



Decline of parasitic and habitat-specialist species drives taxonomic, phylogenetic and functional homogenization of sub-alpine bumblebee communities

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Received: 8 September 2020 / Accepted: 10 June 2021 / Published online: 15 June 2021
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Abstract

The ongoing biodiversity crisis is characterised not only by an elevated extinction rate but also can lead to an increasing similarity of species assemblages. This is an issue of major concern, as it can reduce ecosystem resilience and functionality. Changes in the composition of pollinator communities have mainly been described in intensive agricultural lowland areas. In this context, using a replicated survey of historical and recent bumblebee diversity, we aimed here to test how documented changes in climate and land use influenced the potential homogenization of sub-alpine bumblebee communities in southern Norway. We assessed the change in community composition in terms of taxonomic, phylogenetic and functional (β -)diversity, and estimated the impact of various species traits in probabilities of species gains and losses. Overall, we found a strong reduction in functional diversity, but no change in phylogenetic diversity over time. The β -diversity decreased, especially at high elevations, and this pattern was consistent for taxonomic, phylogenetic and functional β -diversity. The spatial distribution, measured as the average site occupancy, decreased in habitat-specialist species. This was explained by both a higher risk of species loss and a lower probability of species gain for habitat-specialist and parasitic species than for generalist and social species. These findings demonstrate that a narrow niche breadth may contribute to a higher extinction risk in bumblebee species. This non-random impact of disturbance on species may lead to large-scale biotic homogenisation of communities, a pattern that can be detected by investigating biodiversity changes at different scales and across its multiple facets.

Keywords Bombus · Beta-diversity · Mountain · Traits · Historical data

Introduction

Land use and climate change are two of the main contemporary drivers of biodiversity change (Oliver and Morecroft 2014). Such changes are, however, typically not random, but instead depend on species traits (Öckinger et al. 2010; Vandewalle et al. 2010). Therefore, monitoring changes in

the taxonomic composition of biological communities may be insufficient to reveal the impact of anthropogenic disturbance on biodiversity. The most important changes for the resilience of ecosystems should often be described instead in terms of the functional diversity of communities. Indeed, ecosystem functioning depends on the identity and complementarity of species traits and is thus directly affected by a reduction of functional diversity (Cadotte et al. 2011; Gagic et al. 2015). In addition, recently, an emphasis has been put on the conservation of phylogenetic diversity (Winter et al. 2012), both with the aim of preserving evolutionary history and as a proxy for functional diversity (Srivastava et al. 2012). Trends in taxonomic, phylogenetic and functional diversity do not necessarily coincide (Devictor et al. 2010; Monnet et al. 2014; De Palma et al. 2017). For this reason, drawing a comprehensive picture of biodiversity trends requires monitoring at the same time all these aspects of the diversity of assemblages, over large environmental gradients and long periods of time.

Communicated by Ingolf Steffan-Dewenter.

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Changes in biodiversity can also be expressed at different temporal and spatial scales, potentially revealing complex biodiversity trends that can lead to different conclusions about the nature and strength of anthropogenic impact on biodiversity (McGill et al. 2015). For example, globally, the cumulative action of humans has led to an elevated extinction rate and a strong decline in the abundance and distribution of many species (Ceballos et al. 2015, 2017), but there is a lack of evidence for a consistent decline in species richness at local scales (Dornelas et al. 2014). This is evidence that trends observed locally (α -diversity) cannot necessarily be upscaled to describe trends in the regional or global species pool (γ -diversity), and vice-versa. However, a well-documented effect of human disturbance is an increasing similarity of species assemblages across large spatial scales, a process known as biotic homogenisation (Olden et al. 2004). Therefore, the description of the variation of diversity among sites (β -diversity) offers another, equally relevant, view of biodiversity change in the Anthropocene.

These complementary types of biodiversity trends (i.e. changes in α -, β - and γ -diversity) can all be calculated for each of the three facets of diversity (i.e. taxonomic, phylogenetic and functional diversity), which altogether contribute to providing a full account of the processes behind species' response to environmental change. For instance, the fact that human impact on communities is often non-random and typically leads to the replacement of specialist species by more generalist species at the global scale can be described as a functional homogenisation, i.e. a reduction of the functional β -diversity of assemblages (McKinney and Lockwood 1999; Clavel et al. 2011). This type of biotic homogenisation is increasingly recognised as an important aspect of biodiversity change, since functional homogenisation reduces the ability of communities to respond to further human-driven or natural disturbances (Olden et al. 2004), and leads to a deterioration of the ecosystem services they provide (van der Plas et al. 2016).

