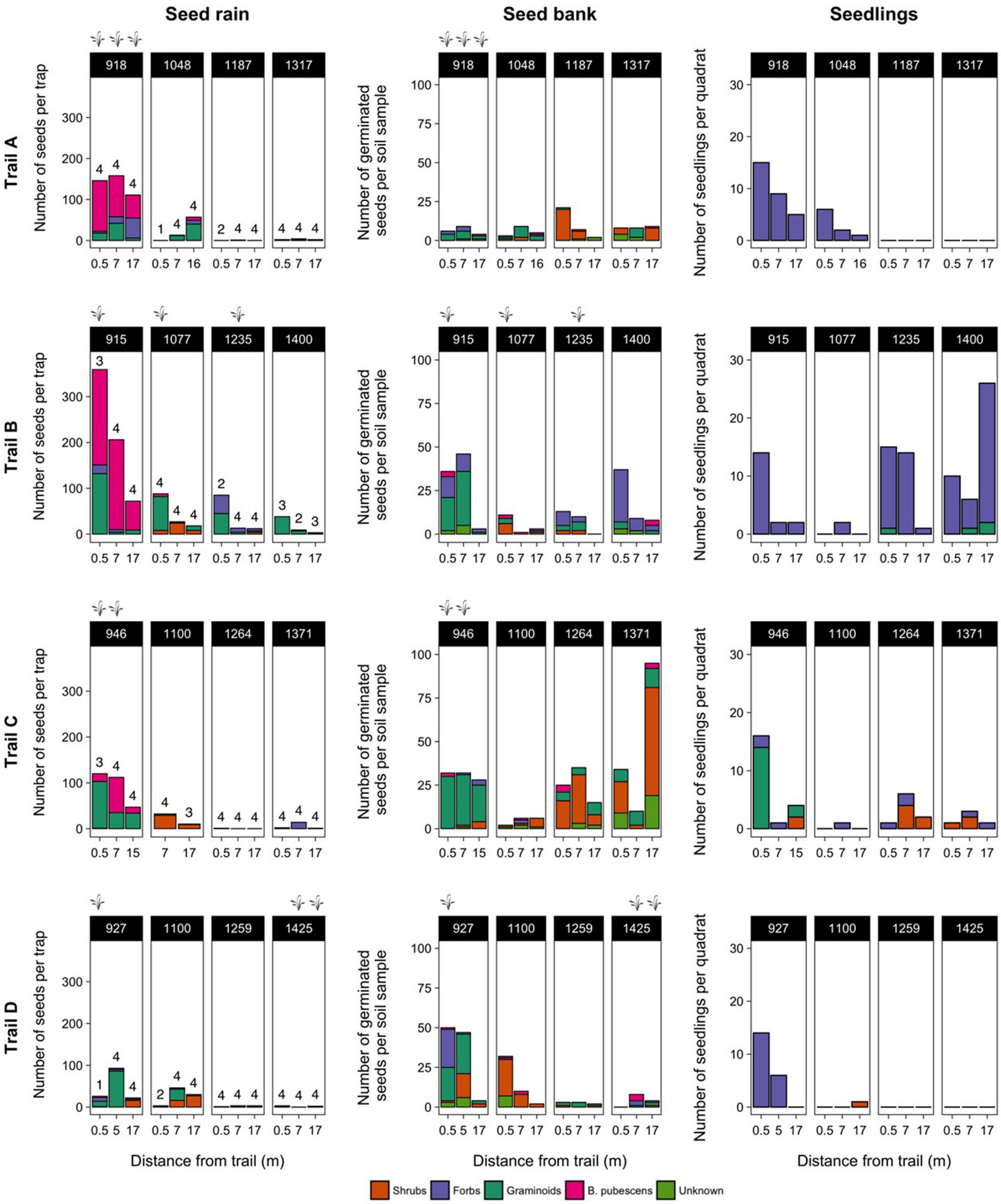

FIGURE 3 Raw number of seeds collected in seed traps, germinated seedlings (seed bank), and seedlings registered at a distance of 0.5, 7 and 17 m from four hiking trails in Dovrefjell, Norway. Note that not all seed traps were recovered/usable: data for each distance at each elevation is sourced from 1–4 traps (numbers in/above histogram bars). Numbers at top of sections denote transect elevations in metres. Grass symbols denote plots in which ≥25% of adult cover surveyed belonged to grass species

TABLE 1 Back-transformed model estimates for the relationship between seed rain, seed bank abundance and seedling density respectively from GLMMs with negative binomial error structure and log-link function

	Seed rain				Germinable seed bank				Seedling density			
Residual *df*	161				182				38			
	Estimate	95% CI	*z*	*p*	Estimate	95% CI	*z*	*p*	Estimate	95%CI	*z*	*p*
Intercept	3.86	**1.44–10.34**	2.81	**0.004**	0.02	**0.01–0.03**	−18.52	**<0.001**	1.12	0.39–3.23	0.22	0.824
Distance to trail	0.68	**0.53–0.87**	−3.21	**0.001**	0.68	**0.51–0.90**	−2.73	**0.005**	0.60	**0.43–0.84**	−3.08	**0.002**
Climate	3.55	**1.99–6.35**	3.37	**<0.001**	1.32	0.83–2.12	1.20	0.194	1.75	0.75–4.07	1.33	0.184
Climate × distance to trail	1.12	0.89–1.40	1.11	0.266	0.71	**0.53–0.95**	−2.39	**0.016**	0.84	0.62–1.13	−1.19	0.233
Grass cover	1.60	**1.02–2.52**	2.21	**0.027**	0.79	0.52–1.20	−1.12	0.259	-	-	-	-
Pellet count	1.38	0.92–2.07	1.57	0.116	0.94	0.65–1.36	−0.33	0.745	0.54	0.18–1.63	−1.12	0.264

Note: Distance from trail, climatic gradient (first axis of a PCA run on the three temperature variables), their interaction and pellet count were included as predictor variables. The seed rain and seed bank models further included grass cover. Significant *p* values at the 0.05 significance level and 95% confidence intervals not including 1 are shown in bold. Original model estimates from the GLMM fits (scaled and on the natural log scale), rescaled estimates, and rescaled and back-transformed estimates are available in Appendix S4.Abbreviations: CI, confidence interval; *df*, degrees of freedom.

The best model for the number of germinable seeds in the seed bank included a significant interaction between climate and distance from the trails, indicating higher numbers close to trails in sites with higher temperatures (Table 1). At thes warmest site, eight times more germinable seeds were found closest to the trail (at 0.5 m) than furthest away (at 17 m, see Appendix S5). At colder sites, lower numbers were found across all distances from the trails, with no significant difference between the coldest (2.4, 95% confidence interval (CI) [0.9, 6.7]) and the warmest locations (1.4, 95% CI [0.6, 3.7]).

Distance to the trail was a main driver of seedling density as well (Table 1). Averaged over all climatic conditions, 3.5 times more seedlings were found in the plots closest to the trail compared to those furthest away (see Appendix S5). While we found some indications for a stronger decrease in seedling density with larger distance from trails at warmer than at colder sites (Table 1, Figure 4), this interaction was only significant when one outlier was included (Appendix S4). The most parsimonious GLMMs for seed rain and seedling density included herbivore pellet count, for seed rain the best model in addition included grass cover; the GLMM for the germinable seed bank included only grass cover in addition to the climate and trail distance variables.

4 | DISCUSSION

We found that seed rain, seed bank abundance and seedling density were higher close to hiking trails, implying that hiking trails are important hotspots of diaspore dispersal and may facilitate vegetation shifts in the Scandes mountains. Additionally, seed rain was higher in warmer locations. The size of the germinable seed bank increased close to trails in warmer sites, while remaining similar at different distances from the trails at colder sites, showing that climate influences seed rain and modulates the effect of trails on the seed banks.

Increases of seed rain, seed bank and seedling emergence towards the trails are rather large. This highlights that further investigation of vegetation shifts, e.g., in relation to a warming climate and land-use changes, should consider distance to trails as a proxy for propagule pressure and disturbance, which both may facilitate establishment (Lembrechts et al., 2016). This is of special importance as trails often access areas of special ecological value (Ballantyne & Pickering, 2015) as well as remote and climatically extreme locations (Liedtke et al., 2020).

We hypothesized that seed rain and seed bank abundance would increase close to trails due to greater seed deposition, seed trapping and higher seed production by trampling resistant species. Our results confirm that hiking trails in Dovre do play a role in seed dispersal, even when the propagule input of trampling-resistant grass species is accounted for. These findings support our hypothesis that seed deposition along trails is higher and corroborate previous evidence that trails may act as dispersal corridors, facilitating colonization (Liedtke et al., 2020). Given this, hiking trails could conceivably play a positive role in maintaining a collection of rare local populations occupying discrete habitat patches, i.e. a metapopulation

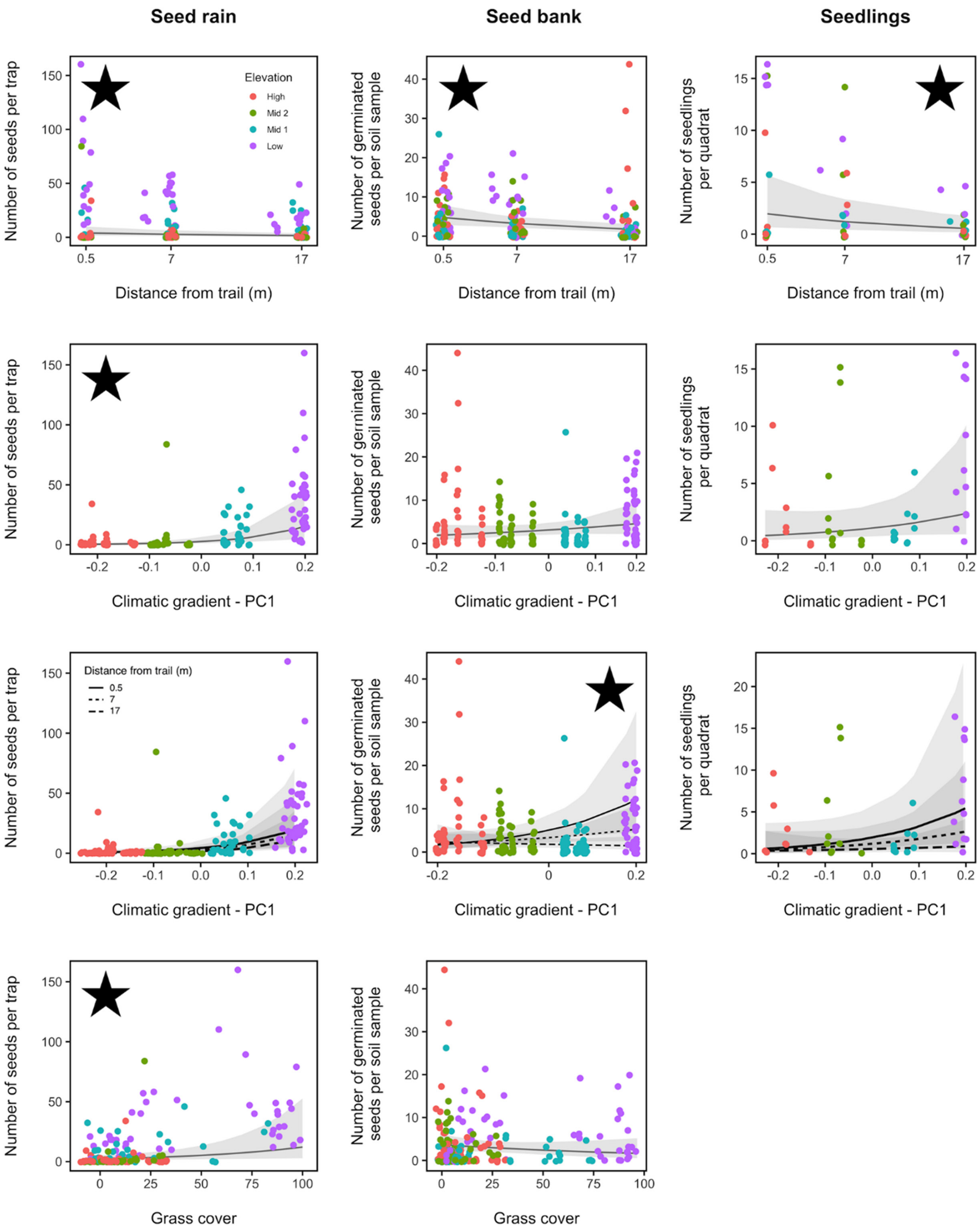

FIGURE 4 Graphical representation of the best models for seed rain, seed bank abundance and seedling density against distance from the trail, the climatic gradient (negative values denote harsher conditions), their interaction, and grass cover, where it was retained in the best model. Grey shading indicates 95% confidence intervals. Stars denote significance in the best model at the $p < 0.05$ level. Raw data are displayed as circles, with red denoting plots located at high, green at medium high, blue at medium low and purple at low elevations

(Hanski, 1998). Related to this, Vandvik & Goldberg (2005) distinguish between patches in which local diversity is either maintained or limited by dispersal. In the former, species richness is maintained at least in part through dispersal; in the latter, species richness would be higher with increased rates of dispersal. By increasing functional connectivity *sensu* Auffret et al. (2017), trails may therefore aid the sustenance of dispersal-maintained local diversity and facilitate the establishment of new species in dispersal-limited locations which may lead to a higher species richness in such locations.

As expected, seed rain is lower in the coldest locations. Of particular interest in this regard is that seed bank abundance is higher at trailsides in warmer locations but is low at all distances from trails at harsher sites, while seed rain consistently decreases away from the trail along the climatic gradient. This pattern follows observations by Thompson (1978), with opposing gradients of disturbance and climatic stress, resulting in higher seed banks at low elevations and at disturbed locations. As we were only measuring the abundance of the germinable seed bank, our observation could be rooted in a lower arrival of seeds in the seed bank, or a lower germinability of seeds after dormancy in colder locations. The five months of cold stratification and subsequent light and temperature regimes used in the seed bank survey may not have been sufficient to trigger dormancy break for some species in the soil seed bank, especially in higher-elevation species (Cavieres & Sierra-Almeida, 2018). It is also likely that for some species, only a proportion of the seeds germinated in response to favourable environmental cues, while the remaining seeds were carried over to germinate the next year, as an adaptation to unpredictable environments such as alpine habitats (Jaganathan et al., 2015) Seed rain rose with an increase in grass cover, as expected, while for the seed bank no significant effect of grass cover was found.

At the harshest locations, neighbouring vegetation is thought to facilitate plant growth and survival by maintaining warmer temperatures and insulating the substrate from growth-stunting abiotic environmental variables such as frost, soil heave from needle ice, drought and wind (Choler et al., 2001; Venn, 2007). As trails may break down such facilitative effects, we expected lower numbers of seedlings close to trails at colder locations. However, the number of seedlings was higher in the vicinity of trails along the whole climatic gradient, and we did not find sufficient support for the hypothesized pattern. This underscores the importance of gaps created by trampling for germination in mountain habitats and is in line with previous studies which found that competition remains important in harsh conditions (Graae et al., 2011; Klanderud et al., 2017; Lembrechts et al., 2016; Milbau et al., 2013) and that the potential for seedling emergence in tundra vegetation is lower in undisturbed closed communities than in disturbed ones (Chambers, 1995). One explanation for this may be that plant physiological response to environmental stress is not necessarily unidirectional along a gradient such as elevation, as climate stress may interact with resource stresses (Holmgren & Scheffer, 2010; Maestre et al., 2009).

At the coldest locations of the four trails there was a large variation in seedling emergence; one plot along trail B (Knutshø) was removed as an outlier, as it held far more seedlings (26) than any other location. Knutshø is known for its extremely rich flora and therefore may represent a variation in general growing conditions (Gjærevoll, 1979). The large variation in seedlings under similar climatic conditions may point to the importance of site-specific limitations to seedling emergence. Especially at harsher sites, seedling emergence may be influenced by microtopography, soil depth and soil substrate with larger emergence in more sheltered sites with deeper soils. This would be in line with findings of previous empirical studies which have demonstrated the importance of microsites and local biotic and abiotic contexts for seedling emergence (Chambers, 1995; Daleo & Iribarne, 2009; Graae et al., 2011; Venn & Morgan, 2009). Minor deviations from optimal conditions within transects may be sufficient to impose an amount of stress large enough to inhibit seedling emergence (Holmgren & Scheffer, 2010). As an additional caveat, we downscaled climate data to a resolution of 30 m based on CHELSA 1-km resolution data, which represent air temperature at 2 m above the ground. However, this does not necessarily represent the growing conditions of seedlings in our plots, as low-stature plants experience microclimates which may greatly differ based on microtopography, moisture and the effects of surrounding vegetation (Graae et al., 2012; Lembrechts et al., 2018; Scherrer & Körner, 2011). Further studies using *in-situ* measurements will therefore aid the understanding of seedling emergence in relation to disturbance and climate in the field.

5 | CONCLUSION

All stages of seedling recruitment 'stick to the trail' with higher seed rain, seed bank abundance and seedling densities on trailsides, highlighting the role of trails as seed dispersal corridors in Dovre, even at colder locations. Trails may thereby increase local diversity by transporting previously dispersal-limited species to uncolonized locations. At the same time, trailsides may help to maintain populations of dispersal-dependent species. This should be taken into consideration when planning for management and conservation, as trails may increase the connectivity between isolated populations, but may also be pathways for the rapid spreading of more ruderal and opportunistic plants into mountain habitats.

AUTHOR CONTRIBUTIONS

Ronja Elisabeth Magdalene Wedegärtner, Aidan Cameron MacDougald, Anaïs Jolivet and Bente Jessen Graae conceived the research idea; Anaïs Jolivet, Aidan Cameron MacDougald and Ronja Elisabeth Magdalene Wedegärtner collected the data, performed statistical analyses and wrote the paper; all authors discussed the results and commented on the manuscript.

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DATA AVAILABILITY STATEMENT

The links to data sets can be found along with the printed version of our data in Appendix S2 and S3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1 Down-scaling of climate data

Appendix S2. Correlation of temperature variables

Appendix S3. Detailed description of results of seed rain, soil seed bank and seedling surveys

Appendix S4. Model estimates from the seed rain, germinable seed bank and seedling emergence

Appendix S5. Predictions based on the best models for seed rain, seed bank and seedling emergence

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Supporting information to the paper
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Appendix S1. Downscaling of climate data.

Data were prepared for downscaling in R 3.5.2 (R Core Team, 2018) using the raster package (Hijmans et al., 2020).
We downloaded annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month for the time period 1979-2013 from the CHELSA data base at a resolution of 30 arcseconds (Karger et al., 2016, 2017). For each region we obtained high resolution digital elevation models (DEMs) using the elevatr package (Hollister & Shah, 2017) at a resolution of 1.2 arcsecond, which corresponds to 1 ca 30 m at this latitude.
We derived the topographic variables from the high resolution DEMs in R and calculated the potential incoming solar radiation for each grid cell of the DEM for the four representative days (equinoxes and solstices) with a six-hour resolution using the SAGA GIS 6.3.0 tool Potential Incoming Solar Radiation (Conrad et al., 2015). Distance from the ocean was downloaded from http://www.soest.hawaii.edu/pwessel/gshhg/ at 1 arcmin resolution (Wessel & Smith, 2017). Downscaling was based on a Geographically Weighted Regression (GWR) approach (Lu et al., 2011) as outlined by Lenoir et al. (2017) using elevation, slope, northness, eastness, distance from the ocean and potential solar radiation as predictor variables. The downscaling was performed on resources provided by the NTNU IDUN/EPIC computing cluster(Själander et al., 2019) using R 3.6.0 and the spgwr package (Bivand & Yu, 2017). Missing data due to omission of missing predictor values were interpolated using the Close Gaps tool of SAGA.

