Thermal niches are more conserved at cold than warm limits in arctic-alpine plant species

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ABSTRACT

Aim Understanding the stability of realized niches is crucial for predicting the responses of species to climate change. One approach is to evaluate the niche differences of populations of the same species that occupy regions that are geographically disconnected. Here, we assess niche conservatism along thermal gradients for 26 plant species with a disjunct distribution between the Alps and the Arctic.

Location European Alps and Norwegian Finnmark.

Methods We collected a comprehensive dataset of 26 arctic-alpine plant occurrences in two regions. We assessed niche conservatism through a multispecies comparison and analysed species rankings at cold and warm thermal limits along two distinct gradients corresponding to (1) air temperatures at 2 m above ground level and (2) elevation distances to the tree line (TLD) for the two regions. We assessed whether observed relationships were close to those predicted under thermal limit conservatism.

Results We found a weak similarity in species ranking at the warm thermal limits. The range of warm thermal limits for the 26 species was much larger in the Alps than in Finnmark. We found a stronger similarity in species ranking and correspondence at the cold thermal limit along the gradients of 2-m temperature and TLD. Yet along the 2-m temperature gradient the cold thermal limits of species in the Alps were lower on average than those in Finnmark.

Main conclusion We found low conservatism of the warm thermal limits but a stronger conservatism of the cold thermal limits. We suggest that biotic interactions at the warm thermal limit are likely to modulate species responses more strongly than at the cold limit. The differing biotic context between the two regions is probably responsible for the observed differences in realized niches.

Keywords Air–soil temperature, biotic interactions, disjunct distribution, distance to tree line, European Alps, niche conservatism, Norwegian Finnmark, realized niche, species distribution models.

INTRODUCTION

Understanding the stability of a species’ environmental niche – both fundamental (i.e. physiological) and realized (i.e. constrained by biotic interactions and dispersal) – is crucial for predicting a species’ response to climate change (Pearman et al., 2008; Lavergne et al., 2010; Salamin et al., 2010; Wiens et al., 2010; Bellard et al., 2012). It was notably suggested that the
fundamental niches of some species might evolve rapidly and this may attenuate the current effects of global change on ecosystems (Hoffmann & Willi, 2008; Hoffmann & Sgrò, 2011). Assessing the differences between populations of a species that occupy geographically disjoint regions or of populations of species that have recently colonized a new geographically separate region (e.g. invasive species) are thus promising ways of providing insight into the possible shifts of species niches (Wiens & Graham, 2005; Pearman et al., 2008; Alexander & Edwards, 2010).

Both abiotic and biotic factors shape the ability of a species to occupy certain environmental conditions (Soberón, 2007). While these factors may change across regions and drive shifts in both fundamental (Hoffmann & Sgrò, 2011) and realized (Schweiger et al., 2008) niches, only the realized niche is easily quantifiable, which limits ecological interpretation. Nonetheless, biotic drivers are thought to have differential effects across environmental gradients (Callaway et al., 2002; Le Roux & McGeoch, 2010). According to the asymmetric abiotic stress limitation hypothesis (AASL), in general, fluctuations of the realized niche due to changing biotic interactions are expected at the warm, more productive end of environmental gradients (Normand et al., 2009; Defossez et al., 2011; Meier et al., 2011). At the cold end, species distributions are primarily limited by physiological tolerance of environmental conditions that are less favourable to growth and reproduction (Pigott & Huntley, 1978; Normand et al., 2009; Meier et al., 2011). Investigating the realized niche of species that spans a wide range of environmental gradients, from warmer, productive conditions to colder, less productive ones, may provide insight into the prevalence of shifts in both fundamental and realized niches.