Mountainous areas are particularly at risk of climate and land-use change. An increase in temperature frequently shifts the treeline towards higher elevation (Harsch et al. 2009), resulting in an alteration of the altitudinal distribution of forest and grassland habitats in addition to the change in climatic conditions. Moreover, although a typical consequence of climate change on mountain species is an upward distribution shifts to track their climatic niche (Chen et al. 2011), the topographic structure of mountains (Elsen and Tingley 2015), as well as the decreasing availability of oxygen at high elevation (Jacobsen 2020), may prevent range shifts to occur, putting alpine species at risk of extinction. By promoting the invasion of warm-adapted species in new environments and the extinction of cold-adapted species, climate change is potentially a strong driver of biotic homogenisation (Magurran et al. 2015). However, although

upward distribution shifts have been shown to be responsible for a gradual altitudinal homogenisation of vegetation communities in Canada (Savage and Vellend 2015), this pattern remains to be detected in a larger range of biogeographical contexts and taxonomic groups. Whether it translates into functional and phylogenetic homogenisation remains an open question too.

Using a replicated survey of historical (1940s–1960s) and recent (2012) bumblebee assemblages in sub-alpine habitats in Norway, we identified a change of bumblebee communities that is consistent with an effect of both climate and land-use change (Fourcade et al. 2019). This is in accordance with studies that have documented two distinctive patterns of the impact of climate change on bumblebees: poleward (Kerr et al. 2015; Biella et al. 2020), and altitudinal (Ploquin et al. 2013; Pyke et al. 2016; Biella et al. 2017) range shifts. Especially, our comparison with historical data revealed a shift towards more thermophilic species and a decline of the regional species pool by ca. 30%, while average local taxonomic diversity remained unchanged. Here, we aimed to investigate whether these patterns were associated with changes in functional and phylogenetic diversity and in β -diversity. Using a phylogeny of bumblebee species as well as a database of traits that we compiled for this study, we explored changes in functional and phylogenetic β -diversity, in addition to taxonomic β -diversity. Then, to study the process of functional homogenisation into more details, we tested how changes in occupancy and species' gains or losses were related to species traits.

Methods

Biodiversity data

A monograph published 50 years ago (Løken 1973), that aimed at providing a comprehensive inventory of Scandinavian bumblebees, served as a basis for historical data of bumblebee communities. This work provides the known localities of observation of all bumblebee species throughout Sweden and Norway, based on a compilation of more than 50,000 specimens carefully examined by the author. Part of these specimens originated from museum collections while the others were collected by the author during field trips carried out between 1940 and 1967 and were latter digitized and made available in Artskart (<https://artskart.artsdatabanken.no/>). Therefore, this database provides an extensive picture of the distribution of bumblebees in Scandinavia during the first half of the twentieth century.

Although details provided by Løken (1973) are insufficient to identify the exact sampling effort put into each inventoried site, we used information from the digitized records in Artskart to extract the collection date of

bumblebee specimens (Fourcade et al. 2019). This allowed us to estimate that, across the 18 sites we revisited (see below), most sites (10) were visited in a single year, while eight other sites were visited more often. Moreover, we also extracted the number of days each site was visited (median = 3), to ensure that our contemporary survey was comparable to the historical data.

We re-surveyed 18 of these sites in 2012, grouped into 9 pairs of sites such that each pair consisted of one site at a high elevation (ca. 1000 m.a.s.l., min. = 730 m, max. = 1000 m) and one site at a low elevation (ca. 500 m.a.s.l., min. = 440 m, max. = 765 m) (Fig. 1A). The selected sites covered a large latitudinal (60.42°–62.62°, ca. 240 km) and longitudinal (24°–10.61°, ca. 180 km) gradient. The study design thus allowed us to study effects of latitude, longitude and elevation separately. The maximum distance between two sites in a pair was 44.4 km, and the minimum distance was 2.6 km (median = 12.3 km). In all the 18 sites, we observed an mean elevation of temperature of +1.46 °C over the period separating historical and contemporary surveys, corresponding to an increase of 0.026 °C/year [min. = 0.003 °C/year (+0.17 °C), max. = 0.040 °C/year (+2.24 °C)]. At the same time, there were significant changes in land use, but no consistent conversion of one land-use type to another (Fourcade et al. 2019).

Because in some cases the location of the sites surveyed in the 1940s–1960s was described only by the combination of the elevation and the name of a farm or village, we surveyed bumblebees in multiple flower-rich habitats within a 1-km-radius circular area around the most likely location. Each site was surveyed twice between July 6 and July 27, 2012. During each visit, two experienced field entomologists visited as many different flower-rich habitats as possible during 2 h within the 1-km circle. The abundance of all bumblebee species encountered was recorded, mostly by visual identification in the field (when necessary, bumblebee specimens were collected for later identification). Accumulation curves of species richness for historical and contemporary

survey showed that our survey protocol likely captured the total species richness (Fourcade et al. 2019). Because bumblebee abundance was not available in the historical data, we used species occurrence data only in analyses.

Many of the rarest species mentioned in the 1940s–1960s inventories were not observed during the 2012 surveys. This pattern could potentially be caused by the non-detection of species occurring at low density, instead of representing a true change of bumblebee communities. To test if this could bias our interpretations, analyses were repeated after removing the eight species present in less than four sites in the historical data. Additional details about historical and contemporary data, study design and site selection can be found in Fourcade et al. (2019).