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Supporting information to the paper
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Appendix S2. Correlation of temperature variables. The three variables are very highly correlated (p-values < 0.001). Data is available for download at: https://doi.org/10.6084/m9.figshare.19410359.

	Mean annual temperature	**Warmest temperature of warmest month**	**Coldest temperature of coldest month**
Mean annual temperature	1	-	-
Warmest temperature of warmest month	0.998	1	-
Coldest temperature of coldest month	0.998	0.992	1

Supporting information to the paper
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Appendix S3. Detailed description of results of seed rain, soil seed bank, and seedling surveys, and list of species recorded in each survey with their total abundances (and densities, if applicable) per transect level.

Seed rain

In total, 1995 seeds belonging to at least 16 families and 24 genera were collected from the seed traps (Figure 3). For these, 17 species were identified to species level. We did not identfy eight genera to species level (Luzula, Festuca, Poa, Carex, Galium, Papaver, Veronica, Cerastium) and we classified seventy seeds belonging to nine different species as unknown forbs or graminoids. Of the seeds identified to genus or species level, the most represented family was Poaceae with at least seven species. Overall, 759 (38%) of the seeds belonged to graminoid species, 146 (7%) to shrubs, 209 (10%) to forbs and 881 (44%) to the tree Betula pubescens (Figure 3). No herbivore pellets were found in the seed traps. Below the tree line at ca 1050 - 1100 m (Paus et al., 2011), we found large numbers of B. pubescens seeds at all distances from the trail, while the number of graminoid seeds was highest in trailside plots and at lower elevations (Figure 3).

Seed bank

During the 11-weeks observation period, a total of 753 seeds germinated in the 192 soil samples, belonging to at least 15 families and 30 genera (Figure 3 b). We identfied 28 species to species level, while 92 seedlings were not identified and were classified as unknown graminoids or forbs. The remaining 78 seedlings were too small for identification and were grouped as unknown. A total of 277 (37%) of the seedlings were classified as graminoids, 248 (33%) as shrubs and 119 (16%) as forbs, while 31 seedlings (4%) were identified as Betula pubescens (Figure 3). The most represented family among the seedlings identified to species or genus level was Poaceae, with at least 13 species. The most abundant species was Empetrum nigrum, with 240 (32%) of the seedlings. At the warmest locations the seedbank was generally dominated by graminoids, while harsher locations showed a larger diversity of functional types, depending on trail identity (Figure 3 b).

Seedling emergence

Overall, 185 seedlings belonging to at least 14 families and 20 genera were recorded in the field. Eighteen species were identified to species level. Some, but not all seedlings from six genera were identified to species level (Alchemilla, Euphrasia, Omalotheca, Luzula, Taraxacum, Vaccinium). Of the seedlings classified as unknown, 16 seedlings were graminoids and 18 forbs. Of the seedlings identified to genus or species level, the most represented families were Rosaceae and Asteraceae (3 species each). We classified 154 of the seedlings as forbs, 12 as shrubs, and 19 as graminoids (Figure 3). The distribution of functional types along the climate and disturbance gradient was highly variable and appeared to be trail-specific.

Table S3a. Total abundance of seeds recovered from seed traps and seedlings surveyed in quadrats, sorted by transect elevation level. Species names and their elevation range classification follow Lid and Lid (2005). A dosnloadable version is available at https://doi.org/10.6084/m9.figshare.19410455 for seed rain and at https://doi.org/10.6084/m9.figshare.19410503 for seedlings.

Species	**Growth form***	**Seed rain**				**Seedlings**			
		Transect level				**Transect level**			
		Low	Mid 1	Mid 2	High	Low	Mid 1	Mid 2	High
Alchemilla alpina	F	-	-	-	-	1	-	-	-
Alchemilla sp.	F	-	-	-	-	-	-	-	2
Anthoxanthum nipponicum	G	45	44	5	11	-	-	-	2
Avenella flexuosa	G	17	-	-	-	-	-	-	-
Betula nana	S	17	13	-	-	-	-	-	-
Betula pubescens	Bp	863	17	1	-	-	-	-	-
Bistorta vivipara	F	2	-	1	4	23	-	7	20
Calamagrostis neglecta	G	4	-	-	-	-	-	-	-
Campanula rotundifolia	F	-	-	-	-	6	2	2	-
Carex sp.	G	-	-	1	-	-	-	-	-
Cerastium sp.	F	1	-	-	-	-	-	-	-
Cerastium alpinum	F	-	-	-	-	2	-	2	6
Deschampsia cespitosa	G	261	29	1	31	-	-	-	-
Empetrum nigrum	S	1	109	4	2	-	-	-	-
Euphrasia frigida	F	-	-	29	-	-	-	-	-
Euphrasia sp.	F	-	-	-	-	-	-	-	5
Festuca sp.	G	87	79	48	3	-	-	-	-
Gallium sp.	F	-	-	1	1	-	-	-	-
Geranium sylvaticum	F	12	2	-	-	-	-	-	-
Luzula sp.	G	-	1	-	18	-	-	-	1
Melampyrum sylvaticum	F	2	2	-	-	-	-	-	-
Myosotis decumbens	F	1	-	-	-	4	-	-	-

Omalotheca sp.	F	-	-	-	-	-	-	1	-
Phleum alpinum	G	15	-	-	-	-	-	-	-
Papaver sp.	F	-	1	-	-	-	-	-	-
Poa sp.	G	8	6	-	4	-	-	-	-
Ranunculus acris	F	30	4	-	-	18	1	12	-
Rumex acetosa	F	12	-	-	-	-	2	-	-
Salix herbacea	S	-	-	-	-	-	-	4	2
Sibbaldia procumbens	F	-	-	1	-	-	-	4	1
Silene acaulis	F	-	-	-	-	-	-	-	1
Solidago virgaurea	F	-	-	-	-	1	2	2	-
Taraxacum sp.	F	-	-	-	-	-	-	-	1
Thalictrum alpinum	F	-	-	-	-	-	-	1	1
Trientalis europaea	F	-	-	-	-	2	1	-	-
Vaccinium vitus-idea	S	-	-	-	-	1	-	2	1
Vaccinium myrtillus	S	-	-	-	-	1	-	-	-
Vaccinium sp.	S	-	-	-	-	-	1	-	-
Veronica sp.	F	1	1	-	-	-	-	-	-
Viola biflora	F	45	2	23	2	1	1	-	-
Viola canina	F	-	-	-	-	1	-	-	-
Unknown 1	-	-	3	2	-	-	-	-	-
Unknown 2	-	-	-	-	1	-	-	-	-
Unknown 3	-	-	-	-	1	-	-	-	-
Unknown 4	-	-	-	-	1	-	-	-	-
Unknown 5	-	1	-	-	-	-	-	-	-
Unknown 6	-	1	-	-	-	-	-	-	-
Unknown 7	-	1	-	-	-	-	-	-	-
Unknown 8	-	-	-	1	-	-	-	-	-
Unknown graminoid	G	47	10	-	1	14	-	1	1
Unknown forb	F	-	-	-	-	11	3	1	3

*G: graminoid; F: forb; S: shrub; Bp: *Betula pubescens*

Table S3b. Total abundance (number of seeds among samples) and corresponding density (number of seeds/ m2) of seedlings for all species recorded in the soil seed bank survey, sorted by transect elevation level. Species names and their elevation range classification follow Lid and Lid (1994).

		Number of seeds in the germinable seed bank				**Seed density (number of seeds/ m^{2})**			
		Transect level				**Transect level**			
		Low	Mid 1	Low	Mid 1	Low	Mid 1	Low	Mid 1
Agrostis capillaris	G	90	8	2	1	424	38	9	5
Alchemilla sp.	F	1	-	-	-	5	-	-	-
Anthoxanthum alpinum	G	-	1	-	-	-	5	-	-
Betula nana	S	-	6	-	-	-	28	-	-
Betula pubescens	*Bp*	7	8	5	11	33	38	24	52
Bistorta vivipara	F	20	-	-	-	94	-	-	-
Calamagrostis sp.	G	7	1	-	-	33	5	-	-
Campanula rotundifolia	F	4	1	-	4	19	5	-	19
Carex sp.	G	58	1	9	2	274	5	42	9
Caryophyllaceae	F	-	-	-	1	-	-	-	5
Cerastium fontanum	F	2	-	-	-	9	-	-	-
Deschampsia caespitosa	G	13	-	-	-	61	-	-	-
Draba norvegica	F	1	-	-	-	5	-	-	-

Empetrum nigrum	S	21	43	81	95	99	203	382	448
Epilobium hornemannii	F	-	1	-	-	-	5	-	-
Euphrasia alpina	F	1	-	-	2	5	-	-	9
Festuca ovina	G	-	1	-	-	-	5	-	-
Luzula sp.	G	14	2	17	33	66	9	80	156
Myosotis decumbens	F	2	-	-	-	9	-	-	-
Omalotheca norvegica	F	-	1	1	-	-	5	5	
Omalotheca supina	F	-	-	1	3	-	-	5	14
Poa alpina	G	1	-	-	-	5	-	-	-
Poa sp.	G	-	1	-	-	-	5	-	-
Potentilla crantzii	F	2	-	-	-	9	-	-	-
Sagina procumbens	F	3	-	-	-	14	-	-	-
Sagina saginoides	F	3	-	3	-	14	-	14	-
Saussurea alpina	F	12	-	-	-	57	-	-	-
Sibbaldia procumbens	F	2	-	4	25	9	-	19	118
Stellaria graminea	F	1	-	-	-	5	-	-	-

Taraxacum sp.	F	-	-	-	1	-	-	-	5
Trifolium pratense	F	1	-	-	-	5	-	-	-
Urtica dioica	F	1	-	-	-	5	-	-	-
Vaccinium uliginosum	S	2	-	-	-	9	-	-	-
Veronica alpina	F	-	-	-	1	-	-	-	5
Veronica serpyllifolia	F	-	1	1	7	-	5	5	33
Viola biflora	F	-	-	1	-	-	-	5	-
Unknown forbs	F	2	2	-	-	9	9	-	-
Unknown graminoids	G	7	-	3	5	33	-	14	24
Unknown seedlings	-	28	12	8	39	132	57	38	184

*G: graminoid; F: forb; S: shrub; Bp: *Betula pubescens*

Supporting information to the paper
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Appendix S4. Model estimates from the seed rain, germinable seed bank and seedling emergence negative binomial GLMM fits (scaled and on the natural log scale), rescaled estimates and rescaled and back-transformed estimates.

Table S4a. Model estimates for the relationship between the number of seeds per seed trap and distance from the trail, climatic gradient, the interaction between climatic gradient and distance from trail, grass cover and pellet count, from a GLMM with negative binomial error structure and log link function (original, rescaled, and rescaled and back-transformed values). Significant p-values are shown in bold. The mean relative difference between rescaled and unscaled coefficients was 0.09990912.

	Original model estimates				**Rescaled estimate**	**Rescaled and back-transformed estimate**
	Estimate	**SE**	**z**	**p-value**		
Intercept	-1.35	0.49	2.74	**0.006**	1.44	4.20
Distance to trail	-0.39	0.12	-3.15	**0.002**	-0.06	0.94
Climate	1.27	0.29	4.36	**< 0.001**	8.61	5505.64
Climate x Distance to trail	0.11	0.113	1.00	0.316	0.07	1.07
Grass cover	0.47	0.23	2.08	**0.038**	0.02	1.02
Pellet count	0.32	0.20	1.60	0.109	0.01	1.01

Table S4b. Model estimates for the relationship between the number of germinable seeds from the soil seed bank per sample and distance from the trail, climatic gradient, the interaction between climatic gradient and distance from trail, grass cover and pellet count from a GLMM with negative binomial error structure and log link function (original, rescaled, and rescaled and back-transformed values). Significant p-values are shown in bold. The mean relative difference between rescaled and unscaled coefficients was 0.5393914.

	Original model estimates				**Rescaled estimate**	**Rescaled and back-transformed estimate**
	Estimate	**SE**	**z**	**p-value**		
Intercept	-3.88	0.21	-18.53	**< 0.001**	-3.21	0.04
Distance to trail	-0.40	0.14	-2.78	**0.005**	-0.06	0.94
Climate	0.30	0.23	1.30	0.194	1.94	6.95
Climate x Distance to trail	-0.34	0.14	-2.40	**0.016**	-0.23	0.80
Grass cover	-0.24	0.21	-1.13	0.259	-0.01	0.99
Pellet count	-0.06	0.18	-0.33	0.745	-0001	1.00

Table S4c. Model estimates for the relationship between the number of seedlings recorded in the field (excluding one outlier) and distance from the trail, climatic gradient, pellet count and the interaction between climatic gradient and distance from trail, from a GLMM with negative binomial error structure and log link function (original, rescaled, and rescaled and back-transformed values). Significant p-values are shown in bold. The mean relative difference between rescaled and unscaled coefficients was 0.3035029

	Original model estimates				**Rescaled estimate**	**Rescaled and back-transformed estimate**
	Estimate	**SE**	**z**	**p-value**		
Intercept	0.12	0.53	0.22	0.824	0.94	2.55
Distance to trail	-0.51	0.17	-3.08	**0.002**	-0.08	0.93
Climate	0.56	0.42	1.33	0.184	3.89	48.74
Climate x Distance to trail	-0.18	0.15	-1.19	0.233	-0.12	0.88
Pellet count	-0.61	0.55	-1.12	0.264	-0.01	0.99

Appendix S4d. Model estimates for the relationship between the number of seedlings recorded in the field (as in Table S4c, yet here including outlier (n=26)) and distance from the trail, climatic gradient, pellet count and the interaction between climatic gradient and distance from trail, from a GLMM with negative binomial error structure and log link function (original, rescaled, and rescaled and back-transformed values). Significant p-values are shown in bold. The mean relative difference between rescaled and unscaled coefficients was 0.5318795.

	Original model estimates				**Rescaled estimate**	**Rescaled and back-transformed estimate**
	Estimate	**SE**	**z**	**p-value**		
Intercept	0.08	0.58	0.13	0.897	0.80	2.22
Distance to trail	-0.35	0.14	-2.41	**0.016**	-0.05	0.95

Climate	0.47	0.45	1.04	0.299	3.24	25.53
Climate x Distance to trail	-0.34	0.127	-2.66	**0.008**	-0.23	0.79
Pellet count	-0.83	0.597	-1.39	0.163	-0.02	0.98

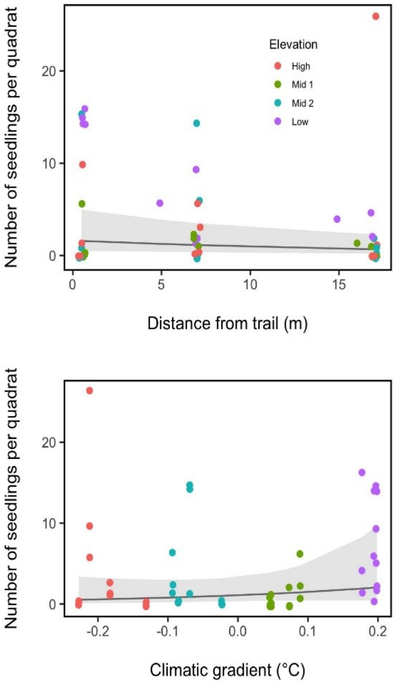

Figure S4. The relationship between distance from the trail, climatic gradient and the predicted number of seedlings per quadrat, based on the best GLMM. One outlier (with n = 26 seedlings) is included, as opposed to Figure 4. Dots represent raw quadrat data, coloured by elevation. 95% confidence intervals of the model are shaded in grey.

Supporting information to the paper
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Appendix S5. Model-based predictions based on the best models for seed rain, seed bank and seedling emergence.

Table S5a. Predictions of seed rain as a function of distance from the trail, adjusted for a mean climatic harshness (PC1 = 0.0) and grasscover (19.8 %) and taking into account random variation between trails and transects. 95 % confidence intervals are given in paratheses.

Distance to the trail edge [m]	Predicted seed rain
0.5	9.38 [7.06, 12.47]
7.0	5.80 [4.81, 7.00]
17.0	2.77 [1.98, 3.85]

Table S5b. Predictions of seed rain as a function of climatic harshness, adjusted for mean distance from the trail (8.75 m) and grasscover (19.8 %) and taking into account random variation between trails and transects. 95 % confidence intervals are given in paratheses.

Climatic harshness	Predicted seed rain
-0.23 (coldest)	2.76 [1.67, 4.58]
0.20 (warmest)	1.27 [0.87, 1.87]

Table S5c. Predictions of the number of germinable seeds in the seed bank as a function of distance from the trail and climatic harshness, adjusted for mean grasscover of 0 % and no herbivore pellets, taking into account random variation between trails and transects. A sample weight of 147 g was taken as the base for these predicitons. 95 % confidence intervals are given in paratheses.

Distance to the trail edge [m]	Climatic harshness	
	-0.23 (coldest)	0.2 (warmest)
0.5	1.67 [0.60, 4.64]	11.74 [4.31, 32.01]
7.0	1.92 [0.83, 4.47]	5.13 [2.40, 10.99]
17.0	2.38 [0.85, 6.65]	1.44 [0.57, 3.65]

Appendix S5d. Predictions of seeding numbers per 0.5 m x 0.5 m quadrat as a function of distance from the trail, adjusted for mean climatic harshness (PC1 = 0.0) and herbivore droppings (16.8) and taking into account random variation between trails and transects. 95 % confidence intervals are given in paratheses.

Distance to the trail edge [m]	Predicted seedling number
0.5	1.96 [0.68, 5.66]
7.0	1.20 [0.43, 3.36]
17.0	0.56 [0.18, 1.80]

Article II

R. E. M. Wedegärtner, J. J. Lembrechts, R. van der Wal, A. Barros, A. Chauvin, I. Janssens, and B. J. Graae

Hiking trails shift plant species' realized climatic niches and locally increase species richness

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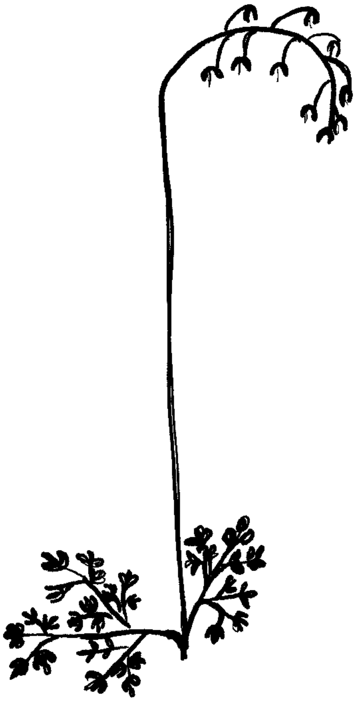

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RESEARCH ARTICLE

Hiking trails shift plant species' realized climatic niches and locally increase species richness

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Abstract

Aim: The presence and use of trails may change plant species' realized climatic niches via modified abiotic and biotic conditions including propagule transport, allowing competition-pressed alpine species to expand their rear edges towards warmer locations and lowland species to extend their leading edges towards cooler locations. We investigated whether mountain trails indeed act as corridors for colonization and shift species' realized climatic niches, resulting in higher species richness in trailsides.

Location: Dovrefjell and Abisko area in the Scandes mountains of Norway and Sweden.