Climatic temporal variations affect the ranges of species and promote the differentiation of their realized niches among disjunct ranges (Hewitt, 2000; Davis & Shaw, 2001; Zimmermann et al., 2009). During the last ice age, ice caps and glaciers covered most of northern Europe and its alpine areas, while most of central Europe comprised cold biomes (Frenzel et al., 1992). With the end of these glaciations, cold-adapted species followed the retreat of the ice toward either higher latitudes or higher elevations, contributing to the current disjunct distribution of those species found both in the Alps and in the Arctic (whose members are referred to as arctic-alpine species; Schönswetter et al., 2005; Espíndola et al., 2012). The separation of species may have caused unequal distributions of the species genetic diversity (Desprès et al., 2002) and genetic isolation (Espíndola et al., 2012). In addition, cryptic refugia in the north may have contributed to the genetic difference in arctic and alpine species (Parducci et al., 2012). This potentially provides the genetic basis for a shift of the fundamental niche (Ackerly, 2003).

Isolated populations without means to exchange genetic material may cause changes to the local fundamental niche and the emergence of ecotypes through adaptations to local environmental conditions (Comes & Kadereit, 1998; Ackerly, 2003; Wiens, 2004; Broennimann et al., 2007; Jay et al., 2012; Manel et al., 2012). Differences existing in abiotic factors may differentially moderate the responses of species across environmental gradients in the two regions. For instance, Billings (1973) suggested that the long separation between the arctic and alpine regions may have created distinct ecotypes. Individuals from alpine populations experience higher light saturation for photosynthesis, undergo maximum photosynthesis rates at higher temperatures and contain a lower chlorophyll content than their Arctic counterparts (Mooney & Johnson, 1965; Billings and Mooney1968; Billings, 1973).

Geographically distant populations may also be part of regionally distinct species pools, such that biotic interactions may influence realized niches differently (Gallien et al., 2010; Pellissier et al., 2010). Plant species richness in the Alps is higher than in the Arctic (Lenoir et al., 2010), potentially causing different competition regimes, which may result in different realized niches. Human pressure also differs: in the Alps, a long history of land use has reshaped the structures of lower alpine grasslands (Gehrig-Fasel et al., 2007), while human impact has been lower in the Arctic. Therefore, one could expect to observe different realized niches for the same species between the Alps and the Arctic, but this has yet to be tested. Hence, a comparison of the Alps and Arctic regions represents a useful case study for considering niche conservatism along the thermal gradient.

For this research, we investigated whether single plant species occupy similar realized niches across the thermal gradients between the Arctic and the Alps. We first collected a comprehensive data set that comprised occurrences of 26 arctic-alpine plant species in the European Alps and in northern Norway. Across the two regions, we compared the rankings of the species when considering their colder and warmer thermal limits according to summer temperature and their distances in elevation from the tree limit. The tree line was shown to be physiologically controlled and conserved world-wide (Körner & Paulsen, 2004; but see Harsch et al., 2009), it therefore constitutes a sound biogeographic reference for the comparison and ranking of non-tree species along thermal gradients (Randin et al., in press).

**MATERIALS AND METHODS**

**Study areas**

The two study areas are the European Alps and Norway’s northernmost counties (Troms and Finnmark, referred to as Finnmark; Fig. 1). These Norwegian counties form the northern frontier of the European continent and are bordered by the Barents Sea to the north and by birch forests and continuous taiga to the south. The western part of the region is characterized topographically by steep hills with peaks of approximately 800–1800 m a.s.l. that are often surrounded by glaciers, deep valleys, narrow fjords or open sea. In the eastern part of Finnmark, the mountain ranges gradually decrease in elevation towards the Barents Sea to plateaus of 300–500 m a.s.l., with the existence of abrupt cliffs interspersed with moderately sloped hills. The Alps represent the most distinct mountain range in central Europe, stretching from Austria and Slovenia in the east to France in the west. Rising up to 4800 m a.s.l., the Alps comprise cold climatic
environments comparable to those of the Arctic, with short growing seasons and long snow cover during the winter. The present study focuses on the areas where the average temperature of the warmest month is less than 11 °C, corresponding to the regions of the subalpine belt and the subarctic tundra.