Species traits database

We compiled a database of nine functional traits that could potentially impact the response of species to land use or climate change (Online resource, Table S1). From Ødegaard et al. (2015), we extracted the following traits:

- (i) Social parasitism, describing whether a species is parasitic (lays its eggs in the nests of other bumblebees and are fed by their host, $N=5$) or not (builds colonies and produces workers, $N=19$). We expect parasitic species to be more susceptible to environmental disturbance as they depend on their host, especially in the context of climate change that can disrupt host-parasite interactions (Sheffield et al. 2013).
- (ii) Nesting habitat (below-, $N=15$; above-ground, $N=4$ or both, $N=4$).
- (iii) The main habitat type a species utilize (open lowland, $N=11$; forest, $N=5$; or alpine/sub-alpine, $N=8$).
- (iv) The number of different habitat types (of those mentioned above, i.e. ranging from 1 to 3) that a species

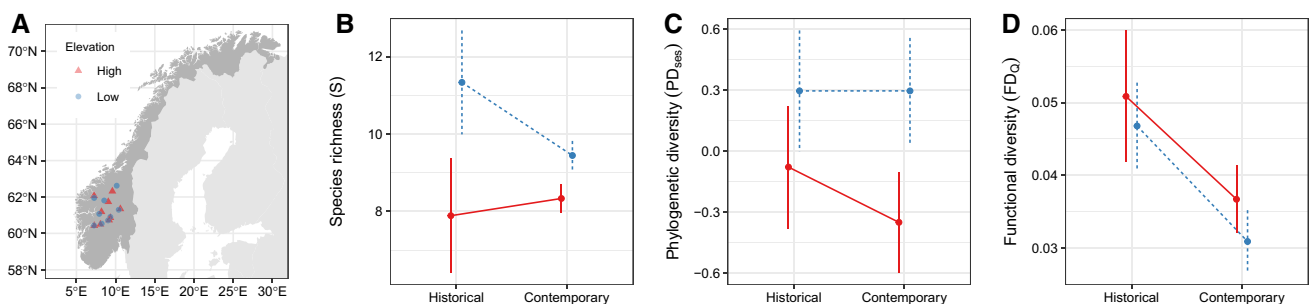


Fig. 1 Map of the 18 sites surveyed in Norway (in dark grey) (A), and variation of species richness (B), standardized phylogenetic diversity (C) and functional diversity (D) between historical and contempo-

rary surveys. In B, C and D, values are the mean \pm s.e.m. across the 9 low- and 9 high-elevation sites. In all plots, low-elevation sites are displayed in blue and high-elevation sites in red

can occupy, as a proxy for niche width (1, $N=8$; 2, $N=3$; 3, $N=13$).

- (v) Queen body length, as a proxy for dispersal ability (Greenleaf et al. 2007), a trait that describes how well a species can colonise new habitats as they become suitable as a result of land-use conversion or climate change.
- (vi) Emergence of the first queen as a proxy for species relative phenologies. Emergence date is also usually correlated with colony size since colonies founded early in the season have a longer reproduction period and can produce larger colonies (Müller and Schmid-Hempel 1992).

Then, we extracted from Ranta (1982) and Persson et al. (2015):

- (vii) Proboscis length, which is linked to foraging preference. It has been suggested that longer proboscis is associated with a more specialised diet (Goulson et al. 2005). Ranta (1982) contained data for all study species but, since there was a more recent compilation of the same trait for a smaller set of species (Persson et al. 2015), that moreover showed substantial differences in the estimated value of proboscis length, we chose to use average values from both studies when possible.

Finally, we extracted the following traits from Rasmont et al. (2015), where these were derived from species distribution models:

- (viii) Species temperature index (STI, the average temperature experienced by a species across its range), to represent the thermal adaptation of species. In a context of climate change, we therefore expect warm-adapted species to perform better.
- (ix) Range size, also related to species climatic niche as it represents the range of temperature conditions that a species can occupy.

After checking for correlations between traits, it appeared that range size, emergence date and habitat type were highly correlated to STI (Online resource, Figure S1). Therefore, we used only the latter in further analyses, resulting in a total of six species traits.

Data analyses

Diversity metrics

We calculated three measures of diversity for each site and for the historical and contemporary surveys. First, we extracted the number of species identified within a community as a measure of species richness (S). Second, we computed a measure of phylogenetic diversity (PD) expressed as the sum of the lengths of all phylogenetic branches spanned