Methods: We surveyed plant community composition and disturbances along 16 hiking trails in summer 2018 (Dovrefjell) and 2019 (Abisko). We linked changes in species' realized climatic niches to their climatic optimum and variation in species richness to climate, trail effects and resident plant community characteristics.

Results: Plant species richness was on average 24% greater in trailside than in interior vegetation plots. Proximity to trails accounted for 9% and climatic harshness for 55% of variation in species richness explained in our model. Trailsides increased in richness, especially in relatively species-poor sites and close to introduction points (each accounting for 24% of variation in our model of species gains). Shifts in rear edges and optima of realized climatic niches along trails related to species' undisturbed climatic optimum, with alpine species being more likely to move into warmer locations. While some disturbance-associated species shifted their leading edges towards colder locations, contrary to expectations this was not the case for lowland species. Overall, shifts in climatic niches resulted in more species' niches overlapping in trailsides than in the interior vegetation.

Main conclusion: Trails can locally increase species richness by creating opportunities for colonizing species and weaker competitors. Because of prevailing disturbance, they may even provide opportunities for persistence and downward expansion of alpine species, aiding conservation efforts.

KEYWORDS
alpine plants, biotic interactions, climate gradient, disturbance, mountain trails, realized niche, species range shifts

1 | INTRODUCTION

Understanding how climate and anthropogenic disturbance influence plant communities in mountains is necessary to protect these ecosystems (IPBES, 2019). While mountain ranges are hotspots of biodiversity and endemism (Steinbauer et al., 2016), they experience rapid warming, especially around the annual 0°C isotherm (Pepin & Lundquist, 2008). Additionally, mountains undergo shifts in land use (Körner et al., 2006) and experience increasing pressure through recreational activities and associated infrastructure such as hiking trails (Debarbieux et al., 2014).

Species range shifts into previously unsuitable higher elevation habitats are expected with climate warming under the assumption of niche-conservatism (Pearman et al., 2008). As strong competitors move their leading range edge into new locations, alpine plant species might lose ground due to increased competition at their rear range edge (Gottfried et al., 2012; Grabherr et al., 1994). However, a plant species' realized climatic niche, and thus spatial distribution in an area, is determined by a much wider set of ecological processes, including dispersal rate (Engler et al., 2009), habitat modification and resulting changes in biotic and abiotic interactions (Lenoir et al., 2010). As hiking trails may facilitate propagule transport (Mount & Pickering, 2009) and influence competitive and facilitative relationships between species through increased disturbance (Bates, 1935), a better understanding of trail effects on species' realized climatic niches and resulting changes in species distribution and richness is called for.

For plants colonizing new locations in high-latitude mountain systems, competition is considered especially important at lower elevations with milder climate, while at higher elevations facilitation of the colonizer by the extant vegetation is thought to be dominating (Bertness & Callaway, 1994; Choler et al., 2001; Paquette & Hargreaves, 2021). Disturbance can disrupt competition and facilitation through removal of plant biomass and creation of gaps in the vegetation (Lembrechts, Pauchard et al., 2016; Nystuen et al., 2014). Where competition is most important, disturbance may lead to competitive release, with gaps in the vegetation promoting establishment by newcomers. In harsher environments, gap formation is expected to reduce facilitation by lessening environmental amelioration by neighbouring plants (Bertness & Callaway, 1994; Lembrechts et al., 2015). Reduced competition in milder locations could result in downward shifts in rear edges of (competitively excluded) alpine species (Chardon et al., 2019; Lenoir et al., 2010; Normand et al., 2009) and thus changes in plant species' realized climatic niche and spatial distribution. Competitive release may not only be limited to the mild end of the climate gradient, though, as there is evidence for a continued importance of competition in alpine plant communities, with gaps increasing colonization even under harsh climatic conditions (Graae et al., 2011; Lembrechts, Pauchard et al., 2016).

Competition and resistance to colonization are influenced by characteristics of resident plant communities (Auffret et al., 2010; Graae et al., 2011; Pollnac & Rew, 2014). Differences may stem from the vegetation structure of a site (Giorgis et al., 2016), the vegetation's susceptibility to disturbance (Graae et al., 2011; Milbau et al., 2013), resource availability (Davis et al., 2000), direct biotic interactions (Cavieres et al., 2008) and species richness as an expression of environmental factors, microheterogeneity and biotic interactions (Elton, 1958; Levine & D'Antonio, 1999; Peng et al., 2019). Herb-dominated and willow shrub-dominated communities are most hospitable for colonization in high-latitude mountain ecosystems (Graae et al., 2011), while dwarf shrub- and lichen-dominated ones, such as *Empetrum nigrum* communities, are more resistant due to their dense growth (Pellissier et al., 2010) and allelopathic properties (Nilsson, 1994).

In the European Alps, lowland species exhibited larger upwards shifts of range edges and a greater increase in abundance than alpine species (Rumpf et al., 2018). Lowland species were also more likely to show establishment lags (Rumpf et al., 2019). As anthropogenic disturbances appear to favour successful colonization by lowland species (Lembrechts, Alexander et al., 2016; Lembrechts, Pauchard et al., 2016), Alexander et al. (2018) hypothesize that such disturbances might decrease establishment lags. Where disturbance facilitates the expansion of species' realized climatic niches, this should lead to a greater number of species' climatic niches overlapping and, therefore, a locally increased species richness.

Mountain trails can be described as features of linear disturbance (Suárez-Esteban et al., 2016) that cut through mountain ecosystems and may influence species' realized niches through disruption of competition and facilitation, and by promoting the transport of diaspores. The construction and use of hiking trails disturbs vegetation mechanically, often resulting in bare soil patches and modified soil conditions (Bates, 1935; Gellatly et al., 1986; Marina et al., 2010), and opening up sites for colonization (Monz, 2002). Both hikers and animals using trails can act as vectors of dispersal by transporting diaspores clinging to footwear, clothes and equipment of people (Huiskes et al., 2014; Mount & Pickering, 2009; Ware et al., 2012) and feet and fur of animals or embedded into their faeces (Bråthen et al., 2016; Fischer et al., 1996). Tourism infrastructure such as cabins, trailheads and ski lifts may act as sources from which propagules of lowland or non-native species spread into mountain areas (Pickering et al., 2007).

Higher plant species richness in trailsides compared with the surrounding vegetation could result from change in realized climatic niches and high diaspore input. This has been observed in different ecosystems (Benninger-Truax et al., 1992; Suárez-Esteban et al., 2016, and references therein), and trails have been shown to promote the spread of non-native species in mountain areas (Anderson et al., 2015; Liedtke et al., 2020). In Arctic, Antarctic and alpine systems, however, findings are contradictory, with decreases in vascular plant species richness along trails in some cases (Crisfield et al., 2012), and in other cases either no clear effect (Jägerbrand & Alatalo, 2015; Monz, 2002) or effects depending on community type, soil moisture (Gremmen et al., 2003), trail type (Hill & Pickering, 2006; Nepal & Way, 2007) and use intensity

(Benninger-Truax et al., 1992). We therefore, need a better understanding of when and to what extent trails affect the colonization of lowland and alpine species into new areas in alpine ecosystems.

In this paper, we examine the effects of hiking trails on species richness, species' realized climatic niches and colonization in an alpine ecosystem. We surveyed the presence and cover of all vascular plants, as well as trail effects along 16 trails spanning steep climatic gradients in two mountain areas. We used this data to model regional species richness, determine the extent to which trails modulate species richness patterns and compare species' realized climatic niche in trailsides and the interior vegetation—undisturbed vegetation away from trails. We hypothesized that: (a) trails act as corridors of colonization for species in mountain ranges, resulting in larger species richness at trailsides; (b) how species colonize new areas along trails is affected by their climatic niche, with lowland plants expanding towards colder locations and alpine plants shifting to warmer locations as competition decreases through disturbance; and (c) in addition to regional drivers of biodiversity, site characteristics such as the recipient community, disturbance and dispersal influence local colonization along trails.

2 | METHODS

2.1 | Study regions

We conducted vegetation surveys along mountain trails in two popular hiking areas in Scandinavia. The Abisko area is situated in Northern Sweden (68.3°N; 18.8°E) and Dovrefjell approximately 700 km south in Southern Norway at 62.2°N; 9.5°E (Figure 1a–d). Both areas are accessible by road and train and are popular tourist destinations with many visitors exploring on foot, mostly following trails (Gundersen et al., 2019; Karlsson, 2016).

At Fokstugu weather station in Dovrefjell (62.11°N, 9.29°E, 979 m.a.s.l.), the mean annual temperature was 1.0°C and mean annual precipitation 445 mm (2002–2019). In Abisko (68.36°N, 18.82°E, 388 m.a.s.l.), the corresponding values were 0.5°C and 340 mm (Norsk Klimaservicesenter, 2020; SMHI, 2020). Both areas are located on the lee-side of mountain ranges, with landscapes shaped by the Weichselian glaciation events (Holdar, 1959; Paus et al., 2011). The bedrock in Abisko area is mostly metamorphic with some acidic and ultrabasic intrusions; in Dovrefjell, it is composed of calcium-rich phyllites. Soils are predominantly thin podzols developed on deposits of glacial till (SGUs Kartvisare, n.d.; Sjögersten et al., 2003), allowing for a rich flora, especially in calcium-rich locations (Gjærevoll, 1979; Koltzenburg & Schipperges, 2014).

The tree line and forest below largely consist of mountain birch (*Betula pubescens*). Low-alpine plateaus host dwarf shrub communities and lichen heaths dominated by *Empetrum nigrum*, *Vaccinium uliginosum*, *V. vitis-idea*, *B. nana* (and *Arctostaphylos uva-ursi* at Dovrefjell), lichens and bryophytes, with considerably denser and more widespread lichen heath in Dovrefjell than in Abisko. The vegetation at higher elevation is a mosaic of dry heath, meadow vegetation, snow beds and sparsely vegetated boulder and scree fields (De Wit et al., 2014; Sjögersten et al., 2003). Vascular plant cover was above 75% in most plots; vascular species richness was highly variable (ranging from 2 to 56 and 1 to 58 species in Dovrefjell and Abisko, respectively). The elevation gradient in the Abisko area spans from 341 m.a.s.l. (Lake Torneträsk) to 2096 m.a.s.l, the top of Sweden's highest mountain (Kebnekaise); at Dovrefjell it spans from 659 m.a.s.l. (Dombås) to 2286 m.a.s.l (Snøhetta mountain).

Sami people traditionally used both areas for reindeer herding (Bergstøl & Reitan, 2008; Emanuelsson, 1987). Today, such practices only take place in the Abisko area (Gabna - Sametinget, 2021). Sheep are grazing in Dovrefjell in summer (kilden.nibio.no, 2021), and a small population of muskoxen is present west of the E6 highway. Trails are used for hiking, and to a lesser extent for biking; in Dovrefjell, some trails are also used for horse riding. The average width of the examined trails was 2.5 m, and the trail surface was mostly bare soil interspersed with remaining vegetation.

2.2 | Data collection

2.2.1 | Field surveys

We surveyed a total of 16 trails, eight in each region, following the trail survey protocol from the Mountain Invasion Research Network (MIREN) as outlined in Liedtke et al. (2020). Trails were surveyed early July to early September, in 2018 for Abisko and 2019 for Dovrefjell. Along each trail, we placed 10 T-shaped transects at intervals of equal elevation from the trailhead to the highest occurrence of vascular plant species along the trail, or the highest point of the trail feasible if this occurred below the limit of vascular vegetation (Figure 1e). Each so-called T-transect consisted of three 2 m × 10 m plots, with the trailside (T) plot directly adjacent to the trail and parallel to its edge forming the short side of the T. Perpendicular to this, the mid-plot (M) and farthest away the interior vegetation plot (F) form the long side of the T (see Figure 1e–f). We are, therefore, capturing a gradient from strongly trail-influenced vegetation (T) to interior vegetation that was not visibly influenced by the trail (F). For each plot, we determined the presence of vascular plant species and estimated their cover (see Appendix S1) alongside that of total vascular vegetation, herbs and forbs, shrubs, dwarf shrubs, bryophytes, rocks and bare soil. We measured the visible extent of mechanical disturbance from trampling exceeding the trail edges and surveyed the number of gaps in the vegetation with exposed soil encountered along a line transect crossing the middle of the plot (see Appendix S1: Figure S1.1). The number of gaps and their representative size were subsequently used to calculate an index of the area covered by gaps (see protocol in Appendix S1). Information about the conservation status of plant species was added to determine whether any threatened species were especially affected by trails (Norwegian Red List, 2015; Swedish Red List 2020, 2020). In each area, three species were listed as near threatened.

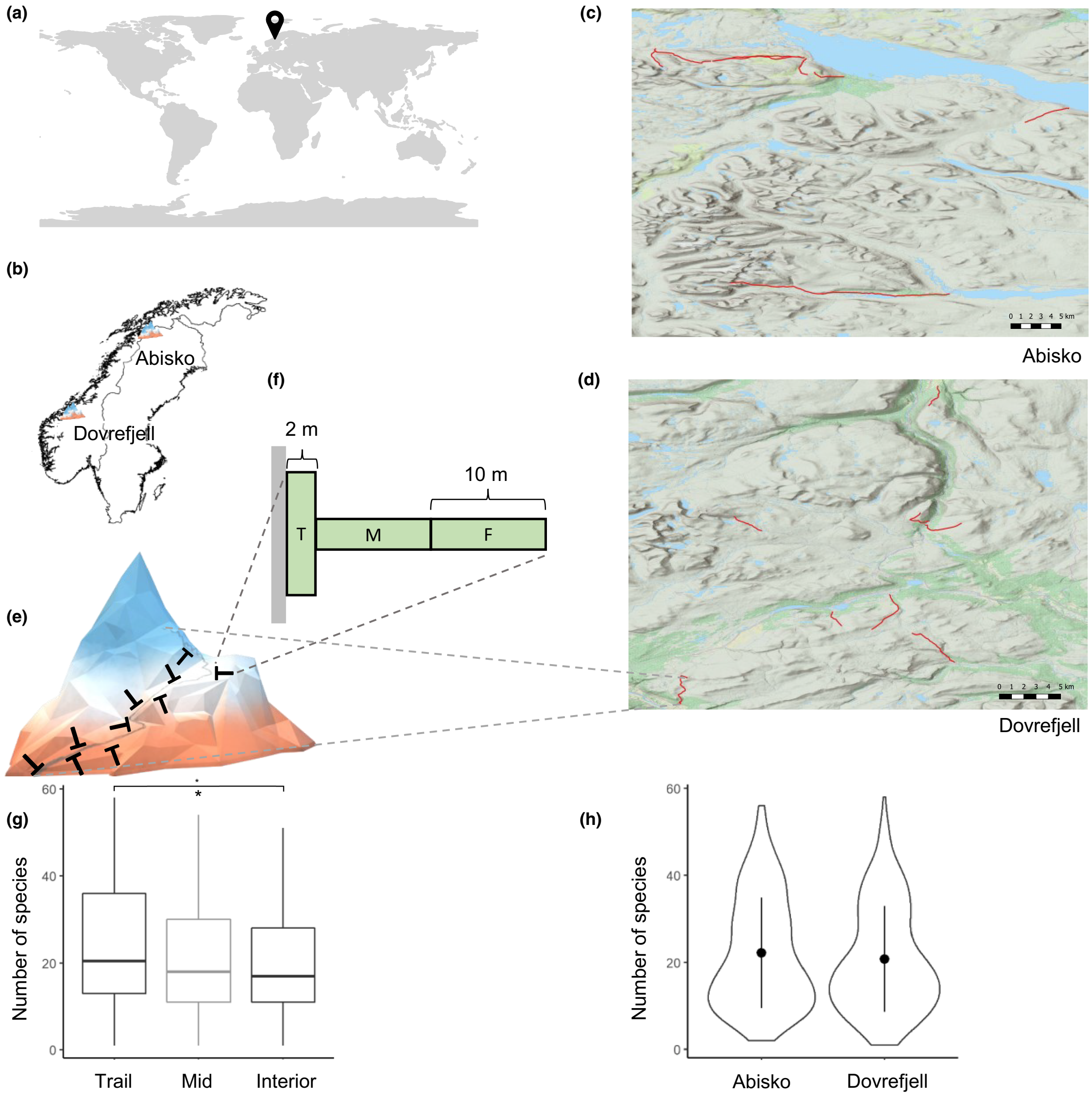


FIGURE 1 Schematic map of (a) the location of the study areas in northern Europe and (b) within the context of Scandinavia, with more detailed maps of surveyed hiking trails in (c) Abisko and (d) Dovrefjell. (e) Shows the study design of 10 T-transects at regular elevation intervals along a trail and (f) the trailside (T), mid- (M) and interior vegetation (F) 2 × 10 m plots that constitute each T-transect. Panel (g) shows the median number and interquartile ranges of species per plot type (with the asterisk denoting a significant difference at the $p < .05$ level between T and F plots, and M plot in grey, as it was not included into the comparison, and (h) depicts the number of species per 20 m^2 plot in the two research areas, with mean (circle), standard error (line) and density function (area). Note for (e) and (f): Trails and T-transect plots are not to scale

2.2.2 | Climate and GIS data

To obtain functionally relevant bioclimatic predictor variables for our models (Elith & Leathwick, 2009), we used high-resolution topographic layers to downscale CHELSA bioclimatic layers (Karger et al., 2017; Karger et al., 2018) with a 30-arcsecond (~1 km) resolution and produce temperature at 1.2-arcsecond (~30 m) resolution. Downscaling followed a geographically weighted regression (GWR) approach (Lu et al., 2011) as described by Lenoir et al. (2017) and was based on elevation, slope, northness, eastness, distance from the ocean and potential solar radiation. These predictor variables have shown good results for predicting temperature in previous studies (Ashcroft & Gollan, 2012; Buytaert et al., 2006; Fridley, 2009; Lenoir et al., 2017). The downscaling process is described in Appendix S1.

To obtain plot-based estimates of climatic harshness, we applied a principal component analysis to high-resolution annual mean temperature, maximum temperature of the warmest month and minimum temperature of the coldest month, as these were highly correlated (see Appendix S2: Table S2.1). The first principal component captured 87% of the variation in climate data and was strongly and negatively correlated with mean annual temperature ($r = -0.97$, $p < .001$) and minimum temperature ($r = -0.98$, $p < .001$), but less so with maximum temperature ($r = -0.53$, $p < .001$). Using this principal component, a climatic harshness value was assigned to each plot.

To determine the distance to the nearest potential propagule introduction source for each plot, we downloaded all roads, railways and buildings for a bounding box surrounding our trails from Open Street Map using the 'osmdata' package (Padgam et al., 2017) and calculated the Euclidian distance. If no such anthropogenic features were present along a trail, additional propagule introduction by humans was considered most likely at the trailhead and, therefore, the distance from there to each plot, along a hiking trail, was taken as distance to the nearest potential introduction source.

2.3 | Analyses

2.3.1 | Trails as corridors of colonization in mountain ranges

We compared median species richness in trailside, intermediate and interior vegetation plots with a Friedman test and paired Wilcoxon signed-rank tests with a Bonferroni correction (Hollander & Wolfe, 1973). For each transect, we compared the presence of species in trailside and mid-distance plots with those found in the associated interior vegetation plot to quantify the number of species lost and gained. We tested for differences in median number of species lost and gained and between trailside and mid-distance plots again using paired Wilcoxon signed-rank tests.