Species data

We selected 34 taxa that are relatively frequent both in the Alps and in Finnmark and that can also be identified in the field with limited risk of confusion. We sought a data set that was as close as possible to an equal-stratified sampling design (Hirzel & Guisan, 2002). Therefore, we stratified our study areas according to WorldClim’s climate grids (Hijmans et al., 2005) at a resolution of 30 arcsec (c. 1 km x 1 km). Three descriptors, representing summer (June–August) temperatures, humidity (June–August) and winter (December–February) precipitation were selected. Summer temperature represents the energy available during the growing season and winter precipitation represents the cover of snow. Each descriptor was divided into three equal classes. By combining these three layers with three classes each, we generated 24 realized climate combinations (strata) in the Alps and 25 in Finnmark, out of the 27 ($3 \times 3 \times 3$) possible classes. Species occurrences were collected for each stratum by using (1) existing observations and (2) a complementary sampling, which filled gaps in the existing data that originated from a non-stratified sampling.

For the previously existing data, we collected exhaustive vegetation inventories for both regions that contained at least one of the selected species. We randomly selected survey points in each climate class from the vegetation data to constitute these classes (with a maximum of 100 survey points). As the acquired data did not cover the entire available environment in the study areas, where the number of historical observation points was insufficient we set up a complementary sampling in Finnmark and in the Alps to achieve equal samples per climate class. To conduct this sampling, we randomly selected 750 m x 750 m plots (hereafter referred to as 750-m plots) in climatic strata with missing data. Each randomly selected plot was subsampled by randomly selecting four 100 m x 100 m subplots (hereafter, 100-m subplots) that were separated from one another by at least 200 m. Within each 100-m subplot, we visited nine subplots of 2 m x 2 m (hereafter, 2-m subplots) and inventoried the species along a planned route. We first set a 2-m subplot at the centre of a 100-m subplot and recorded all of the target species present. We then moved 25 m to the north-east to sample the second 2-m subplot, moved another 25 m further to the north-east to sample the third 2-m subplot, and then returned to the central point. We performed similar sampling procedures for the other three directions (i.e. north-west, south-east and south-west). Additionally, we recorded whether the target species were present in the routes between the 2-m subplots. This nested design, with three plot levels of 750, 100 and 2 m, was chosen over a standard random sampling because accessibility to Finnmark’s northern regions is limited and this procedure has proven to be the most cost efficient (Pellissier et al., 2010).

Environmental data

We calculated the average summer temperature (hereafter referred to as the 2-m temperature) as the mean of the recorded temperatures for June, July and August. We considered average summer temperature only because: (1) it is physiologically more meaningful to alpine species than other temperature variables (Körner, 2003); (2) the altitude of the global tree line is also best explained by the average temperature of the summer growing season (Körner & Paulsen, 2004; Gehrig-Fasel et al., 2008); and (3) other climatic variables that could have been derived from WorldClim, such as degree-days measured with the approach of Zimmermann & Kienast (1999), show anyway a high correlation to June–August average temperature ($R^2 = 0.9$ in the Alps and $R^2 = 0.7$ in Finnmark) and therefore were not expected to prove more informative than the summer average for our analyses.

We obtained the temperature layer from WorldClim (Hijman et al., 2005), which is based on 2-m air measurements from meteorological stations. To obtain more precise climatic
information at the sites, we downscaled WorldClim data from a 30-arcsec resolution to a 100-m resolution using a digital elevation model (for details see Engler et al., 2011). While the temperature layer gives fairly robust results with this downscaling approach, the method is less reliable when applied to the precipitation layer (Gyalistras, 2003; Daly et al., 2008; Randin et al., in press). Consequently, we only analysed thermal niches in the present study. All other thermal variables from WorldClim or derived variables show a high correlation with the June–August average and we therefore did not consider them in the analyses.