by the species present (Faith 1992). We obtained phylogenetic data from the molecular-based phylogeny of bumblebee species of Cameron et al. (2007), available at TreeBase (treebase.org: study 1927, tree Tr2906). Since phylogenetic diversity is highly correlated with species richness, we standardized PD by extracting its effect size (PD_{ses}) compared to a null model in which species were randomly shuffled across the tips of the phylogenetic tree (Kembel 2009). The tree was reshuffled 1000 times and PD_{ses} was calculated as the deviation of the observed PD from the mean value of PD across all reshuffled trees divided by the standard deviation of the PD values from the reshuffled trees. PD and PD_{ses} were computed with the “picante” R package (Kembel et al. 2010), using the “rotl” R package (Michonneau et al. 2016) to access the phylogenetic tree. Finally, we also computed a measure of functional diversity based on the functional traits that we compiled. We chose to use Rao’s quadratic entropy Q index as a measure of functional diversity (hereafter referred to as FD_Q) as it has been shown to be independent of species richness (Mouchet et al. 2010). FD_Q was calculated using the “FD” R package (Laliberte and Legendre 2010). We used linear mixed models to assess whether S , PD_{ses} and FD_Q differed between periods (historical and contemporary surveys). We also tested whether these diversity metrics varied geographically by including the elevation (low or high), longitude and latitude of sites and their interactions with the period of survey. Since surveyed sites were grouped by pairs of high- and low-elevation sites, we included the identity of site pairs as a random effect. Note that variation of species richness was already analysed in Fourcade et al. (2019), and the purpose is here to test whether the pattern identified in species richness still holds when considering phylogenetic and functional diversity.

Community composition and beta diversity

To visualize differences in community composition between sites and their temporal trajectories, we performed a Non-metric Multidimensional Scaling analysis (NMDS), based on the Jaccard dissimilarity index. We tested for statistical differences in community composition between elevations and between sampling periods using a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) with 10,000 permutations to assess significance. To test for different temporal trajectories between low and high elevations, we included as predictors in the PERMANOVA the interaction between elevation and sampling period. We also added the interaction between latitude and longitude to control for spatial autocorrelation. Moreover, we tested for differences in the dispersion of assemblages between historical and contemporary surveys, separately for high and low-elevation sites. NDMS, PERMANOVA and dispersion

analyses were performed using the “vegan” R package (Oksanen et al. 2015).

Beta-diversity was assessed by calculating the pairwise community dissimilarity between sites based on the Jaccard index. Specifically, we computed dissimilarity values for each period and among all high elevation sites, among all low-elevation sites, and between low- and high-elevation sites for each pair of sites. We estimated not only the classical taxonomic β -diversity based on species identity, but also the phylogenetic β -diversity which measures the phylogenetic distance between sets of taxa, and the functional β -diversity based on the intersection of convex hulls in the multidimensional functional space (Villegger et al. 2011). The three types of β -diversity were decomposed into their turnover component, which reflects the replacement of species between sites, and their nestedness component, which reflects the loss or gain of species from site to site (Baselga 2010). In addition, we estimated the temporal change in species assemblages within each site using the same measures of taxonomic, phylogenetic and functional β -diversity, calculated here between the historical and contemporary surveys. All indices of β -diversity were based on pairwise community dissimilarity measures computed using the “betapart” R package (Baselga and Orme 2012). We ran ANOVAs and post hoc Tukey tests to assess whether the various measures of β -diversity significantly changed between historical and contemporary surveys. For β -diversity among high- or low-elevation sites, we included the elevation and its interaction with the period of survey as additional predictors.

Association between community trends and species traits

We aimed to identify whether the patterns of community shifts that we observed were driven by changes in the distribution of species sharing similar traits. For this purpose, we adopted three complementary approaches. First, we described graphically the density distribution of each of the four continuous species’ traits in the historical and contemporary datasets, separating between low- and high-elevation sites. This way, we could assess whether the mean values of traits have changed over time, while also visualising their variance. For categorical traits (social parasitism and nesting habitat), we simply reported the proportion of each category of traits found in historical and contemporary sampling, again for low- and high-elevation sites separately. Note that since we work with presence-only data, traits’ distributions and proportions do not account for relative species abundance but depend only on the number of occurrences of species exhibiting these traits across the 18 sampling sites.

Second, we assessed the effect of species traits on the change in (apparent) site occupancy between the historical and contemporary surveys. Occupancy represents, for each species, the proportion of sites occupied. We modelled

the change in occupancy—expressed as the ratio of occupancy in the contemporary sampling to the occupancy in the historical sampling—as a generalized linear model with a Gaussian distribution of errors and a log link to normalise the residuals.

Third, we estimated the effect of species traits on apparent colonisations and extinctions between the historical and contemporary time periods. Since we do not know for sure whether the detection of a new species in a site or its apparent extirpation reflect a true, long term, colonisation or extinction, we referred to these events as gains and losses (in the sense of species ‘gained’ and ‘lost’ from the data, whatever the underlying ecological process). Specifically, losses and gains were represented as follow: a loss was coded 0 for a species that was reported in a given site in the 1960s and was found again in the 2012 survey, and 1 if the species was not reported anymore. Reciprocally, gains were coded 0 for a species that was not detected in a site neither in the historical nor in the contemporary survey, and 1 if the species was reported in this site in 2012. Probabilities of gain and loss were modelled using binomial generalized linear mixed models with logit link and the following random effects: site pair, site identity nested within site pair, and species identity.