Next, relationships between plot-level species richness and distance to trail, regional drivers of species richness such as microclimate, distance to potential introduction sites and the research area were analysed with generalized linear mixed-effect models (GLMMs, with a Poisson error distribution) using the 'glmmTMB' package (Brooks et al., 2017). Transect nested within trail was chosen as based on a selection of the random effects model with lowest Akaike Information Criterion (AIC, Akaike, 1974) starting with the most complex possible random effects structure as described in Zuur et al. (2009). We modelled species richness as a function of climatic harshness, distance from trail edge, distance to nearest introduction point, research area (Abisko vs. Dovrefjell) and the interactions of distance from the trail, climatic harshness and distance to introduction point. Then, we employed backward model selection based on AIC to find the optimal model for species richness using the 'MASS' package (Venables & Ripley, 2002). To determine how much of the variation in richness each of the predictor variables explained, we constructed nested partial models and used a variance partitioning approach (Legendre & Legendre, 2012).

2.3.2 | Range shifts along trails

For all species with more than 6 occurrences in each plot type (i.e. trail, mid, interior) in both research areas, we calculated the rear edge (warmest occurrence), leading edge (coldest occurrence), climatic range and optimum position (mean occurrence along the gradient weighted by species cover, as outlined in Lembrechts, Alexander et al., 2016) along the gradient of climatic harshness. To evaluate how proximity to a trail can influence realized climatic niche, we determined species-specific shifts in rear edge, leading edge, optimum and climatic range between trailside and interior vegetation plots. The influence of a species' realized niche on range shifts was tested through linear regression analysis, modelling changes in rear edge, leading edge, climatic range and optimum as a function of a species' climatic optimum in the interior vegetation.

2.3.3 | Site-level drivers of colonization

To examine how the interplay between regional drivers of richness and site-level properties influences colonization along trails, we calculated the difference in species richness between each pair of interior vegetation and trailside plots and modelled this change in richness using a linear mixed-effect model with a Gaussian error

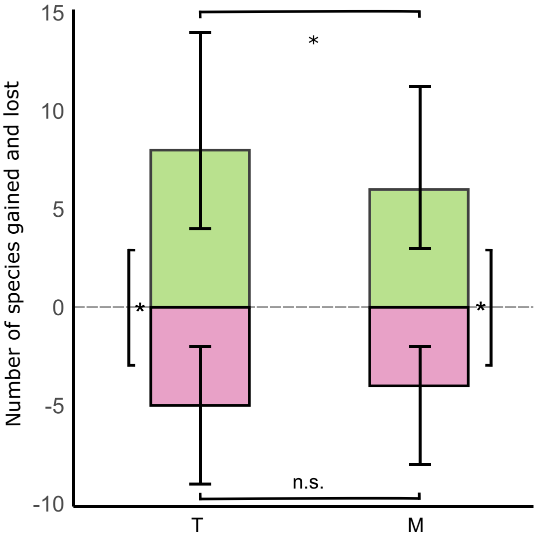


FIGURE 2 Bar plots of median and interquartile ranges of number of species gained (green, positive values) and lost (pink negative values) for trailside (T) and mid-distance (M) vegetation relative to the number of species present in interior vegetation. We compared lost with gained, within T and M, respectively, and differences in lost and gained between T and M. significance of each pairwise Wilcoxon comparison with Bonferroni correction at the $p < .05$ level is denoted by an asterisk (full summary table Appendix S2: Table S2.5)

distribution (Bates et al., 2015). We included regional drivers of colonization (distance to introduction source, interaction between climatic harshness and research area), site-level properties related to disturbance by trails (disturbance extent into the vegetation, gap index and total vegetation cover), properties of the recipient plant community (species richness of the interior vegetation, herb cover and dwarf shrub cover of the colonized plot) into our beyond optimal model. To find the best model, we again used AIC-based backward model selection. Trail identity was included as a random effect after determining the optimal random effects structure using AIC. Contributions of the different variables were analysed using variance partitioning.

3 | RESULTS

3.1 | Trails as corridors for colonization

We found a total of 325 species of vascular plants, of which 296 could be identified to species level (Appendix S2: Tables S2.2 and S2.3). The number of species per plot varied considerably within both regions, but their means were rather similar (Figure 1h; Abisko, 24.0 ±13.5 [*SD*]; Dovrefjell, 23.4 ±13.9). Plots next to trails had on average 24% more species than plots in the interior vegetation (Figure 1g; median 4 [95% CI: 1–6] species more; Appendix S2: Table S2.4). Trailside and mid-distance plots gained more species than they lost (Figure 2; trailside: median 3 [95% CI: 2–4] mid-distance: median 2 [95% CI, 1–3] more species gained than lost; Appendix S2: Table S2.5), and trailside plots gained on average two more species than the mid-distance plot (Figure 2; Appendix S2: Table S2.5).

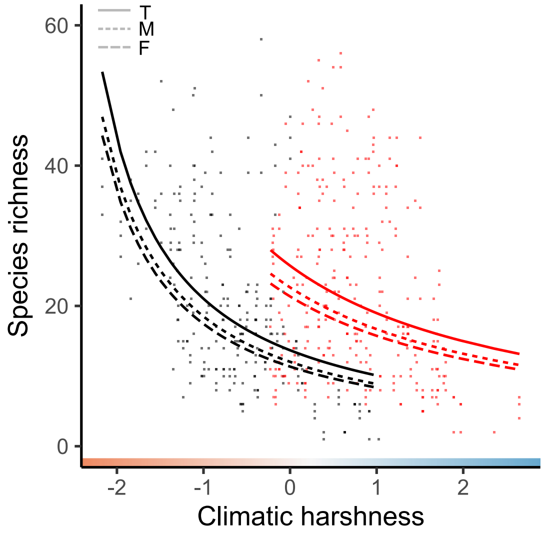


FIGURE 3 Predicted species richness as function of climatic harshness and distance from the trail for Dovrefjell (black line) and Abisko (red line). Raw data from Dovrefjell (black dots) and Abisko (red dots) are plotted as is, to show variability among recorded plots. The coloured bar at the bottom illustrates the climatic harshness gradient from warmer (red) to colder (blue)

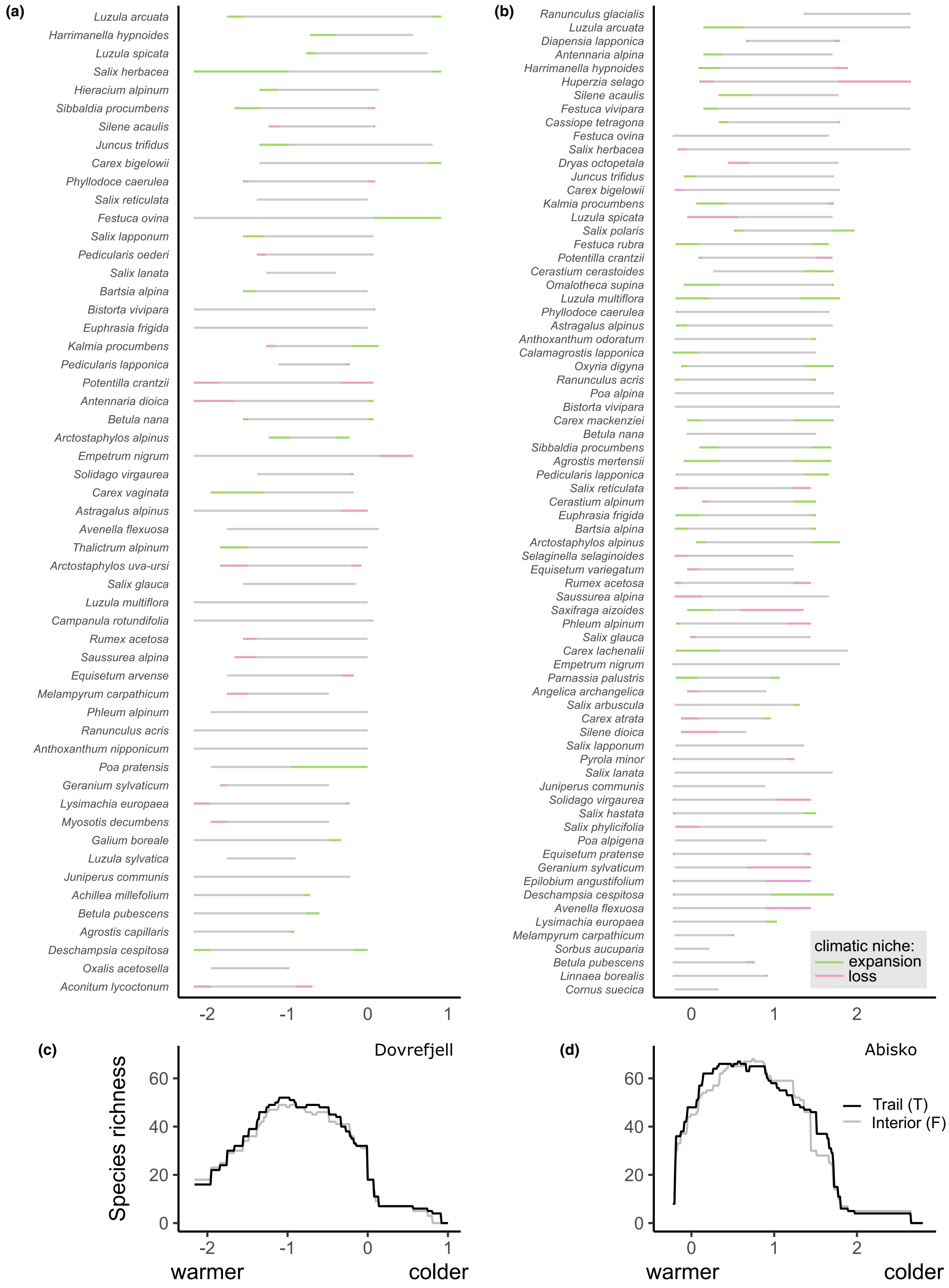
Species that were frequently gained in trailside plots included grasses such as *Poa annua*, *Phleum alpinum* and *P. alpina*, low-stature forbs such as *Sibbaldia procumbens* and *Euphrasia frigida*, and some species associated with agriculture such as the forbs *Trifolium repens* and *T. pratense*, but also occasional occurrences of red-listed species that were not found in the interior plots, such as *Draba lactea* and the orchid *Platanthera obtusata* (see Appendix S2: Tables S2.2 and S2.3).

Variation in species richness may stem from a multitude of interacting drivers. Our best GLMM captured 17% of the variation observed (marginal R^2). Of this explained variance, climatic harshness was the main determinant of plot-based species richness (Figure 3; 55%, with greatest richness at lowest climatic harshness; see Appendix S2: Tables S2.6 and S2.7 for model parameters and variance partitioning), followed by study area (10%, with greater richness in Dovrefjell than in Abisko) and distance from trail (9%, with higher richness at trailsides). Distance to introduction source only explained 1% of the variance in our model of plot-based richness.

3.2 | Trail influence on occupied climatic niches

Shifts in realized climatic niche when growing close to trails could be examined for 73 species from Abisko and 54 from Dovrefjell; this included 37 species sufficiently present in both study areas (Figure 4; see Appendix S2: Tables S2.8–S2.11, Figures S2.2–S2.7). Shifts were species- and area-specific. While shifts in optimum were small for some species, over half of them shifted their optimum towards warmer locations (Dovrefjell 59%, Abisko 53%) close to trails. The rest of the species shifted their optimum towards colder locations. In Dovrefjell, the shares of species that expanded their rear edges towards warmer (28%) or retracted towards colder (26%) locations were similar, and the proportion of stable rear edges was high (47%), whereas in Abisko more species lost ground at their rear edges (57%) and the proportion of stable rear edges was lower (23%). More species expanded their leading edges towards colder locations (Dovrefjell 30%, Abisko 38%) rather than losing ground (Dovrefjell

FIGURE 4 Species range changes along trails in comparison with the interior vegetation, with pink parts of the bar denoting a loss of range along trails, green range expansion along trails, and grey ranges occupied both along the trails and in the interior vegetation in (a) Dovrefjell and (b) Abisko area. Species are ordered according to their optimum in the interior vegetation, with those found at the coldest locations on the top. Cumulative number of species ranges overlapping at any given point (i.e., species richness) along the climatic gradient in the interior vegetation (grey) and in trailsides (black) are shown in (c) Dovrefjell and (d) Abisko


(a)
Luzula arcuata
Harrimanella hypnoides
Luzula spicata
Salix herbacea
Hieracium alpinum
Sibbaldia procumbens
Silene acaulis
Juncus trifidus
Carex bigelowii
Phyllodoce caerulea
Salix reticulata
Festuca ovina
Salix lapponum
Pedicularis oederi
Salix lanata
Bartsia alpina
Bistorta vivipara
Euphrasia frigida
Kalmia procumbens
Pedicularis lapponica
Potentilla crantzii
Antennaria dioica
Betula nana
Arctostaphylos alpinus
Empetrum nigrum
Solidago virgaurea
Carex vaginata
Astragalus alpinus
Avenella flexuosa
Thalictrum alpinum
Arctostaphylos uva-ursi
Salix glauca
Luzula multiflora
Campanula rotundifolia
Rumex acetosa
Saussurea alpina
Equisetum arvense
Melampyrum carpathicum
Phleum alpinum
Ranunculus acris
Anthoxanthum nipponicum
Poa pratensis
Geranium sylvaticum
Lysimachia europaea
Myosotis decumbens
Galium boreale
Luzula sylvatica
Juniperus communis
Achillea millefolium
Betula pubescens
Agrostis capillaris
Deschampsia cespitosa
Oxalis acetosella
Aconitum lycoctonum
-2
-1
0
1
(b)
Ranunculus glacialis
Luzula arcuata
Diapensia lapponica
Antennaria alpina
Harrimanella hypnoides
Huperzia selago
Silene acaulis
Festuca vivipara
Cassiope tetragona
Festuca ovina
Salix herbacea
Dryas octopetala
Juncus trifidus
Carex bigelowii
Kalmia procumbens
Luzula spicata
Salix polaris
Festuca rubra
Potentilla crantzii
Cerastium cerastoides
Omalotheca supina
Luzula multiflora
Phyllodoce caerulea
Astragalus alpinus
Anthoxanthum odoratum
Calamagrostis lapponica
Oxyria digyna
Ranunculus acris
Poa alpina
Bistorta vivipara
Carex mackenziei
Betula nana
Sibbaldia procumbens
Agrostis mertensii
Pedicularis lapponica
Salix reticulata
Cerastium alpinum
Euphrasia frigida
Bartsia alpina
Arctostaphylos alpinus
Selaginella selaginoides
Equisetum variegatum
Rumex acetosa
Saussurea alpina
Saxifraga aizoides
Phleum alpinum
Salix glauca
Carex lachenalii
Empetrum nigrum
Parnassia palustris
Angelica archangelica
Salix arbuscula
Carex atrata
Silene dioica
Salix lapponum
Pyrola minor
Salix lanata
Juniperus communis
Solidago virgaurea
Salix hastata
Salix phylicifolia
Poa alpigena
Equisetum pratense
Geranium sylvaticum
Epilobium angustifolium
Deschampsia cespitosa
Avenella flexuosa
Lysimachia europaea
Melampyrum carpathicum
Sorbus aucuparia
Betula pubescens
Linnaea borealis
Cornus suecica
0
1
2
climatic niche:
expansion
loss
(c)
Dovrefjell
Species richness
60
40
20
0
-2
-1
0
1
warmer
colder
(d)
Abisko
60
40
20
0
0
1
2
Trail (T)
Interior (F)
warmer
colder

22%, Abisko 28%) but a relatively high proportion of species had leading edges that remained stable (49% and 33%). Considering the 37 species shared between areas, 35% of species consistently shifted their optimum towards warmer locations and 21% shifted towards colder locations in both areas. The remaining species (44%) responded inconsistently between areas (see Figure 4a,b).

Linking direction and magnitude of shift to information about species climatic preferences, we found that climatic optimum in the interior vegetation predicted changes in species' realized climatic niche in trailsides. In trailsides, alpine species were more likely to shift their rear edges and optima towards warmer locations and lowland species towards colder locations (Figure 5; Table 1; see Appendix S2: Table S2.12). For example, alpine species such as *Luzula multiflora* and *Silene acaulis* shifted their optima towards warmer locations, and lowland species such as *Geranium sylvaticum* and *Juniperus communis* towards colder locations along trails. The general pattern was consistent across the two areas, but with stronger support from Dovrefjell; for Abisko only the rear-edge shifts were statistically significant. No general pattern for leading edge shifts could be found, but in the Abisko area many species with their optimum in the subalpine range (e.g. *Bartsia alpina*, *Omalotheca supina* and *Sibbaldia procumbens*) showed an expansion of their leading edge towards colder locations along trails (Figure 4a,b). Plotting species ranges in the interior vegetation and along trails (Figure 4c,d) illustrates how the cumulative change in ranges can lead to an increase in richness by allowing more overlapping species ranges at a given climatic locality.

3.3 | What drives differences in richness between interior and trailside plots?

The best LMM of the difference in species number between interior and trailside plots accounted for 25% of variation (see Appendix S2: Tables S.2.13 and S2.14). Increases in species richness next to trails were greater when closer to introduction points such as trailheads (variances explained by all factors are summarized in Table 2). Distance to the nearest introduction point accounted for 24% of the variation explained by the model. Interior vegetation species richness explained 24% of variation in differences between trailside and interior vegetation with largest gains in less rich communities. When keeping all other factors constant, the gain in trailside species richness increased with increasing herbaceous cover, while more dwarf shrubs close to trails led to smaller gains or in extreme cases even to a loss of species. Gap area was negatively related to gain in richness at trailsides, while trailsides were more likely to increase in richness in sites with a higher total vegetation cover or with a larger disturbance extent. Factors associated with disturbance through trails added up to explaining 21% of the variance in the model.

4 | DISCUSSION

Contrary to previous observations in cold ecosystems (Crisfield et al., 2012; Gremmen et al., 2003; Jägerbrand & Alatalo, 2015;

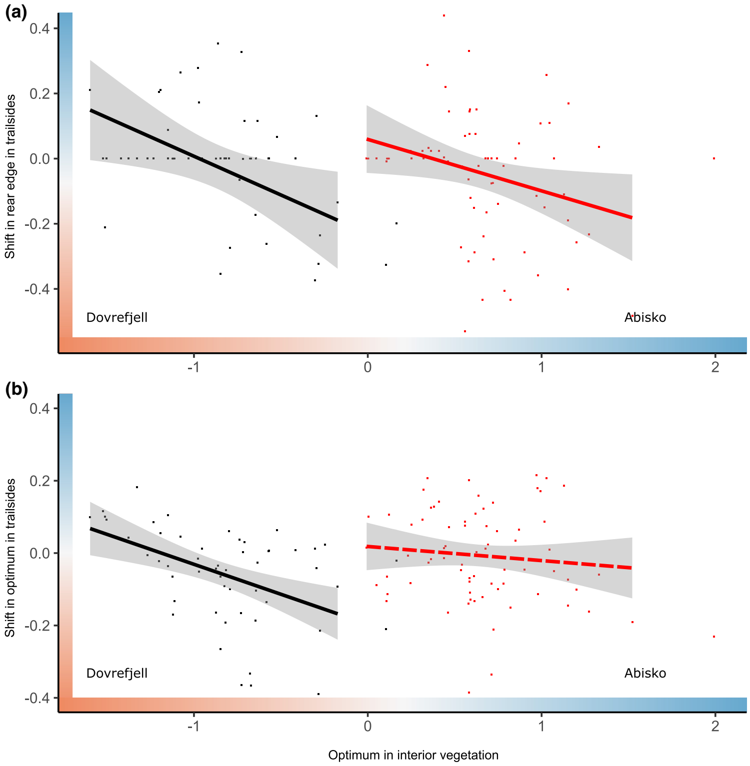


FIGURE 5 Predicted shifts between interior vegetation and trailsides (with 95% confidence intervals) in (a) rear edges and (b) optimum of species plotted against each species' optimum in the interior vegetation along the climatic gradient studied in the Dovrefjell ($n = 52$, black) and Abisko ($n = 72$, red) areas. Solid lines denote significance at $p < .05$. The colour gradient on the axes illustrates the climatic gradient from warmer (red) to colder (blue). Positive values on the x-axis correspond to harsher climate. Positive values on the y-axis represent shifts towards colder locations in trailsides

TABLE 1 Model parameters from linear models of shifts in climatic optimum, rear edge, leading edge, climatic range of vascular plant species in the trailside compared with the interior vegetation after removal of outliers in Dovrefjell ($n = 52$) and Abisko ($n = 72$), as a function of species' climatic optimum in the interior vegetation

	Dovrefjell				Abisko			
	Optimum	Rear edge	Leading edge	Amplitude	Optimum	Rear edge	Leading edge	Amplitude
Intercept	**0.00** (0.00)	**0.00** (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	−0.00 (0.00)
Optimum interior vegetation	**−0.17** (0.05)	**−0.24** (0.09)	−0.02 (0.09)	0.21 (0.14)	−0.04 (0.04)	**−0.16** (0.07)	0.04 (0.10)	0.20 (0.13)
n	52	52	52	52	72	72	72	72
Adj. R^2	0.19	0.09	−0.02	0.03	−0.00	0.05	0.00	0.02

Note: The standard error of coefficients is given in parentheses. Significance at the $p < .05$ level is denoted by bold lettering.