We also estimated thermal differences in relation to the calculated distance to the potential local tree line (TLD), as tree lines are good biogeographic reference points for comparing and ranking non-tree species (Randin et al., in press). For the two regions, we extracted data at a resolution of 100 m per pixel of forest-occupied areas of the land-cover layers of CORINE, for Europe, and GEOSTAT, for Switzerland. With this information, we calculated the elevations of the forest-occupied areas. After delineating a square window of 5 km × 5 km, we calculated the potential tree line of each 100-m pixel by computing the maximum of forest elevation within each window, following the procedure defined by Paulsen & Körner (2001) and Gehrig-Fasel et al. (2007). For each 100-m pixel, we subtracted the elevations of the pixel from the elevations of potential tree lines to obtain the distances in elevation to the potential tree line, one of the most relevant temperature proxies in cold environments.

Rankings of species across thermal gradients

We compared the warm and cold thermal limit values for the averaged 2-m temperature and calculated TLD in the Alps and in Finnmark. To investigate whether the rankings of species across temperature gradients are similar between the two regions, we considered the cold and warm thermal limits to be the 20th and 80th percentiles of the 2-m temperature and TLD gradients for both study regions. We preferred using the 20th and 80th percentiles rather than the absolute minima and maxima because they are less sensitive to outliers. We extracted the 2-m temperature and TLD at the locations where the species were recorded and calculated the 20th and 80th percentiles of the distribution of those values. Our analysis is thus based on presence only. We then tested for rank conservatism using Kendall’s rank correlation of the 20th and 80th percentile values in the Alps and Finnmark. The formal null hypothesis for the conservatism of thermal limits in species is that the slope representing the relationship of two regions is equal to one while the intercept is zero. However, an alternative hypothesis can also be that, due to microclimatic differences between the two regions, the thermal niche limits are related but with a slope different from 1 and a non-zero intercept. We tested these alternative hypotheses using the slope.test function of the smatr R package using the standard major axis method, with and without the intercept fixed to the origin (Warton et al., 2006).

RESULTS

Species sampling

In total, we obtained 6320 plots in the Alps and 2819 in Finnmark. Of the 34 species sampled, only 26 occurred with sufficient frequency in both regions to support further analyses (number of occurrences > 20; Table 1).

Warm thermal limit

The most interesting finding of this study is that the range of warm thermal limits demonstrated by the 26 species was much larger in the Alps than in Finnmark both when measured with 2-m temperature (4 °C in the Alps and 1 °C in Finnmark; Fig. 2) and with the TLD (350 m in the Alps and 180 m in Finnmark; Fig. 3). As a consequence, the relationships between the ranks of the warm thermal limits of the species in the two regions were weak (2-m temperature, \( R^2 = 0.23; \) Kendall tau = 0.3, \( P = 0.04; \) TLD, \( R^2 = 0.31, \) Kendall tau = 0.38, \( P = 0.005 \). The estimated slopes of those relationships differed from one with zero-forced intercept (TLD, slope = 2.16, confidence interval = 1.47–3.16) and with non-zero estimated intercept (2-m temperature, slope = 4.04, confidence interval = 2.81–5.79; TLD, slope = 1.84, confidence interval = 1.31–1.84), except along the 2-m gradient with zero-forced intercept (slope = 0.96, confidence interval = 0.9–1.02). This occurred because the points were equally distributed across both sides of (but not along) the 1 : 1 line (Fig. 2).

Cold thermal limit

We found a better correspondence of species limit in the Alps and Finnmark toward cold temperatures. We found a positive relationship between the ranks of cold thermal limits of the 26 species in the two regions measured with 2-m temperature (\( R^2 = 0.41, \) Kendall tau = 0.5, \( P = 0.0005 \). Yet, the slope of this relationship was unequal to one, being systematically biased, whether tested with zero-forced intercept (slope = 0.76, confidence interval = 0.71–0.82) or with non-zero estimated intercept (slope = 2.25, confidence interval = 1.64–3.07). The species with the coldest thermal limits tolerated colder 2-m temperatures in the Alps than in Finnmark, while species located in warmer conditions in the Alps and in Finnmark exhibited more equivalent cold thermal limits (Fig. 2). Except for one species (Antennaria dioica), along the TLD gradient the points were closer to the 1 : 1 relationship (Fig. 3). When excluding this outlying species, the correlation was high (\( R^2 = 0.51, \) Kendall tau = 0.48, \( P = 0.0007; \) when not excluded \( R^2 = 0.28, \) Kendall tau = 0.38, \( P = 0.005 \). The estimated slopes with zero-forced intercept (slope = 0.98, confidence interval = 0.88–1.08) were similar to one, and the lower bound of the confidence interval was close to one with non-estimated intercept (slope = 1.65, confidence interval = 1.15–2.39; Fig. 3).
At the warm thermal limits, the less climatically severe and more productive ends of the gradients for species, we found a low conservatism of species limit rankings, with lower variation in thermal limits in Finnmark compared with the Alps. In contrast, we found higher correspondences in species rankings at the cold thermal limits across the two regions (especially along the TLD).