For the three models, we included in a first step parasitism, queen length, STI, niche width and nesting habitat as explanatory variables. In a second step, we aimed to test the effect of proboscis length, which could not be included in the first step because parasitic species do not produce workers. Therefore, we ran the same models for non-parasitic species only, replacing social parasitism by proboscis length from the explanatory variables. Since the nesting habitat of *Bombus cingulatus* is unknown (Mossberg and Cederberg 2012), we excluded this species from these analyses. However, we verified that assigning either below-ground, above-ground or both as nesting habitat for this species would not change the results qualitatively.

Results

Changes in regional and local diversity

We already identified in Fourcade et al. (2019) that the total observed number of species decreased from 23 in the historical survey to 16 in the contemporary survey (Online resource, Table S2). Similar to the pattern for species richness (see Fourcade et al. 2019, and Fig. 1B), standardised phylogenetic diversity per site was higher in low-elevation sites but did not change between the historical and contemporary surveys (Table 1 and Fig. 1C). However, we observed here that the average functional diversity of bumblebee assemblages was similar at low and high elevation and exhibited a strong reduction over time (Table 1, Fig. 1D).

Table 1 Results of the linear mixed models that tested the effect of survey period, elevation and geography on (standardized) phylogenetic and functional diversity per site

	Phylogenetic diversity (PD _{ses})			Functional diversity (FD _Q)		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Period	1, 23.98	0.32	0.56	1, 23.85	6.69	0.02
Elevation	1, 24.08	4.19	0.05	1, 23.94	0.77	0.39
Latitude	1, 6.23	0.55	0.49	1, 6.06	1.34	0.29
Longitude	1, 6.48	2.94	0.13	1, 6.27	0.01	0.91
Year × elevation	1, 23.98	0.32	0.58	1, 23.85	0.02	0.88

F tests are reported for each factor, with *P* values < 0.05 highlighted in bold font. We also report marginal and conditional R^2 . Species richness was analysed in (Fourcade et al. 2019) and showed that the number of species detected was larger at higher elevation but did not significantly change between the historical and contemporary surveys

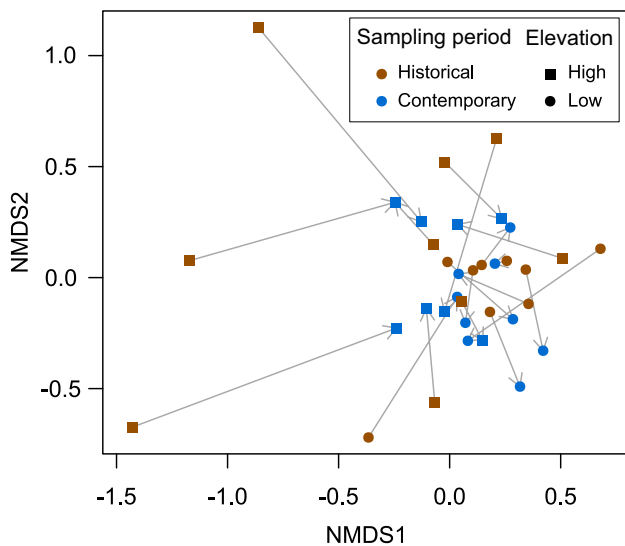


Fig. 2 Nonmetric multidimensional scaling representation of the historical (brown) and contemporary (blue) bumblebee sampling. Arrows show the temporal trajectory of each sampling site. Sites of high and low elevation are presented as squares and dots, respectively

This pattern remained when the eight rarest species were excluded from the analyses (Online resource, Table S3).

Changes in β -diversity

The NDMS demonstrated a shift in community composition over time (Fig. 2). This was confirmed by the PERMANOVA ($F_{1,29} = 2.11$, $P = 0.03$) which also revealed differences in community composition between sites at high and low elevations ($F_{1,29} = 3.54$, $P < 0.01$) as well as a longitudinal trend in community composition ($F_{1,29} = 2.36$, $P = 0.02$), but no interaction between elevation or longitude and year. These patterns remain when the eight rare species were excluded from the analysis (Online resource, Table S4).

Over time, high-elevation communities had become more similar to low-elevation communities (Fig. 2). Specifically, in the historical data, high-elevation sites had much more

heterogeneous species compositions than low-elevation sites, as evidenced by the dispersion around the mean (high elevation = 0.44, low elevation = 0.23, $F_{1,16} = 7.73$, $P = 0.01$), but in the contemporary data there was no such difference (0.26 vs 0.23, $F_{1,16} = 0.62$, $P = 0.44$). This was because species assemblages at high elevations had become more homogenous over time (0.44 vs. 0.26, $F_{1,16} = 8.92$, $P = 0.01$), while the dispersion at low-elevation sites did not change (0.23 vs. 0.23, $F_{1,16} = 0.01$, $P = 0.94$). We obtained similar results when the eight rarest species were excluded (Online resource, Table S5).