Monz, 2002), trailsides in the Scandes mountains had higher species richness than the surrounding vegetation. Trail effects appeared to have resulted in increased overlap in species' ranges due to transport to new locations and competitive release. Many alpine species shifted their rear edges and climatic optima towards warmer locations in trailsides. For lowland species' leading edges, no general shift was detected. Trailside plots close to introduction points and with fewer species in the interior vegetation had a larger increase in species number, and species gain was higher when the interior plot was dominated by herbaceous and lower in dwarf shrub-dominated vegetation. Altogether, this highlights that trails in the Scandes mountains provide plants with opportunities to shift realized niches, resulting in greater local plant species richness.

4.1 | Trails increase species richness

We observed a higher species richness in trailside plots than in the interior vegetation. An increased overlap in species' realized climatic niches along the climatic gradient contributed to this increase in species richness, with trails acting as conduits for seed transport and providing seedling establishment opportunities. Higher richness and expansion of alpine species' ranges towards lower elevation were also found along mountain roads in Scandinavia. There, roads led to a lower cover of *E. nigrum* and moss, which otherwise may inhibit germination and establishment (Lembrechts et al., 2014). Higher species richness along trails contrasts with other studies from cold ecosystems, all finding no or negative effects (Crisfield et al., 2012; Gremmen et al., 2003; Jägerbrand & Alatalo, 2015; Monz, 2002). However, we surveyed 16 trails extending more than 100 km and cutting through a variety of alpine communities, capturing the effects of trails on species richness across a larger spatial scale than previous studies. Our study emphasizes that the impact of trails on species richness should not be underestimated, especially when taking into consideration that trails often reach more remote and climatically extreme locations (Liedtke et al., 2020). While research has mostly focussed on the role of trails as corridors for the invasion of non-native species into mountain areas (e.g. Liedtke et al., 2020), we suggest that they also allow alpine species to colonize new locations.

4.2 | Climatic niche shifts along trails

Trails influenced the realized climatic niche of species. For alpine species, the expansion of their rear edge towards warmer locations is a sign of competitive release caused by disturbance (Chardon et al., 2019; Herrmann et al., 2021). Trailsides may thus potentially help preserve populations even under the condition of lowland plants moving into alpine habitats (Chardon et al., 2019). Corridors along trails could, therefore, act as temporary escape routes for alpine species such as *Harrimanella hypnoides*

TABLE 2 Direction of effect of factors retained in the best linear mixed model on change in species number between interior vegetation and trailside plots, and percentage of variance explained

Driver	Species gains ↑ or losses ↓ at trails relative to interior vegetation	Variance explained [%]
Distance to introduction point	↓	24.0
Interior vegetation species richness	↓	23.9
Vegetation cover	↑	9.5
Dwarf shrub cover	↓	9.4
Herb cover	↑	7.0
Gap index	↓	7.0
Disturbance extent	↑	4.9

Note: R^2 values on which the calculated variances are based and additional information regarding coefficients and shared variances can be found in Appendix S2: Tables S2.13 and S2.14.

and *Sibbaldia procumbens*, which prefer low-stature neighbours (Coker, 1966). However, as trailsides only comprise a small fraction of the total mountain area, it remains unclear how stable the observed changes in realized niche are over time, as they might be the result of source-sink dynamics (Lembrechts, Alexander et al., 2016). Overall, our observations of downward shifts of alpine plants with disturbance corroborate patterns found along trails in the Rocky mountains (Chardon et al., 2019), but expand those by relating rear-edge shifts of the whole community to their optimum along the climatic harshness gradient. Contrary to our expectations, lowland species' leading edges did not generally shift towards colder locations in trailsides. However, trails allowed lowland species to increase in abundance particularly in colder parts of their niche, which resulted in a shift of climatic optima towards colder locations. In contrast to our findings, mountain roads allowed native lowland species to expand their leading edges towards higher elevations in the same ecosystem (Lembrechts, Alexander et al., 2016). Our results suggest that many lowland species might (a) benefit less from disturbances by trails than alpine species (Le Roux et al., 2013), (b) have their leading edge detected at their true temperature limit as trails reached higher elevations than roads which might provide truncated climatic gradients, (c) might be insufficiently equipped to deal with additional stresses in the alpine zone such as drought and wind exposition or (d) that the disturbance intensity of trails in our research area was too weak to break down limiting biotic resistance at the upper range edge of lowland species (Graae et al., 2011; Lembrechts, Pauchard et al., 2016; Milbau et al., 2013).

We did, however, find that some species expanded their leading edges towards colder locations along trails. This included the trampling-resistant grass *Deschampsia cespitosa*. In Abisko we saw that, for example, the forbs *Cerastium cerastoides*, *Omalotheca supina*, *Oxyria digyna*, *Sibbaldia procumbens*, *Euphrasia frigida* and *Bartsia alpina* expanded from the sub-alpine belt towards the alpine zone. Many of these species are associated with snowbeds (Coker, 1966; Taylor & Rumsey, 2003; Totland & Schulte-Herbrüggen, 2003; Väre et al., 1997), which are moist environments; they may, therefore, be favoured by increases in moisture along trails resulting from soil compaction and funnelling of precipitation (Kuss, 1986; Tuomi et al., 2020), while, for example, *Cerastium cerastoides* and *Euphrasia frigida* are known to explicitly benefit from disturbances (Nyléhn & Totland, 1999; Totland & Schulte-Herbrüggen, 2003). This underlines that trails can allow disturbance-adapted species to move into colder locations.

4.3 | Where do trailsides gain species?

Characteristics of the recipient plant community influenced the gain of species in the trailside compared with the interior vegetation. In sites with species-poor interior vegetation, which in our study was dominated by graminoids like *Luzula arcuata*, *Carex bigelowii* and *Juncus trifidus*, the prostrate dwarf shrub *Salix herbacea*, the herb *Ranunculus glacialis* or by dwarf shrubs, trailsides gained more species, while in more species-rich sites frequently associated with meadows and willow shrub communities, trailsides gained fewer species. Decreasing establishment with higher diversity was also found by Olsen & Klanderud, 2014. Richer communities may already accommodate a broader range of niches than poorer ones due to higher in-site environmental variability, and thus the net effect of disturbance on niche availability might be weaker or even negative (Hofer et al., 2008; Palmer & Dixon, 1990). At similar levels of richness, a larger cover of herbaceous vegetation was associated with larger and more dwarf shrubs with smaller increases of species richness in trailsides. This corroborates experimental studies of establishment in different vegetation types after disturbance finding higher resistance of dwarf shrub heaths to colonization but greater invasibility of meadows dominated by herbaceous vegetation (Graae et al., 2011; Milbau et al., 2013; Opedal et al., 2021). Distance to the closest potential point of propagule introduction, such as ski lifts or trailheads, also had a strong effect, with a greater gain of species in trailsides close to introduction points concurring with findings of Pickering et al., 2007. The fact that t function as corridors for colonization in alpine ecosystems aligns with their role played in other ecosystems such as coniferous mountain forests in North America (Benninger-Truax et al., 1992).

Disturbance is known to create microsites for germinations and subsequent establishment also in alpine systems (e.g. Lembrechts, Pauchard, et al., 2016). However, under harsh climatic conditions the establishment in large gaps could be too difficult for successful establishment, as theoretically predicted by Lembrechts et al. (2015). Our findings lend careful support to this prediction, as richness in trailsides increased less in plots with larger gaps yet was positively associated with a larger area over which disturbance was spread.

5 | CONCLUSION

While disturbance and trampling on paths evidently suppress plants, our findings demonstrate that trailsides may also offer opportunities for alpine species, weaker competitors and disturbance-associated species, through competitive release and propagule transport. Changes in species ranges along trails increased plant diversity in trailsides in our study, which underscores their importance as corridors of colonization for notably weaker competitors and alpine species. As communities showed differential reactions to disturbances along trails, a further integration of such field findings into management is called for in the planning of trails. However, the species richness enhancing effects of trails should be considered in a broader perspective, as disturbances may also destroy rare communities or rare and trampling-sensitive species. In this context, species- and region-specific understanding of trail effects is required.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.17040770.

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BIOSKETCH

The research team is part of the Mountain Invasions Research Network (MIREN), which aims to understand the effects of global change drivers such as climate and land-use change on species' distributions and biodiversity in mountainous areas. We perform observational and experimental studies along elevation gradients to evaluate and quantify the processes and mechanisms that shape mountain plant communities at regional to global scales. One part of our focus is evaluating the effects of trails on plant communities in mountains around the globe. More information about our work in Scandinavia can be found on the MIREN trails Scandinavia webpage.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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Appendix I -Methods

Hiking trails shift plant species' occupied climatic niches and locally increase species richness. Ronja E. M. Wedegärtner et al., 2021. *Diversity and Distributions*.

Cover estimates

Cover of the total vascular vegetation, herbaceous cover, and dwarf shrub cover were estimated per 2 x 10 m plot in the field and classified according to the following cover classes:

0 = none
1 = 1 %
2 = 1 - <=5 %
3 = 5 > - <=25 %
4 = 25 > - <=50 %
5 = 50 > - <=75 %
6 = 75 > - <=95 %
7 = 95 > - <=99 %
8 = 99 > - <=100 %

Downscaling of climate data

Data were prepared for downscaling in R 3.5.2 (R Core Team 2018) using the *raster* package (Hijmans et al. 2020).

We downloaded annual mean temperature, maximum temperature of the warmest month, and minimum temperature of the coldest month for the time period 1979-2013 from the CHELSA database (Dirk N. Karger et al., 2018; Dirk Nikolaus Karger et al., 2017) at a resolution of 30 arcseconds. For each region we obtained high resolution digital elevation models (DEMs) using the elevatr package (Hollister and Shah 2017) at 1.2 arcsecond resolution which corresponds to approximately 30 m at this latitude.

We derived the topographic variables from the high resolution DEMs in R and calculated the potential incoming solar radiation for each grid cell of the DEM for the four representative days (equinoxes and solstices) with a six-hour resolution using the SAGA GIS 6.3.0 tool Potential Incoming Solar Radiation (Conrad et al. 2015). Distance from the ocean was downloaded from http://www.soest.hawaii.edu/pwessel/gshhg/ at 1 arcmin resolution (Wessel and Smith 2017). Downscaling was based on a Geographically Weighted Regression (GWR) approach (Lu, Charlton, & Fotheringham, 2011) as outlined by Lenoir et al. (2017) using elevation, slope, northness, eastness, distance from the ocean and potential solar radiation as predictor variables.

The downscaling was performed on resources provided by the NTNU IDUN/EPIC computing cluster (Själander, Jahre, Tufte, & Reissmann, 2019) using R 3.6.0 and the *spgwr* package (Bivand & Yu, 2017). Missing data due to omission of missing predictor values were interpolated using the Close Gaps tool of SAGA.

Gap index

To estimate the gradient of mechanical disturbances in the plots of the T-transect all gaps were mapped. Gaps in this context are clearly delineated areas of bare ground, that are therefore a competitor free space (Bullock, 2000). A 10 m measuring tape was placed along the middle of each 10 x 2 m plot and we counted the number of clearly delineated gaps that it intersected. At up to five randomly predetermined distances along the tape we measured the nearest intersected gap. Gaps were measured at their greatest (a) extent and perpendicular to this at their maximal extent (b). The size of the gap was roughly estimated using the formula to calculate the area of an ellipsoid ($a*b\pi$). We calculated the gap index as approximate estimate of trampling by multiplying mean gap area by the number of gaps encountered along the tape transect.

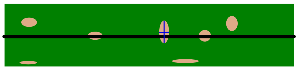

Figure S1: A 2 x 10 m plot (not to scale) with gaps in brown and the transect walked to count and measure gaps in black. Gaps were measured as indicated by the blue lines and the mean gap area was calculated.

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Appendix 2

Hiking trails shift plant species' occupied climatic niches and locally increase species richness. Ronja E. M. Wedegärtner et al., 2021. *Diversity and Distributions*.

Raw data are available on figshare. DOI: 10.6084/m9.figshare.17040770.

Table S2.1: Pearson correlations between downscaled climatic data in the 2 research areas. Bold: ($p < 0.01$)

	Bio1	**Bio5**	**Bio6**
Bio1	**1**	**0.72**	**0.91**
Bio5		1	**0.38**
Bio6			1

Table S2.2: List of species found in Dovrefjell transects with the total number of occurrences in all plots, the number of occurrences in the trailside, but not in the interior vegetation (gained), the number of occurrences in the interior vegetation, but not in the trailside (lost), the netto and percent change between trailside and interior vegetation plots, and the red list category (NA= not applicable, LC 0 Least concern, NT= nearly threatened) according to the Norwegian Red List (2020).

Species	**Total**	**Gained**	**Lost**	**Netto**	**Percent change**	**Red list category**
Achillea millefolium	15	7	0	7	47	LC
Achnatherum calamagrostis	1	1	0	1	100	NA
Aconitum lycoctonum	16	3	5	-2	-13	NA
Agrostis capillaris	18	6	1	5	28	LC
Agrostis mertensii	8	4	0	4	50	LC
Alchemilla alpina	7	3	3	0	0	LC
Alnus incana	2	NA	NA	NA	NA	LC
Alopecurus pratensis	1	1	0	1	100	LC
Andromeda polifolia	3	2	0	2	67	LC
Antennaria dioica	29	19	3	16	55	LC
Anthoxanthum nipponicum	37	13	8	5	14	LC
Anthriscus sylvestris	2	2	0	2	100	LC
Arabis alpina	1	NA	NA	NA	NA	LC
Arctostaphylos alpinus	23	14	2	12	52	NA
Arctostaphylos uva-ursi	20	9	4	5	25	LC
Astragalus alpinus	19	9	5	4	21	LC
Astragalus frigidus	6	2	3	-1	-17	LC
Avenella flexuosa	44	4	14	-10	-23	LC
Avenula pubescens	4	1	2	-1	-25	LC
Bartsia alpina	19	9	4	5	26	LC

Betula nana	58	4	5	-1	-2	LC
Betula pubescens	26	6	4	2	8	LC
Bistorta vivipara	51	22	5	17	33	LC
Botrychium lunaria	3	3	0	3	100	LC
Calluna vulgaris	10	5	0	5	50	LC
Caltha palustris	1	NA	NA	NA	NA	LC
Campanula rotundifolia	37	19	3	16	43	LC
Carex atrata	1	1	0	1	100	LC
Carex atrofusca	1	0	1	-1	-100	LC
Carex bigelowii	60	13	6	7	12	LC
Carex brunnescens	3	1	2	-1	-33	LC
Carex canescens	1	0	1	-1	-100	LC
Carex capillaris	4	4	0	4	100	LC
Carex capitata	2	1	1	0	0	LC
Carex dioica	1	0	1	-1	-100	LC
Carex ericetorum	3	2	1	1	33	LC
Carex flava	1	1	0	1	100	LC
Carex limosa	1	0	1	-1	-100	LC
Carex mackenziei	2	1	1	0	0	LC
Carex macloviana	2	1	0	1	50	LC
Carex media	1	0	1	-1	-100	LC
Carex microglochin	1	1	0	1	100	LC
Carex myosuroides	2	2	0	2	100	NA
Carex nigra	4	2	1	1	25	LC
Carex pallescens	2	0	1	-1	-50	LC
Carex panicea	1	NA	NA	NA	NA	LC
Carex rupestris	2	1	1	0	0	LC
Carex saxatilis	3	2	1	1	33	LC
Carex simpliciuscula	1	1	0	1	100	NA
Carex stenolepis	1	0	1	-1	-100	NA
Carex vaginata	19	8	3	5	26	LC
Cerastium alpinum	10	4	5	-1	-10	LC
Cerastium fontanum	9	6	0	6	67	LC
Chamorchis alpina	1	1	0	1	100	LC
Cherleria biflora	1	1	0	1	100	NA
Circaea alpina	1	0	1	-1	-100	LC
Cirsium helenioides	1	0	1	-1	-100	NA
Comarum palustre	1	NA	NA	NA	NA	LC
Dactylorhiza viridis	3	2	1	1	33	NA
Deschampsia atropurpurea	1	0	1	-1	-100	NA
Deschampsia cespitosa	32	12	2	10	31	LC
Diapensia lapponica	3	1	1	0	0	LC
Diphasiastrum alpinum	6	0	5	-5	-83	LC
Draba incana	1	1	0	1	100	LC
Draba lactea	1	1	0	1	100	NT
Draba norvegica	1	1	0	1	100	LC

Dryas octopetala	1	NA	NA	NA	NA	LC
Empetrum nigrum	65	8	2	6	9	LC
Epilobium angustifolium	7	4	2	2	29	NA
Epilobium davuricum	1	0	1	-1	-100	LC
Epilobium lactiflorum	1	0	1	-1	-100	LC
Epilobium latifolium	1	1	0	1	100	NA
Equisetum arvense	13	2	5	-3	-23	LC
Equisetum hyemale	1	0	1	-1	-100	LC
Equisetum palustre	1	0	1	-1	-100	LC
Equisetum pratense	7	4	1	3	43	LC
Equisetum sylvaticum	1	NA	NA	NA	NA	LC
Equisetum variegatum	2	1	1	0	0	LC
Erigeron uniflorus	2	NA	NA	NA	NA	LC
Eriophorum angustifolium	2	1	1	0	0	LC
Eriophorum vaginatum	1	0	1	-1	-100	LC
Euphrasia alpina	1	1	0	1	100	NA
Euphrasia frigida	19	11	2	9	47	NA
Euphrasia stricta	7	4	0	4	57	LC
Festuca ovina	58	11	6	5	9	LC
Festuca rubra	14	9	2	7	50	LC
Festuca vivipara	1	0	1	-1	-100	LC
Filipendula ulmaria	6	0	5	-5	-83	LC
Fragaria vesca	3	0	1	-1	-33	LC
Galium boreale	21	4	4	0	0	LC
Galium uliginosum	7	3	1	2	29	LC
Galium verum	2	1	0	1	50	LC
Gentiana nivalis	1	NA	NA	NA	NA	LC
Gentianella amarella	2	2	0	2	100	LC
Geranium sylvaticum	19	3	2	1	5	LC
Geum rivale	6	2	3	-1	-17	LC
Glechoma hederacea	1	1	0	1	100	LC
Gymnocarpium brittonianum	4	0	3	-3	-75	NA
Harrimanella hypnoides	12	5	1	4	33	LC
Hieracium alpinum	19	8	2	6	32	NA
Hieracium umbrosum	2	2	0	2	100	NA
Huperzia selago	7	2	4	-2	-29	LC
Juncus alpinoarticulatus	1	1	0	1	100	LC
Juncus arcticus	1	1	0	1	100	LC
Juncus filiformis	1	0	1	-1	-100	LC
Juncus trifidus	50	18	2	16	32	LC
Juncus triglumis	5	4	1	3	60	LC
Juniperus communis	41	3	5	-2	-5	LC
Kalmia procumbens	25	11	2	9	36	LC
Knautia arvensis	2	0	2	-2	-100	LC
Linnaea borealis	5	0	2	-2	-40	LC
Lotus corniculatus	2	2	0	2	100	LC