**Table 1** List of the arctic-alpine species sampled in the Alps (A) and in Finnmark (F), including the total number of occurrences (Pres.) obtained in each region. Nomenclature from Aeschimann et al. (2004).

<table>
<thead>
<tr>
<th>Abbrev.</th>
<th>Species</th>
<th>Family</th>
<th>Growth form</th>
<th>Pres. (A)</th>
<th>Pres. (F)</th>
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<tr>
<td>ALALP</td>
<td>Alchemilla alpina</td>
<td>Rosaceae</td>
<td>Forb</td>
<td>95</td>
<td>178</td>
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<tr>
<td>ANDIO</td>
<td>Antennaria dioica</td>
<td>Asteraceae</td>
<td>Forb</td>
<td>278</td>
<td>81</td>
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<td>Brassicaceae</td>
<td>Forb</td>
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<td>25</td>
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<td>ARCAL</td>
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<td>Ericaceae</td>
<td>Dwarf shrub</td>
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<td>223</td>
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<td>DEFLE</td>
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<td>862</td>
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<td>Spore plant</td>
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<td>57</td>
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<td>1089</td>
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<td>Forb</td>
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<td>Forb</td>
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<td>Forb</td>
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<td>Forb</td>
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<td>Caryophilaee</td>
<td>Forb</td>
<td>67</td>
<td>8</td>
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<td>Salicaceae</td>
<td>Dwarf shrub</td>
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<td>Asteraceae</td>
<td>Forb</td>
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<td>Forb</td>
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<td>Forb</td>
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<td>Forb</td>
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<td>VIBIF</td>
<td>Viola biflora</td>
<td>Violaceae</td>
<td>Forb</td>
<td>235</td>
<td>303</td>
</tr>
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</table>

**Figure 2** Relationship between (a) the warm (80th percentile) and (b) cold (20th percentile) thermal limits of species in the Alps and Finnmark for summer temperature. The straight line indicates the expected 1 : 1 relationship, which has a slope of one and passes through the origin. Abbreviations refer to Table 1.
With a low tolerance for competition may have been able to
and alpine vegetation belts (Gobet et al., 2003). Human settlers have, since the Neolithic, freed low alpine grassland from shrubs and small trees (lowering the tree line as far as 300 m down-slope), which created less gradual vegetation transitions than those found in Finnmark (Tinner & Theurillat, 2003). Many alpine species probably took the opportunity to extend their distribution in microniches in the subalpine belt after clearing. Furthermore, domesticated reindeer have been present for centuries in Finnmark (Muga, 1986), but only recently at high densities (Bråthen et al., 2007). As a consequence, alpine plants with a low tolerance for competition may have been able to colonize habitats towards much lower elevations than the potential tree line in the Alps, while the ecotone heath vegetation in Finnmark has probably limited the distribution of alpine plant species at their warm thermal limits. While this effect is mostly apparent at a local scale, it has been demonstrated that such effects can also have range-shaping influences, thus affecting the geographic distribution of species up to a large spatial extent (Meier et al., 2012).