Historically, taxonomic, functional and phylogenetic β -diversity were higher at high-elevation sites, but decreased over time. At the same time, total β -diversity remained constant at low elevation, so that there were no differences in β -diversity of any of these biodiversity facets between high and low elevations in the contemporary data (Table 2, Fig. 3). More specifically, the declines in taxonomic and phylogenetic β -diversity were driven by a decrease in the nestedness component of β -diversity. At high (but not at low) latitudes, this was the case also for functional β -diversity (Table 2, Fig. 3). Although the turnover component of β -diversity did not change at high elevation, low-elevation sites exhibited an increase in taxonomic turnover that balanced the decreased in nestedness, which explained why total taxonomic β -diversity remained constant at low elevation (Table 2, Fig. 3).

Overall, the β -diversity between high and low elevations did not change over time, but for taxonomic β -diversity there was a shift from the between-elevations β -diversity being explained mainly by nestedness historically to being explained mainly by turnover in the contemporary data (Table 2, Fig. 3).

Traits distribution, occupancy and species' gains/losses

We could not detect any clear and consistent change in the distribution of queen length or proboscis length (Fig. 4).

Table 2 Results of models explaining the variation of taxonomic, phylogenetic and functional β -diversity (measured as the pairwise dissimilarity between sites, and partitioned between their nestedness and turnover components)

	Total		Nestedness		Turnover	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Taxonomic β -diversity						
<i>Within elevations</i>	<i>F</i> _{1, 140}	<i>P</i>	<i>F</i> _{1, 140}	<i>P</i>	<i>F</i> _{1, 140}	<i>P</i>
Period	40.57	< 0.01	56.47	< 0.01	5.00	0.03
Elevation	46.79	< 0.01	2.42	0.12	13.68	< 0.01
Period \times elevation	27.22	< 0.01	1.26	0.26	8.31	0.01
<i>Between elevations</i>	<i>F</i> _{1, 15}	<i>P</i>	<i>F</i> _{1, 15}	<i>P</i>	<i>F</i> _{1, 15}	<i>P</i>
Period	1.66	0.22	7.63	0.01	5.23	0.04
Phylogenetic β -diversity						
<i>Within elevations</i>	<i>F</i> _{1, 140}	<i>P</i>	<i>F</i> _{1, 140}	<i>P</i>	<i>F</i> _{1, 140}	<i>P</i>
Period	23.08	< 0.01	28.11	< 0.01	0.93	0.34
Elevation	7.47	0.01	2.07	0.15	2.11	0.15
Period \times elevation	6.39	0.01	0.84	0.36	3.50	0.06
<i>Between elevations</i>	<i>F</i> _{1, 15}	<i>P</i>	<i>F</i> _{1, 15}	<i>P</i>	<i>F</i> _{1, 15}	<i>P</i>
Period	2.12	0.17	1.83	0.20	0.03	0.87
Functional β -diversity						
<i>Within elevations</i>	<i>F</i> _{1, 132}	<i>P</i>	<i>F</i> _{1, 132}	<i>P</i>	<i>F</i> _{1, 132}	<i>P</i>
Period	3.04	0.08	5.64	0.02	1.58	0.21
Elevation	5.54	0.02	0.39	0.54	24.54	< 0.01
Period \times elevation	3.60	0.06	2.69	0.10	0.07	0.79
<i>Between elevations</i>	<i>F</i> _{1, 15}	<i>P</i>	<i>F</i> _{1, 15}	<i>P</i>	<i>F</i> _{1, 15}	<i>P</i>
Period	0.05	0.83	0.69	0.42	0.87	0.37

Significant factors are highlighted in bold font

However, as reported in Fourcade et al. (2019), there was a shift towards higher values of species temperature index. We also observed a tendency towards higher values of niche width, i.e. there was an increase in the occurrence of generalist species (adapted to three habitat types) at the expense of species inhabiting one or two habitats. Generally, we found slightly more often species using above-ground habitats in the contemporary survey than in the past. There was also a reduction in the proportion of parasitic species (Fig. 4).

Among the 23 bumblebee species, the regional occupancy had declined for 16, six had expanded and one remained stable. The change in species' occupancy patterns was not significantly related to any trait (Table 3). We note, though, that there was a near significant ($P=0.07$) tendency for an increase in the occupancy of species with a larger niche.

A total of 36 apparent colonisations (i.e. gains of new species in sites where they were previously absent) were detected, 23 occurred at high elevation and 13 at low elevation. Forty-nine apparent extinctions (i.e. species lost from sites where they were detected in the historical data) occurred between the historical and contemporary surveys, among which 19 were observed at high elevation and 30 at low elevation. Analyses showed both a risk of species loss and a lower probability of species gain in species with a narrow niche (Table 3 and Fig. 5). Probabilities of gaining or losing species were also explained by social parasitism

(Table 3). Parasitic species had a much higher risk of disappearing from a given site, and were also slightly less likely to be found in new sites (Fig. 5). Surprisingly, species with a low temperature index, i.e. those adapted to colder climates, were more likely to be found in new sites (Table 3 and Fig. 4). When only non-parasitic species were analysed, proboscis length also appeared to be a significant predictor of both species gain and loss. Species with a longer proboscis were slightly more likely to be detected in new sites in the contemporary compared to historical survey, and less likely to have been lost (Table 3 and Fig. 5).