Luzula arcuata	16	4	4	0	0	LC
Luzula multiflora	29	16	4	12	41	LC
Luzula spicata	21	7	3	4	19	LC
Luzula sudetica	4	0	1	-1	-25	LC
Luzula sylvatica	10	0	3	-3	-30	LC
Lycopodium clavatum	6	1	3	-2	-33	LC
Lysimachia europaea	32	5	10	-5	-16	LC
Maianthemum bifolium	5	0	3	-3	-60	LC
Melampyrum carpathicum	16	3	5	-2	-13	NA
Melica nutans	4	0	3	-3	-75	LC
Micranthes stellaris	2	1	1	0	0	LC
Milium effusum	2	0	2	-2	-100	LC
Moneses uniflora	1	0	1	-1	-100	LC
Myosotis decumbens	12	3	3	0	0	LC
Nardus stricta	8	5	2	3	38	LC
Neottia cordata	1	1	0	1	100	NA
Omalotheca norvegica	4	3	0	3	75	LC
Omalotheca supina	12	9	0	9	75	LC
Orthilia secunda	2	0	2	-2	-100	LC
Oxalis acetosella	9	1	2	-1	-11	LC
Oxyria digyna	2	0	1	-1	-50	LC
Oxytropis lapponica	4	3	1	2	50	LC
Paris quadrifolia	1	1	0	1	100	LC
Parnassia palustris	7	5	1	4	57	LC
Pedicularis lapponica	14	3	4	-1	-7	LC
Pedicularis oederi	25	8	9	-1	-4	LC
Phleum alpinum	14	8	0	8	57	LC
Phyllodoce caerulea	30	9	8	1	3	LC
Pilosella lactucella	3	1	0	1	33	LC
Pimpinella saxifraga	1	1	0	1	100	LC
Pinguicula vulgaris	9	4	4	0	0	LC
Pinus sylvestris	6	2	4	-2	-33	LC
Plantago major	2	2	0	2	100	LC
Plantago media	2	2	0	2	100	LC
Poa alpina	14	10	1	9	64	LC
Poa nemoralis	2	0	1	-1	-50	LC
Poa pratensis	9	3	1	2	22	LC
Poa supina	2	2	0	2	100	NA
Polygonatum verticillatum	1	1	0	1	100	LC
Potentilla crantzii	16	9	5	4	25	LC
Potentilla erecta	5	3	1	2	40	LC
Potentilla virgata	1	1	0	1	100	NA
Primula scandinavica	1	0	1	-1	-100	LC
Prunella vulgaris	8	6	1	5	63	LC
Prunus padus	2	0	1	-1	-50	LC
Pseudorchis albida	1	0	1	-1	-100	NT

Pulsatilla vernalis	8	5	2	3	38	LC
Pyrola media	4	0	2	-2	-50	LC
Pyrola minor	8	3	2	1	13	LC
Pyrola rotundifolia	5	1	2	-1	-20	LC
Ranunculus acris	23	10	2	8	35	LC
Ranunculus glacialis	1	NA	NA	NA	NA	NT
Ranunculus repens	1	NA	NA	NA	NA	LC
Rhinanthus minor	14	12	2	10	71	LC
Rhodiola rosea	8	4	3	1	13	LC
Ribes spicatum	1	0	1	-1	-100	LC
Rubus chamaemorus	2	1	1	0	0	LC
Rubus parvifolius	3	1	1	0	0	NA
Rubus saxatilis	7	0	6	-6	-86	LC
Rumex acetosa	19	4	6	-2	-11	LC
Rumex acetosella	3	3	0	3	100	LC
Salix arbuscula	7	5	1	4	57	LC
Salix caprea	1	0	1	-1	-100	LC
Salix glauca	39	12	9	3	8	LC
Salix hastata	4	1	1	0	0	LC
Salix herbacea	42	20	2	18	43	LC
Salix lanata	12	6	2	4	33	LC
Salix lapponum	35	9	13	-4	-11	LC
Salix myrsinifolia	8	3	0	3	38	LC
Salix myrsinites	6	2	1	1	17	LC
Salix pentandra	1	1	0	1	100	LC
Salix phylicifolia	5	3	0	3	60	LC
Salix polaris	6	4	2	2	33	LC
Salix reticulata	12	6	1	5	42	LC
Saussurea alpina	30	6	8	-2	-7	LC
Saxifraga aizoides	5	2	3	-1	-20	LC
Saxifraga cespitosa	1	1	0	1	100	LC
Saxifraga oppositifolia	4	2	2	0	0	LC
Scorzoneroides autumnalis	18	15	0	15	83	LC
Selaginella selaginoides	13	10	0	10	77	LC
Sibbaldia procumbens	14	7	4	3	21	LC
Silene acaulis	13	4	5	-1	-8	LC
Silene dioica	8	3	4	-1	-13	LC
Silene suecica	2	1	1	0	0	NA
Solidago virgaurea	31	5	4	1	3	LC
Spinulum annotinum	8	2	6	-4	-50	NA
Stellaria borealis	1	1	0	1	100	LC
Stellaria graminea	5	1	2	-1	-20	LC
Stellaria nemorum	1	NA	NA	NA	NA	LC
Thalictrum alpinum	22	8	5	3	14	LC
Tofieldia pusilla	7	5	2	3	43	LC
Trifolium pratense	3	3	0	3	100	LC

Trifolium repens	14	10	0	10	71	LC
Tussilago farfara	1	0	1	-1	-100	LC
Urtica dioica	4	1	3	-2	-50	LC
Vaccinium myrtillus	40	8	15	-7	-18	LC
Vaccinium uliginosum	48	15	7	8	17	LC
Vaccinium vitis-idaea	67	3	4	-1	-1	LC
Valeriana officinalis	1	1	0	1	100	NT
Veronica alpina	6	1	2	-1	-17	LC
Veronica fruticans	1	1	0	1	100	LC
Veronica officinalis	4	3	1	2	50	LC
Veronica serpyllifolia	4	3	1	2	50	LC
Vicia cracca	4	1	1	0	0	LC
Vicia sepium	1	0	1	-1	-100	LC
Viola biflora	21	2	5	-3	-14	LC
Viola canina	3	0	1	-1	-33	LC
Viola palustris	2	0	1	-1	-50	LC
Viola riviniana	1	NA	NA	NA	NA	LC

Table S2.3: List of species found in Abisko transects with the total number of occurrences in all plots, the number of ocurrences in the trailside, but not in the interior vegetation (gained), the number of occurrences in the interior vegetation, but not in the trailside (lost), the netto and percent change between trailside and interior vegetation plots, and the red list category (NA= not applicable, LC 0 Least concern, NT= nearly threatened) according to the Swedish Red List (2015).

Species	**Total**	**Gained**	**Lost**	**Netto**	**Percent change**	**Red list category**
Achillea millefolium	6	4	1	3	50	NA
Agrostis capillaris	17	12	2	10	59	NA
Agrostis mertensii	28	21	3	18	64	NA
Andromeda polifolia	5	3	1	2	40	NA
Angelica archangelica	17	2	6	-4	-24	NA
Antennaria alpina	22	8	3	5	23	NA
Anthoxanthum monticola	4	0	2	-2	-50	NA
Anthoxanthum nitens	1	NA	NA	NA	NA	NA
Anthoxanthum odoratum	45	10	6	4	9	NA
Anthriscus sylvestris	2	NA	NA	NA	NA	NA
Arabidopsis arenosa subsp. arenosa	1	1	0	1	100	NA
Arabis alpina	9	4	4	0	0	NA
Arctostaphylos alpinus	17	6	5	1	6	NA
Asplenium viride	1	1	0	1	100	NA
Astragalus alpinus	38	10	9	1	3	NA
Avenella flexuosa	45	8	7	1	2	NA
Bartsia alpina	35	12	6	6	17	NA
Betula nana	44	5	3	2	5	NA
Betula pubescens	31	4	3	1	3	NA
Bistorta vivipara	70	25	3	22	31	NA

Botrychium lunaria	3	3	0	3	100	NT
Calamagrostis lapponica	32	6	8	-2	-6	NA
Calamagrostis purpurea	4	0	4	-4	-100	NA
Calamagrostis stricta	6	2	2	0	0	NA
Campanula rotundifolia	6	2	3	-1	-17	NA
Cardamine bellidifolia	10	6	3	3	30	NA
Cardamine pratensis	1	0	1	-1	-100	NA
Carex aquatilis	1	0	1	-1	-100	NA
Carex atrata	15	7	4	3	20	NA
Carex bigelowii	67	21	9	12	18	NA
Carex buxbaumii	1	0	1	-1	-100	NA
Carex canescens	1	0	1	-1	-100	NA
Carex capillaris	1	NA	NA	NA	NA	NA
Carex crassiflora	9	8	0	8	89	NA
Carex dioica	1	0	1	-1	-100	NA
Carex echinata	1	1	0	1	100	NA
Carex hartmanii	1	1	0	1	100	VU
Carex lachenalii	28	18	2	16	57	NA
Carex lapponica	3	3	0	3	100	NA
Carex limosa	3	1	1	0	0	NA
Carex mackenziei	18	10	4	6	33	NA
Carex panicea	1	1	0	1	100	NA
Carex parallela	5	2	1	1	20	NA
Carex vaginata	12	2	9	-7	-58	NA
Cassiope tetragona	23	6	3	3	13	NA
Cerastium alpinum	14	6	4	2	14	NA
Cerastium arcticum	7	5	1	4	57	NA
Cerastium cerastoides	17	10	5	5	29	NA
Cerastium fontanum	8	4	3	1	13	NA
Cherleria biflora	1	1	0	1	100	NA
Cirsium helenioides	3	1	2	-1	-33	NA
Corallorhiza trifida	1	0	1	-1	-100	NA
Cornus suecica	14	2	5	-3	-21	NA
Cystopteris montana	2	0	2	-2	-100	NA
Cystopteris montserratii	1	1	0	1	100	NA
Dactylorhiza viridis	1	0	1	-1	-100	NA
Deschampsia cespitosa	38	22	3	19	50	NA
Diapensia lapponica	20	7	6	1	5	NA
Diphasiastrum alpinum	10	2	8	-6	-60	NA
Draba nivalis	1	1	0	1	100	NA
Dryas octopetala	10	3	1	2	20	NA
Eleocharis macrostachya	1	0	1	-1	-100	NA
Elymus alaskanus	1	0	1	-1	-100	NA
Elymus caninus	2	2	0	2	100	NA
Elymus mutabilis	1	0	1	-1	-100	NA
Elymus repens	1	1	0	1	100	NA

Empetrum nigrum	77	14	10	4	5	NA
Epilobium anagallidifolium	5	2	2	0	0	NA
Epilobium angustifolium	15	5	3	2	13	NA
Epilobium hornemannii	3	1	2	-1	-33	NA
Equisetum palustre	5	3	1	2	40	NA
Equisetum pratense	43	7	8	-1	-2	NA
Equisetum scirpoides	4	1	0	1	25	NA
Equisetum sylvaticum	1	0	1	-1	-100	NA
Equisetum variegatum	16	5	5	0	0	NA
Erigeron uniflorus	9	5	2	3	33	NA
Eriophorum angustifolium	4	4	0	4	100	NA
Eriophorum scheuchzeri	2	2	0	2	100	NA
Euphrasia frigida	25	11	7	4	16	NA
Euphrasia stricta	5	3	1	2	40	NA
Festuca ovina	23	9	5	4	17	NA
Festuca rubra	28	14	7	7	25	NA
Festuca vivipara	32	10	3	7	22	NA
Gentiana nivalis	16	11	1	10	63	NA
Geranium sylvaticum	18	5	6	-1	-6	NA
Geum rivale	1	0	1	-1	-100	NA
Gymnadenia conopsea	1	NA	NA	NA	NA	NA
Gymnocarpium brittonianum	10	1	6	-5	-50	NA
Harrimanella hypnoides	39	10	10	0	0	NA
Huperzia selago	26	6	15	-9	-35	NA
Juncus alpinoarticulatus	1	1	0	1	100	NA
Juncus arcticus	3	3	0	3	100	NA
Juncus biglumis	2	1	1	0	0	NA
Juncus filiformis	1	1	0	1	100	NA
Juncus trifidus	48	21	6	15	31	NA
Juncus triglumis	3	2	0	2	67	NA
Juniperus communis	13	2	6	-4	-31	NA
Kalmia procumbens	23	11	8	3	13	NA
Leontodon hispidus	2	0	1	-1	-50	NT
Linnaea borealis	21	4	5	-1	-5	NA
Luzula alopecurus	2	1	0	1	50	NA
Luzula arcuata	36	13	6	7	19	NA
Luzula multiflora	32	18	6	12	38	NA
Luzula spicata	19	12	4	8	42	NA
Luzula wahlenbergii	2	2	0	2	100	NA
Lycopodium clavatum	12	1	9	-8	-67	NA
Lysimachia europaea	20	8	4	4	20	NA
Melampyrum carpathicum	13	1	6	-5	-38	NA
Melampyrum pratense	5	2	2	0	0	NA
Melica nutans	1	1	0	1	100	NA
Menyanthes trifoliata	2	0	1	-1	-50	NA
Micranthes foliolosa	1	0	1	-1	-100	NA

Micranthes stellaris	10	6	4	2	20	NA
Milium effusum	5	0	4	-4	-80	NA
Moneses uniflora	5	2	1	1	20	NA
Myosotis decumbens	8	0	5	-5	-63	NA
NA	1	NA	NA	NA	NA	NA
Neottia cordata	1	1	0	1	100	NA
Omalotheca norvegica	16	12	1	11	69	NA
Omalotheca supina	39	26	2	24	62	NA
Orthilia secunda	2	0	2	-2	-100	NA
Oxyria digyna	21	11	4	7	33	NA
Parnassia palustris	25	10	3	7	28	NA
Pedicularis hirsuta	3	0	3	-3	-100	NA
Pedicularis lapponica	27	9	9	0	0	NA
Petasites frigidus	3	2	1	1	33	NA
Phegopteris connectilis	1	1	0	1	100	NA
Phleum alpinum	42	25	5	20	48	NA
Phyllodoce caerulea	49	13	13	0	0	NA
Pinguicula alpina	4	1	3	-2	-50	NA
Pinguicula vulgaris	8	7	1	6	75	NA
Plantago major	1	1	0	1	100	NA
Platanthera obtusata	1	1	0	1	100	EN
Poa alpigena	10	4	2	2	20	NA
Poa alpina	43	17	5	12	28	NA
Poa annua	16	16	0	16	100	NA
Poa palustris	2	0	2	-2	-100	NA
Poa pratensis	4	1	2	-1	-25	NA
Poa pratensis subsp. pratensis	1	1	0	1	100	NA
Potentilla crantzii	27	9	6	3	11	NA
Pyrola minor	34	12	12	0	0	NA
Pyrola rotundifolia	1	1	0	1	100	NA
Ranunculus acris	33	15	3	12	36	NA
Ranunculus glacialis	9	3	1	2	22	NA
Ranunculus nivalis	7	6	0	6	86	NA
Ranunculus pygmaeus	1	1	0	1	100	NA
Ranunculus sulphureus	4	2	1	1	25	VU
Rhinanthus minor	6	6	0	6	100	NA
Rhodiola rosea	7	3	3	0	0	NA
Rhododendron lapponicum	1	0	1	-1	-100	NA
Rubus chamaemorus	6	1	1	0	0	NA
Rubus saxatilis	8	1	4	-3	-38	NA
Rumex acetosa	37	10	8	2	5	NA
Sagina caespitosa	1	1	0	1	100	NT
Sagina nivalis	4	3	1	2	50	NA
Sagina saginoides	14	9	4	5	36	NA
Salix arbuscula	26	13	5	8	31	NA
Salix caprea	5	0	4	-4	-80	NA

Salix glauca	18	6	9	-3	-17	NA
Salix hastata	29	12	10	2	7	NA
Salix herbacea	58	11	7	4	7	NA
Salix lanata	35	14	3	11	31	NA
Salix lapponum	46	16	12	4	9	NA
Salix myrsinifolia	6	5	1	4	67	NA
Salix myrsinites	5	0	4	-4	-80	NA
Salix phylicifolia	14	8	2	6	43	NA
Salix polaris	22	8	4	4	18	NA
Salix reticulata	22	7	6	1	5	NA
Saussurea alpina	44	4	16	-12	-27	NA
Saxifraga aizoides	11	5	4	1	9	NA
Saxifraga cernua	6	3	3	0	0	NA
Saxifraga oppositifolia	7	6	0	6	86	NA
Scorzoneroides autumnalis	1	0	1	-1	-100	NA
Selaginella selaginoides	23	8	4	4	17	NA
Sibbaldia procumbens	31	17	4	13	42	NA
Silene acaulis	29	11	6	5	17	NA
Silene apetala	1	1	0	1	100	NA
Silene dioica	10	1	4	-3	-30	NA
Silene suecica	1	0	1	-1	-100	NA
Solidago virgaurea	58	16	9	7	12	NA
Sorbus aucuparia	10	3	4	-1	-10	NA
Spinulum annotinum	14	7	3	4	29	NA
Stellaria borealis	9	1	4	-3	-33	NA
Stellaria graminea	1	1	0	1	100	NA
Stellaria nemorum	3	0	3	-3	-100	NA
Thalictrum alpinum	30	6	7	-1	-3	NA
Tofieldia pusilla	12	10	1	9	75	NA
Trifolium pratense	2	2	0	2	100	NA
Trifolium repens	3	3	0	3	100	NA
Tripleurospermum subpolare	1	1	0	1	100	NA
Trisetum spicatum	24	16	3	13	54	NA
Trollius europaeus	24	4	6	-2	-8	NA
Tussilago farfara	5	3	1	2	40	NA
Vaccinium myrtillus	46	8	10	-2	-4	NA
Vaccinium uliginosum	56	11	13	-2	-4	NA
Vaccinium vitis-idaea	69	9	13	-4	-6	NA
Veronica alpina	29	14	0	14	48	NA
Viola biflora	47	8	12	-4	-9	NA

Table S2.4: Results of two-sided Wilcoxon post-hoc test for differences in species richness between distances from trail with n = 174 for all groups and Bonferroni adjusted p values.

Estimate	**Group 1**	**Group 2**	***W***	**Conf. lower**	**Conf. higher**	**Adjusted *p*-value**
3.0	N	M	17056.5	0.0	5.0	0.123
4.0	N	F	17811	1.0	6.0	0.013
1.0	M	F	15894.5	-1.0	3.0	1

Table S2.5: Results of two-sided Wilcoxon post-hoc test for differences in species gains and losses in trailside and mid-distance plots, compared to the interior vegetation plots between distances from trail with n = 174 for all groups and Bonferroni adjusted p values.