**Warm thermal limits are different across arctic and alpine populations**

We found little similarity between the Alps and Finnmark in the realized niches at the warm thermal limits. While species limits were distributed across the environmental gradients examined in the Alps and extended far below the potential tree line, the warm thermal limit of all species in Finnmark was narrower and was situated in closer proximity to the potential tree line than in the Alps (Fig. 3). Thus, temperature appears to be structuring species sequences at the warm thermal limit across environmental gradients in the Alps, but the same degree of structuring was not reached in Finnmark. In the latter, Müller (1952) suggested intense competitive effects from dwarf shrubs in the lower Arctic. Similarly, Pellissier et al. (2010) documented a large competitive effect of a dominant dwarf shrub in subarctic tundra. In comparison, because the land-use history of the Alps has been more intense, the heath vegetation is severely reduced or almost absent in the transitional zone (ecotone) between the subalpine and alpine vegetation belts (Gobet et al., 2003). Human settlers have, since the Neolithic, freed low alpine grassland from shrubs and small trees (lowering the tree line as far as 300 m down-slope), which created less gradual vegetation transitions than those found in Finnmark (Tinner & Theurillat, 2003). Many alpine species probably took the opportunity to extend their distribution in microniches in the subalpine belt after clearing. Furthermore, domesticated reindeer have been present for centuries in Finnmark (Muga, 1986), but only recently at high densities (Bråthen et al., 2007). As a consequence, alpine plants with a low tolerance for competition may have been able to colonize habitats towards much lower elevations than the potential tree line in the Alps, while the ecotone heath vegetation in Finnmark has probably limited the distribution of alpine plant species at their warm thermal limits. While this effect is mostly apparent at a local scale, it has been demonstrated that such effects can also have range-shaping influences, thus affecting the geographic distribution of species up to a large spatial extent (Meier et al., 2012).

**Realized niche conservatism at the cold thermal limit**

Arctic and alpine plant populations occupy more similar rank positions in cold compared with warm thermal limits of their range, especially along TLD gradients where the distribution is relatively close to the 1 : 1 line. This is in accordance with the asymmetric abiotic stress limitation hypothesis, which states that the cold temperature end of a gradient should be less affected by biotic interactions (Callaway et al., 2002) because it tends to be closer to the fundamental niche and its physiological limits (Normand et al., 2009). Our results corroborate those of Wiens & Graham (2005), who also documented strong niche similarities for northern latitudes in invasive species between native and invaded ranges. Here we used the different distances in elevation from the tree line as a proxy for thermal difference. A clearer relationship may have been found if the units for these differences in elevation were transformed from metres to thermal units (K) using a local lapse rate (Randin et al., 2011). As a consequence, alpine plants with a low tolerance for competition may have been able to colonize habitats towards much lower elevations than the potential tree line in the Alps, while the ecotone heath vegetation in Finnmark has probably limited the distribution of alpine plant species at their warm thermal limits. While this effect is mostly apparent at a local scale, it has been demonstrated that such effects can also have range-shaping influences, thus affecting the geographic distribution of species up to a large spatial extent (Meier et al., 2012).

**Discrepancies between analyses of distances to tree line and 2-m temperature**

Our findings indicate a stronger similarity among realized niches at the cold than at the warm thermal limit in the Alps and
regions with complex topography, and would particularly allow future research on climatic niche dynamics, particularly in regions with complex topography, and would particularly allow

us to assess more precisely whether genetic differences across regions may be associated with distinct tolerances to environmental conditions.

ACKNOWLEDGEMENTS

We would like to thank those who helped with the field work, the Swiss Biodiversity Monitoring programme and Torbjørn Alm at Tromsø University Museum for data and Sophie Cotting for help with the GIS. We further thank the Norwegian Coast Guard that helped us reach several of the remote field sites in Finnmark. This study was supported by the NSF grant no. 31003A-125145 (BIOASSEMBLE) project to A.G. and by the European Commission FP6 ECOCHANGE project to A.G., E.M., N.E.Z., W.T., K.A.B. and N.G.Y. W.T. received funding from the European Research Council under the European 80 Community’s Seven Framework Programme FP7/2007–2013 Grant Agreement no. 281422 (TEEMBIO). L.P. was supported by The Danish Council for Independent Research grant n°12-126430.

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**Editor:** Arndt Hampe