Discussion

The replication of an inventory of bumblebees from 50 to 70 years ago that we described in this study revealed substantial changes in the composition of sub-alpine bumblebee communities in Norway. Importantly, most of these changes could not have been identified by a basic record of the identity of species in individual sites (i.e. taxonomic α -diversity). Although there was no net change in local species richness (Fourcade et al. 2019), we detected a considerable loss of functional diversity in bumblebee assemblages, along with a taxonomic, phylogenetic and functional homogenization of these assemblages (i.e. a decrease in β -diversity). This

Fig. 3 Taxonomic, phylogenetic and functional β -diversity in the historical and contemporary surveys, expressed as the total, nestedness and turnover dissimilarity. Measures of β -diversity are presented as the mean pairwise Jaccard dissimilarity index \pm standard errors between assemblages of high (red solid lines) and low (blue dotted lines) elevations. Identical letters within a sub-plot indicate values that do not significantly differ in post hoc tests. Significance of main effects and interactions can be found in Table 2. Green dotted lines show the same measures of β -diversity presented between high- and low-elevation sites for a given site pair, with significant differences between contemporary and historical surveys highlighted by a star

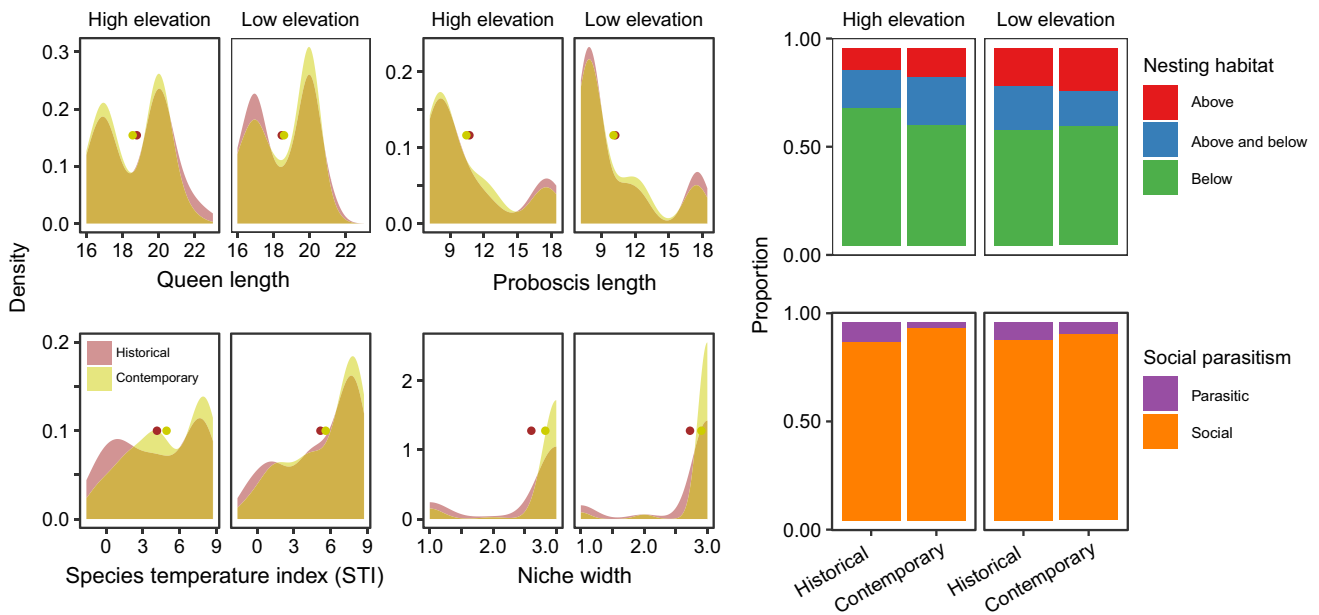
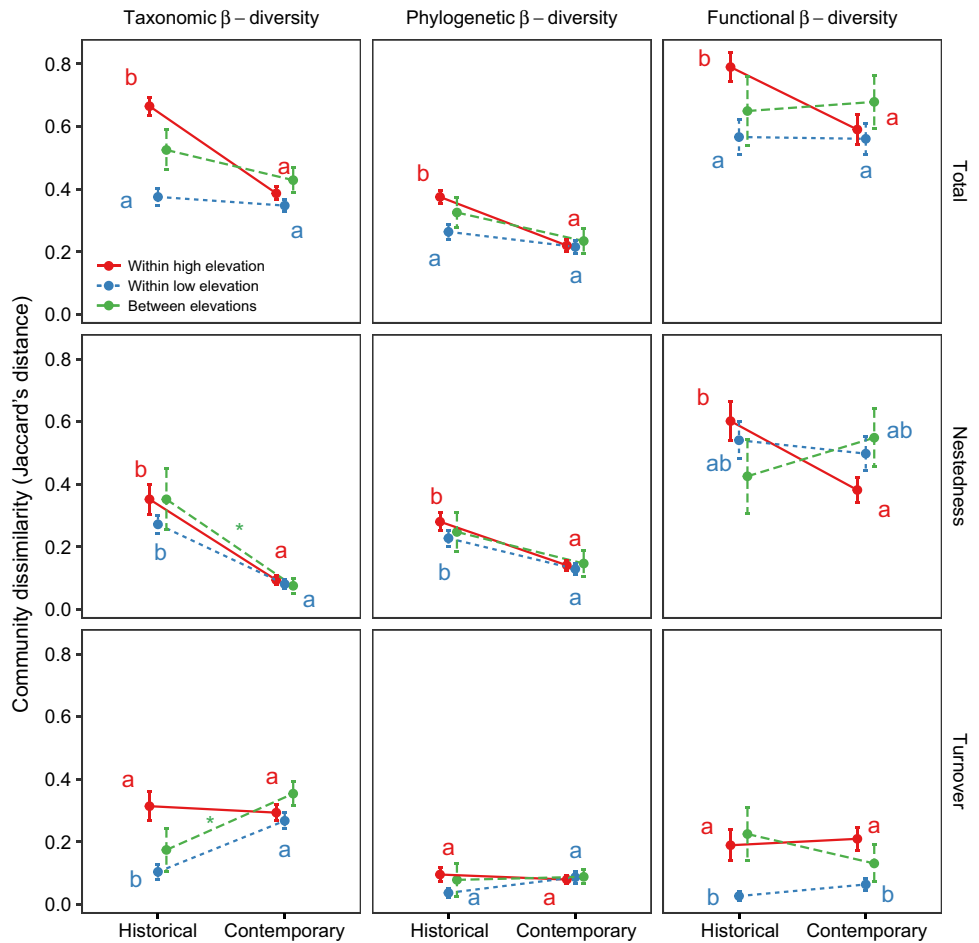