Estimate	**Group 1**	**Group 2**	***W***	**Conf. lower**	**Conf. higher**	**Adjusted *p*-value**
2.0	gained_T	gained_M	12507.5	1.0	3.0	<0.01
2.0	gained_M	lost_M	18647.5	1.0	3.0	<0.01
1.0	gained_M	lost_T	17482	0.0	2.0	0.23
3.0	gained_T	lost_T	20458.5	2.0	4.0	<0.01
-1.0	lost_M	lost_T	14157	-1.0	0.0	0.91

Table S2.6: Model parameters of the best GLMM (Family Poisson) for species richness along hiking trails with 526 observations, and transect nested in trail as random term (transect:trail, 177; trail, 16).

	Estimate	**Std. Error**	***z* value**	**Pr(>|z|)**	**Variance explained [%]**
Intercept	-0.47	0.84	-0.56	**0.58**	
Climatic harshness	-1.06	0.25	-4.18	**< 0.001**	55
Plot M	-0.13	0.02	-5.57	**< 0.001**	9
Plot F	-0.19	0.02	-8.01	**< 0.001**	
Distance introduction	-0.05	0.06	-0.8	0.42	10
Region (Norway)	-0.63	0.22	-2.85	**0.004**	1
Plot M: Dist. intro	0.06	0.03	2.35	**0.02**	
Plot F: Dist. intro	0.11	0.03	4.35	**< 0.001**	

Table S2.7: Partitioning of variance. Fixed and Full R^2 are shown for the best model and sub-models with all variables separately and models with specific variables excluded. The variance percentage is calculated based on the fixed R^2 for the model with only the specific variable ('factor'), for the model without that focal variable ('other'), and shared variance ('shared').

Model	**Fixed R^2**	**Full R^2**
Best	0.17	0.88
Climate only	0.16	0.9
Plot only	0.02	0.9
Distance to introduction only	0.05	0.89
Area only	0.01	0.89

No climate	0.08	0.89	
No plot	0.15	0.88	
No distance to introduction	0.17	0.88	
No area	0.15	0.9	
Model	**Factor**	**Shared**	**Other**
Climate	0.55	0.42	0.03
Plot	0.09	0.01	0.91
Distance to introduction	0.01	0.31	0.67
Area	0.1	-0.07	0.97

Table S2.8: Shifts of rear edges in trailside plots compared to the interior vegetation in Abisko and Dovrefjell.

Dovrefjell			**Abisko**		
no shift	**warmer**	**colder**	**no shift**	**warmer**	**colder**
Achillea millefolium	*Arctostaphylos alpinus*	*Aconitum lycoctonum*	*Anthoxanthum odoratum*	*Agrostis mertensii*	*Angelica archangelica*
Agrostis capillaris	*Bartsia alpina*	*Antennaria dioica*	*Avenella flexuosa*	*Antennaria alpina*	*Carex atrata*
Anthoxanthum nipponicum	*Betula nana*	*Arctostaphylos uva-ursi*	*Betula nana*	*Arctostaphylos alpinus*	*Carex bigelowii*
Astragalus alpinus	*Carex vaginata*	*Geranium sylvaticum*	*Betula pubescens*	*Astragalus alpinus*	*Cerastium alpinum*
Avenella flexuosa	*Deschampsia cespitosa*	*Kalmia procumbens*	*Bistorta vivipara*	*Bartsia alpina*	*Deschampsia cespitosa*
Betula pubescens	*Harrimanella hypnoides*	*Lysimachia europaea*	*Cerastium cerastoides*	*Calamagrostis lapponica*	*Diapensia lapponica*
Bistorta vivipara	*Hieracium alpinum*	*Melampyrum carpathicum*	*Cornus suecica*	*Carex lachenalii*	*Dryas octopetala*
Campanula rotundifolia	*Juncus trifidus*	*Myosotis decumbens*	*Festuca ovina*	*Carex mackenziei*	*Epilobium angustifolium*
Carex bigelowii	*Luzula arcuata*	*Pedicularis oederi*	*Geranium sylvaticum*	*Cassiope tetragona*	*Equisetum pratense*
Empetrum nigrum	*Luzula spicata*	*Phyllodoce caerulea*	*Juniperus communis*	*Empetrum nigrum*	*Equisetum variegatum*
Equisetum arvense	*Pedicularis lapponica*	*Potentilla crantzii*	*Linnaea borealis*	*Euphrasia frigida*	*Huperzia selago*
Euphrasia frigida	*Salix herbacea*	*Rumex acetosa*	*Lysimachia europaea*	*Festuca rubra*	*Luzula spicata*
Festuca ovina	*Salix lapponum*	*Saussurea alpina*	*Melampyrum carpathicum*	*Festuca vivipara*	*Potentilla crantzii*
Galium boreale	*Sibbaldia procumbens*	*Silene acaulis*	*Poa alpigena*	*Harrimanella hypnoides*	*Pyrola minor*
Juniperus communis	*Thalictrum alpinum*		*Poa alpina*	*Juncus trifidus*	*Rumex acetosa*
Luzula multiflora			*Ranunculus glacialis*	*Kalmia procumbens*	*Salix glauca*
Luzula sylvatica			*Salix lanata*	*Luzula arcuata*	*Salix hastata*
Oxalis acetosella				*Luzula multiflora*	*Salix herbacea*
Phleum alpinum				*Omalotheca supina*	*Salix lapponum*
Poa pratensis				*Oxyria digyna*	*Salix phylicifolia*

Ranunculus acris	Parnassia palustris	Salix reticulata
Salix glauca	Pedicularis lapponica	Saussurea alpina
Salix lanata	Phleum alpinum	Selaginella selaginoides
Salix reticulata	Phyllodoce caerulea	Silene dioica
Solidago virgaurea	Ranunculus acris	Solidago virgaurea
	Salix arbuscula	
	Salix polaris	
	Saxifraga aizoides	
	Sibbaldia procumbens	
	Silene acaulis	
	Sorbus aucuparia	

Table S2.9: Shifts of optima in trailside plots compared to the interior vegetation in Abisko and Dovrefjell.

Dovrefjell			**Abisko**		
no shift	**warmer**	**colder**	**no shift**	**warmer**	**colder**
	Antennaria dioica	*Achillea millefolium*		*Agrostis mertensii*	*Angelica archangelica*
	Anthoxanthum nipponicum	*Aconitum lycoctonum*		*Antennaria alpina*	*Anthoxanthum odoratum*
	Arctostaphylos alpinus	*Agrostis capillaris*		*Arctostaphylos alpinus*	*Avenella flexuosa*
	Arctostaphylos uva-ursi	*Betula nana*		*Astragalus alpinus*	*Betula nana*
	Astragalus alpinus	*Betula pubescens*		*Bartsia alpina*	*Bistorta vivipara*
	Avenella flexuosa	*Campanula rotundifolia*		*Betula pubescens*	*Carex atrata*
	Bartsia alpina	*Carex bigelowii*		*Calamagrostis lapponica*	*Carex bigelowii*
	Bistorta vivipara	*Deschampsia cespitosa*		*Deschampsia cespitosa*	*Carex lachenalii*
	Carex vaginata	*Empetrum nigrum*		*Diapensia lapponica*	*Carex mackenziei*
	Equisetum arvense	*Festuca ovina*		*Empetrum nigrum*	*Cassiope tetragona*
	Euphrasia frigida	*Galium boreale*		*Epilobium angustifolium*	*Cerastium alpinum*
	Harrimanella hypnoides	*Geranium sylvaticum*		*Equisetum variegatum*	*Cerastium cerastoides*
	Hieracium alpinum	*Juncus trifidus*		*Euphrasia frigida*	*Cornus suecica*
	Luzula arcuata	*Juniperus communis*		*Festuca ovina*	*Dryas octopetala*
	Luzula multiflora	*Kalmia procumbens*		*Festuca rubra*	*Equisetum pratense*
	Luzula spicata	*Lysimachia europaea*		*Festuca vivipara*	*Geranium sylvaticum*
	Luzula sylvatica	*Melampyrum carpathicum*		*Harrimanella hypnoides*	*Juncus trifidus*
	Myosotis decumbens	*Oxalis acetosella*		*Huperzia selago*	*Juniperus communis*

Pedicularis oederi	*Pedicularis lapponica*	*Kalmia procumbens*	*Linnaea borealis*
Phleum alpinum	*Phyllodoce caerulea*	*Luzula arcuata*	*Luzula spicata*
Poa pratensis	*Salix herbacea*	*Luzula multiflora*	*Oxyria digyna*
Potentilla crantzii	*Salix reticulata*	*Lysimachia europaea*	*Pedicularis lapponica*
Ranunculus acris		*Melampyrum carpathicum*	*Poa alpigena*
Rumex acetosa		*Omalotheca supina*	*Potentilla crantzii*
Salix glauca		*Parnassia palustris*	*Pyrola minor*
Salix lanata		*Phleum alpinum*	*Salix glauca*
Salix lapponum		*Phyllodoce caerulea*	*Salix herbacea*
Saussurea alpina		*Poa alpina*	*Salix lanata*
Sibbaldia procumbens		*Ranunculus acris*	*Salix phylicifolia*
Silene acaulis		*Ranunculus glacialis*	*Salix polaris*
Solidago virgaurea		*Rumex acetosa*	*Salix reticulata*
Thalictrum alpinum		*Salix arbuscula*	*Saussurea alpina*
		Salix hastata	*Sibbaldia procumbens*
		Salix lapponum	*Silene dioica*
		Saxifraga aizoides	
		Selaginella selaginoides	
		Silene acaulis	
		Solidago virgaurea	
		Sorbus aucuparia	

Table S2.10: Shifts of leading edges in trailside plots compared to the interior vegetation in Abisko and Dovrefjell.

Dovrefjell			**Abisko**		
no shift	**warmer**	**colder**	**no shift**	**warmer**	**colder**
Anthoxanthum nipponicum	*Aconitum lycoctonum*	*Achillea millefolium*	*Angelica archangelica*	*Avenella flexuosa*	*Agrostis mertensii*
Avenella flexuosa	*Arctostaphylos uva-ursi*	*Agrostis capillaris*	*Antennaria alpina*	*Betula pubescens*	*Anthoxanthum odoratum*
Bartsia alpina	*Astragalus alpinus*	*Antennaria dioica*	*Astragalus alpinus*	*Cassiope tetragona*	*Arctostaphylos alpinus*
Campanula rotundifolia	*Bistorta vivipara*	*Arctostaphylos alpinus*	*Betula nana*	*Diapensia lapponica*	*Bartsia alpina*
Carex vaginata	*Empetrum nigrum*	*Betula nana*	*Calamagrostis lapponica*	*Epilobium angustifolium*	*Bistorta vivipara*
Euphrasia frigida	*Equisetum arvense*	*Betula pubescens*	*Carex lachenalii*	*Equisetum pratense*	*Carex atrata*
Geranium sylvaticum	*Lysimachia europaea*	*Carex bigelowii*	*Cornus suecica*	*Equisetum variegatum*	*Carex bigelowii*
Harrimanella hypnoides	*Pedicularis lapponica*	*Deschampsia cespitosa*	*Dryas octopetala*	*Geranium sylvaticum*	*Carex mackenziei*
Hieracium alpinum	*Phyllodoce caerulea*	*Festuca ovina*	*Empetrum nigrum*	*Harrimanella hypnoides*	*Cerastium alpinum*
Juncus trifidus	*Potentilla crantzii*	*Galium boreale*	*Festuca ovina*	*Huperzia selago*	*Cerastium cerastoides*
Juniperus communis	*Sibbaldia procumbens*	*Kalmia procumbens*	*Festuca vivipara*	*Kalmia procumbens*	*Deschampsia cespitosa*

Luzula multiflora	*Silene acaulis*	*Luzula arcuata*	*Juncus trifidus*	*Melampyrum carpathicum*	*Euphrasia frigida*
Luzula spicata		*Oxalis acetosella*	*Juniperus communis*	*Phleum alpinum*	*Festuca rubra*
Luzula sylvatica		*Poa pratensis*	*Luzula arcuata*	*Phyllodoce caerulea*	*Linnaea borealis*
Melampyrum carpathicum		*Salix herbacea*	*Luzula spicata*	*Potentilla crantzii*	*Luzula multiflora*
Myosotis decumbens		*Solidago virgaurea*	*Poa alpigena*	*Pyrola minor*	*Lysimachia europaea*
Pedicularis oederi			*Ranunculus glacialis*	*Rumex acetosa*	*Omalotheca supina*
Phleum alpinum			*Salix glauca*	*Salix reticulata*	*Oxyria digyna*
Ranunculus acris			*Salix herbacea*	*Saxifraga aizoides*	*Parnassia palustris*
Rumex acetosa			*Salix lanata*	*Solidago virgaurea*	*Pedicularis lapponica*
Salix glauca			*Salix phylicifolia*	*Sorbus aucuparia*	*Poa alpina*
Salix lanata			*Saussurea alpina*		*Ranunculus acris*
Salix lapponum			*Selaginella selaginoides*		*Salix arbuscula*
Salix reticulata			*Silene acaulis*		*Salix hastata*
Saussurea alpina					*Salix lapponum*
Thalictrum alpinum					*Salix polaris*
					Sibbaldia procumbens
					Silene dioica

Table S2.11: Shared shifts in optima between the Abisko and Dovrefjell.

Warmer optimum	**Colder optimum**
Arctostaphylos alpinus	*Betula nana*
Astragalus alpinus	*Carex bigelowii,*
Bartsia alpina	*Geranium sylvaticum*
Euphrasia frigida	*Juncus trifidus*
Harrimanella hypnoides	*Juniperus communis*
Luzula arcuata	*Pedicularis lapponica*
Luzula multiflora	*Salix herbacea*
Phleum alpinum	*Salix reticulata*
Ranunculus acris	
Rumex acetosa	
Salix lapponum	

Silene acaulis

Solidago virgaurea

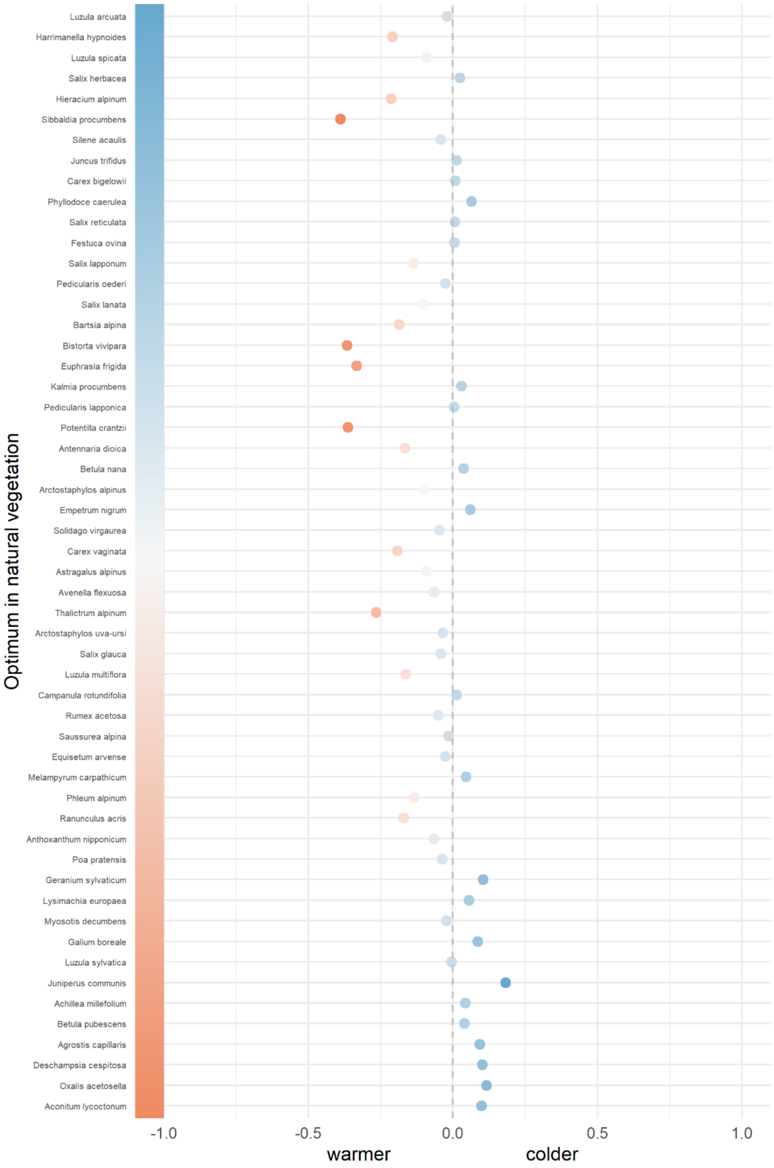


Figure S2.2: Dovrefjell – changes in optimum between interior vegetation and trailsides towards warmer (negative values) and colder (positive values) locations. Species are ordered according to their climatic optimum in the interior vegetation, from colder (top) to warmer (bottom).

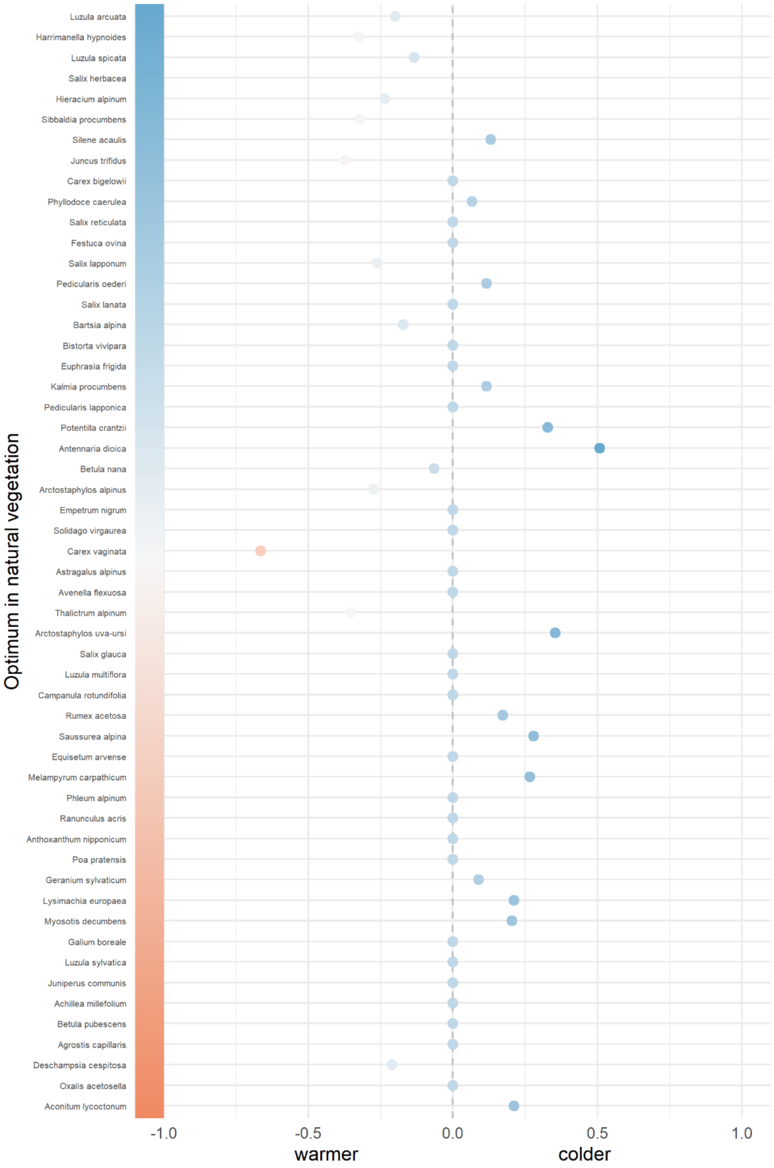


Figure S2.3: Dovrefjell – changes in rear edge between interior vegetation and trailsides towards warmer (negative values) and colder (positive values) locations. Species are ordered according to their climatic optimum in the interior vegetation, from colder (top) to warmer (bottom).

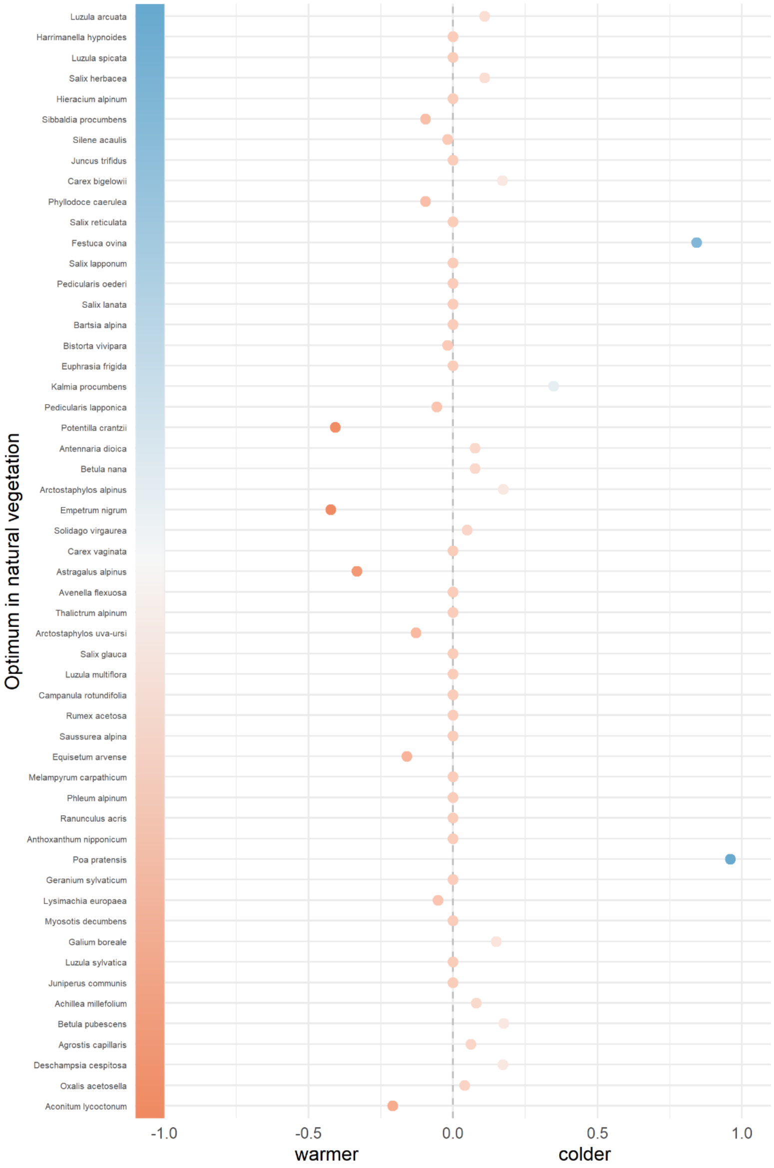


Figure S2.4: Dovrefjell – changes in leading edge between interior vegetation and trailsides towards warmer (negative values) and colder (positive values) locations. Species are ordered according to their climatic optimum in the interior vegetation, from colder (top) to warmer (bottom).

Figure S2.5: Abisko – changes in optimum between interior vegetation and trailsides towards warmer (negative values) and colder (positive values) locations. Species are ordered according to their climatic optimum in the interior vegetation, from colder (top) to warmer (bottom).

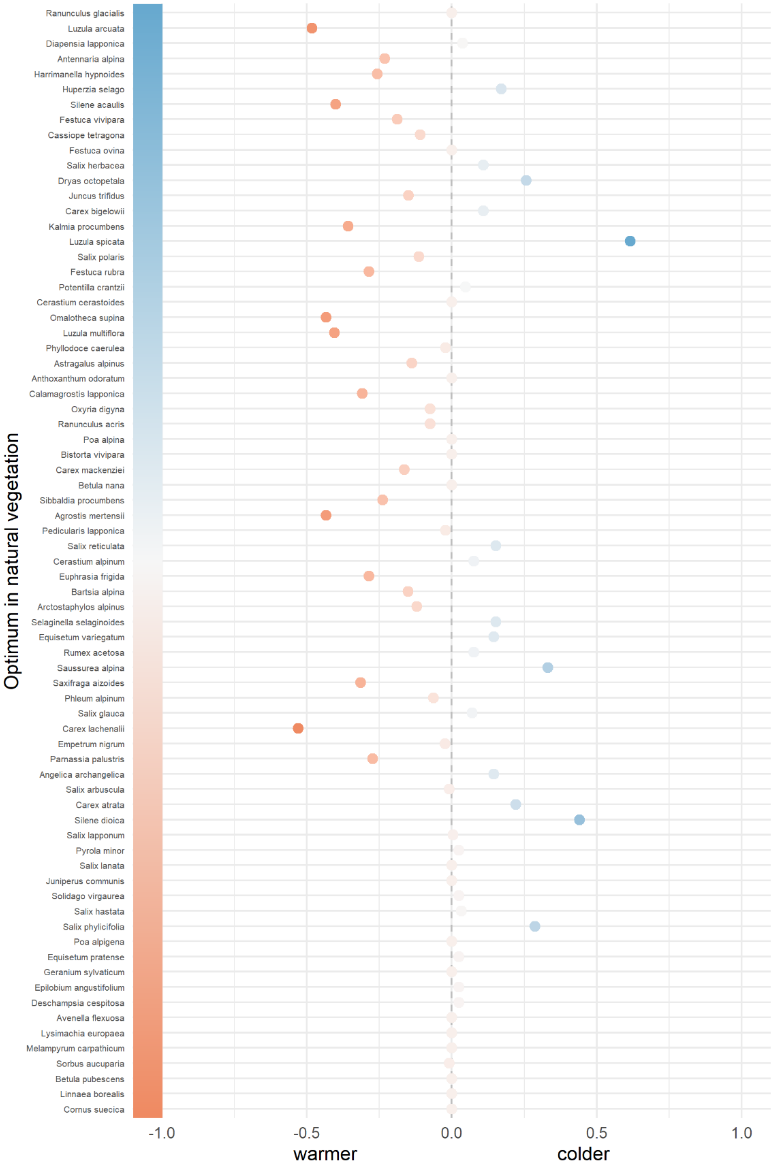


Figure S2.6: Abisko – changes in rear edge between interior vegetation and trailsides towards warmer (negative values) and colder (positive values) locations. Species are ordered according to their climatic optimum in the interior vegetation, from colder (top) to warmer (bottom).

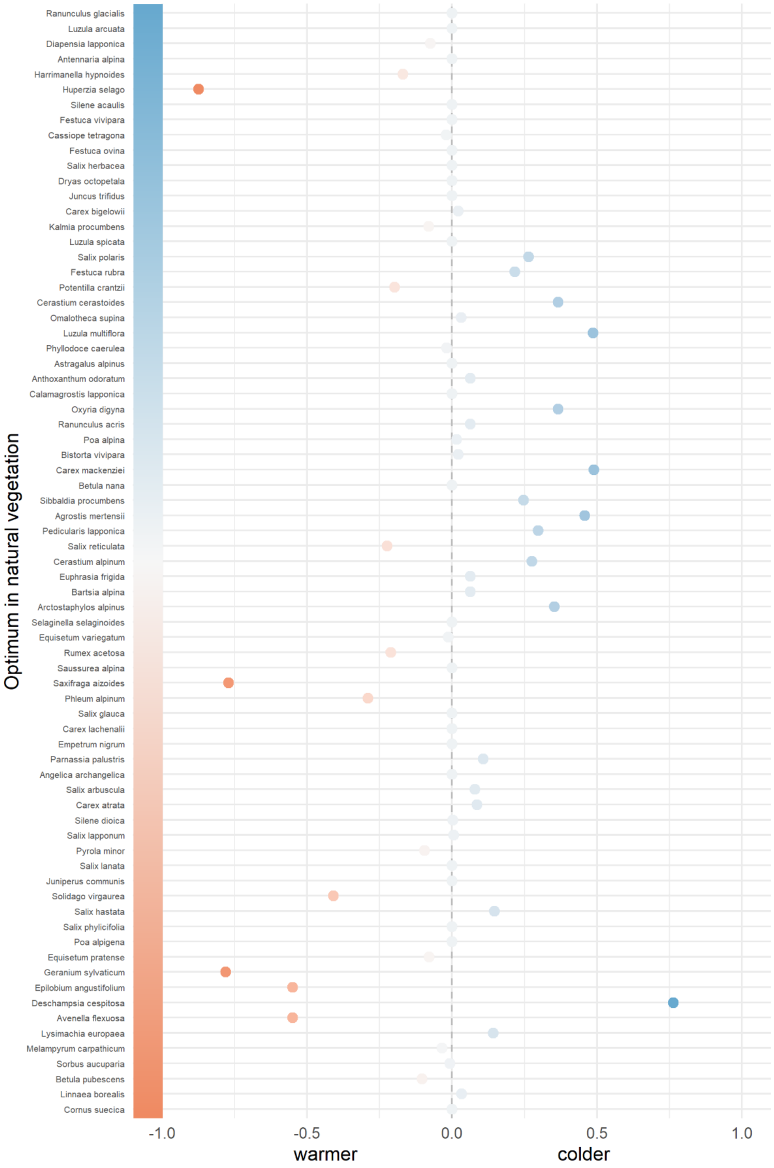


Figure S2.7: Abisko – changes in leading edge between interior vegetation and trailsides towards warmer (negative values) and colder (positive values) locations. Species are ordered according to their climatic optimum in the interior vegetation, from colder (top) to warmer (bottom).

Table S2.12: Model parameters from linear models of shifts in climatic optimum, rear edge, leading edge, climatic range of vascular plant species in the trailside compared to the interior vegetation including outliers in Dovrefjell (n = 55) and Abisko (n = 73), as a function of species' climatic optimum in the interior vegetation. The standard error of coefficients is given in parentheses.

	Dovrefjell				**Abisko**			
	Optimum	**Rear edge**	**Leading edge**	**Amplitude**	**Optimum**	**Rear edge**	**Leading edge**	**Amplitude**
Intercept	-0.00***	-0.00**	0.00	0.00*	0.00	0.00	-0.00	-0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Optimum	-0.14***	-0.24**	-0.01	0.22	-0.06	-0.12	0.03	0.16
	(0.04)	(0.08)	(0.07)	(0.12)	(0.04)	(0.06)	(0.09)	(0.11)
R^2	0.19	0.14	0.00	0.07	0.03	0.05	0.00	0.03
Adj. R^2	0.18	0.12	-0.02	0.05	0.02	0.04	-0.01	0.01

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Table S2.13: Model parameters best LMM for change in richness between interior vegetation and trailside plot. 167 observations, trail as random effect.

	Estimate	Std.Error	DF	t-value	*p*-value	Variance explained [%]
Intercept	4.161	2.315	144	1.798	0.07	
Dwarf shrub cover	-0.162	0.069	144	-2.356	0.02	9.38
Dist. introduction	-2.275	0.63	144	-3.614	< 0.001	23.96
Vegetation cover	0.151	0.066	144	2.272	0.03	9.45
Herb cover	0.148	0.077	144	1.926	0.06	7.01
Disturbance extent	1.081	0.672	144	1.607	0.11	4.92
Gap index	-1.286	0.664	144	-1.936	0.06	6.97
Richness interior vegetation	-0.262	0.07	144	-3.739	< 0.001	23.86

Table S2.14: Partitioning of variance for change in richness between interior vegetation and trailside plots. Adjusted R^2 is shown for the best model and sub-models with all variables separately and models with specific variables excluded. The variance percentage is calculated based on the fixed R2 for the model with only the specific variable (‘factor’), for the model without that focal variable (‘other’), and shared variance (‘shared’).

Model	R2 adjusted
Best	0.2519
Richness interior vegetation	7e-04
Disturbance extent	0.0103
Total vegetation cover	0.039
Dwarf shrub cover	0.0216
Herbaceous cover	0.0916
Gap index	0.0242
Distance to introduction	0.0103
No richness interior vegetation	0.1918
No disturbance extent	0.2395
No total vegetation cover	0.2281
No dwarf shrub cover	0.2283
No herbaceous cover	0.2342
No gap index	0.2343
No distance to introduction	0.1915

Model	Factor	Shared	Other
Richness interior vegetation	0.2386	-0.2359	0.9972
Disturbance extent	0.0492	-0.0081	0.9589
Total vegetation cover	0.0945	0.0603	0.8452
Dwarf shrub cover	0.0938	-0.0079	0.9141
Distance to introduction	0.2396	-0.1985	0.9589
Gap index	0.0697	0.0266	0.9038
Herbaceous cover	0.0701	0.2935	0.6364

Article III

R. E. M. Wedegärtner, J. J. Lembrechts, R. van der Wal, and B. J. Graae

Closing the gap: facilitation is important but depends on life stage, stress type, and gap size in tundra vegetation

In preparation for resubmission to Journal of Ecology.

Article III

This paper is awaiting publication and is not included in NTNU Open

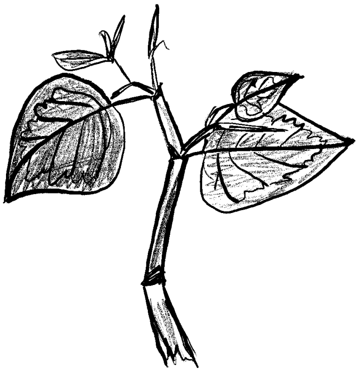
Article IV

S. Geange*, A. D. Barraclough*, R. E. M. Wedegärtner*, D. Urbach, L. A. Cavieres, C. Chisholm, J. J. Lembrechts, A. Pauchard, J. C. Pizarro, I. Rashid, T. Seipel, M. Snethlage, and V. Vandvik

Global survey on invasive species impacts and management in mountains

* Denotes co-lead authorship

Manuscript.



Article IV

This article is awaiting publication and is not included

Supplementary Materials S.1 – S.7
Global survey on invasive species impacts and management in mountains

Sonya Geange*, Alicia D Barraclough*, Ronja E. M. Wedegärtner*, Davnah Urbach, Lohengrin A. Cavieres, Chelsea Chisholm, Jonas J. Lembrechts, Aníbal Pauchard, J. Cristóbal Pizarro, Irfran Rashid, Tim Seipel, Mark Snethlage, Vigdis Vandvik

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This supplementary material is not included in NTNU Open

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

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

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*

1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as

1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)

1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)

2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities

2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia

2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem

2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype

2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose

2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming

2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals

2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.
2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism

2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh
2019	Knut Jørgen Egelie	PhD Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	PhD Biology	Adaptive responses to enviromental stochasticity on different evolutionary time-scales
2019	Kwaslema Malle Hariohay	PhD Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	PhD Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Joseph Mbyati Mukeka	PhD Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	PhD Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	PhD Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	PhD Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	PhD Biology	Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer
2019	Emma-Liina Marjakangas	PhD Biology	Understanding species interactions in the tropics: dynamics within and between trophic levels

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

2021	Monica Shilereyo	PhD Biology	Small Mammal Population Ecology and Ectoparasite Load: Assessing Impacts of Land Use and Rainfall Seasonality in the Serengeti Ecosystem, Tanzania
2021	Vanessa Bieker	PhD Biology	Using historical herbarium specimens to elucidate the evolutionary genomics of plant invasion
2021	Håkon Austad Langberg	PhD Biology	Fate and transport of forever chemicals in the aquatic environment: Partitioning and biotransformation of mixtures of Per- and Polyfluoroalkyl Substances (PFAS) from different point sources and resulting concentrations in biota
2021	Julie Renberg	PhD Biology	Muscular and metabolic load and manual function when working in the cold
2021	Olena Meleshko	PhD Biology	Gene flow and genome evolution on peatmosses (*Sphagnum*)
2021	Essa Ahsan Khan	PhD Biology	Systems toxicology approach for evaluating the effects of contaminants on fish ovarian development and reproductive endocrine physiology:A combination of field-, in vivo and ex vivo studies using Atlantic cod (*Gadus morhua*)
2021	Tanja Kofod Petersen	PhD Biology	Biodiversity dynamics in urban areas under changing land-uses
2021	Katariina Vuorinen	PhD Biology	When do ungulates override the climate? Defining the interplay of two key drivers of northern vegetation dynamics
2021	Archana Golla	PhD Biology	Impact of early life stress on behaviour and dorsal raphe serotonergic activity in zebrafish (*Danio rerio*)
2021	Aksel Alstad Mogstad	PhD Biology	Underwater Hyperspectral Imaging as a Tool for Benthic Habitat Mapping
2021	Randi Grønnstad	PhD Biology	Per- and polyfluoroalkyl substances (PFAS) in ski products: Environmental contamination, bioaccumulation and effects in rodents
2021	Gaspard Philis	PhD Biology	Life cycle assessment of sea lice treatments in Norwegian net pens with emphasis on the environmental tradeoffs of salmon aquaculture production systems
2021	Christoffer Høyvik Hilde	PhD Biology	Demographic buffering of vital rates in age-structured populations”
2021	Halldis Ringvold	Dr.Philos	Studies on Echinodermata from the NE Atlantic Ocean - Spatial distribution and abundance of Asteroidea, including taxonomic and molecular studies on Crossaster and Henricia genera- Value-chain results, including test fishery, biology, market and nutritional analysis, on Parastichopus tremulus (Holothuroidea) from the Norwegian coast
2021	Elise Skottene	PhD Biology	Lipid metabolism and diapause timing in Calanus copepods. The impact of predation risk, food availability and oil exposure

2021	Michael Le Pepke	PhD Biology	The ecological and evolutionary role of telomere length in house sparrows
2022	Niklas Erik Johansson	Dr. Philos	On the taxonomy of Northern European Darwin wasps (Hymenoptera: Ichneumonidae).
2022	Jonatan Fredricson Marquez	PhD Biology	Understanding spatial and interspecific processes affecting population dynamics in a marine ecosystem.
2022	Anne Mehlhoop	PhD Biology	Evaluating mitigation measures to reduce negative impacts of infrastructure construction on vegetation and wildlife.
2022	Malene Østreng Nygård	PhD Biology	Integrative biosystematics and conservation genomics – holistic studies of two red-listed plants in Norway
2022	Martin René Ellegaard	PhD Biology	Human Population Genomics in Northern Europe in the Past 2000 years
2022	Gaute Kjærstad	PhD Biology	The eradication of invasive species using rotenone and its impact on freshwater macroinvertebrates
2022	Stefan Vriend	PhD Biology	On the roles of density dependence and environmental fluctuations in driving eco-evolutionary dynamics of hole-nesting passerines
2022	Zaw Min Thant	PhD Biology	Anthropogenic and Environmental factors driving the Human-Elephant Conflict in Myanmar
2022	Prashann Guragain	PhD Biology	Population analysis and structure and RNA interference to understand salmon lice biology and a review of the principles of controlling infestation in aquaculture facilities.