Fig. 4 Density distribution of four continuous species traits, and proportion of parasitic/non-parasitic species, and of each type of nesting habitat, in the historical and contemporary surveys, separately

for low- and high-elevation sites. For better visualisation of potential shifts in continuous traits, mean values are also plotted as dots in the middle of density distribution graphs

Table 3 Summary table of the generalized linear (mixed) models explaining change in occupancy, colonisation probability and extinction probability as a function of species traits

	Change in occupancy		Probability of species loss		Probability of species gain	
	Estimate ± SE	P	Estimate ± SE	P	Estimate ± SE	P
(a) With parasitic species						
Intercept	-7.74 ± 6.78	0.27	15.59 ± 6.66	0.02	-18.19 ± 7.20	0.01
Parasitic status ^a	1.38 ± 1.17	0.26	-3.75 ± 1.16	<0.01	2.64 ± 0.79	<0.01
Nesting habitat ^b						
A/B	0.50 ± 1.65	0.77	-0.56 ± 1.27	0.66	1.80 ± 1.17	0.13
B	-0.44 ± 1.49	0.77	-0.22 ± 1.05	0.84	-0.81 ± 0.90	0.37
Niche width	1.32 ± 0.57	0.04	-1.86 ± 0.56	<0.01	3.80 ± 0.91	<0.01
Queen length	0.22 ± 0.34	0.54	-0.41 ± 0.29	0.16	0.42 ± 0.32	0.19
STI	-0.06 ± 0.16	0.71	-0.11 ± 0.15	0.47	-0.47 ± 0.17	<0.01
(b) Without parasitic species						
Intercept	-8.67 ± 10.3	0.42	8.18 ± 5.79	0.16	-16.37 ± 6.95	0.02
Nesting habitat ^b						
A/B	1.74 ± 2.17	0.44	-0.32 ± 1.18	0.79	1.70 ± 1.42	0.23
B	0.21 ± 1.90	0.91	0.00 ± 0.98	1.00	-1.11 ± 0.85	0.19
Proboscis length	0.17 ± 0.23	0.48	-0.28 ± 0.15	0.07	0.52 ± 0.18	<0.01
Niche width	1.44 ± 0.71	0.07	-1.77 ± 0.50	<0.01	4.15 ± 1.00	<0.01
Queen length	0.17 ± 0.51	0.75	-0.05 ± 0.31	0.88	0.14 ± 0.35	0.69
STI	0.05 ± 0.21	0.82	-0.23 ± 0.17	0.16	-0.40 ± 0.19	0.02

Models were run with all species and including social parasitism as an explanatory variable, or with non-parasitic species only and including proboscis length. Significant variables are highlighted in bold font

^aNon-parasitic taken as reference

^bAbove ground taken as reference (B: below, A/B: above and below)

is in accordance with other findings that showed that trends in these different facets of the diversity of assemblages may sometimes be largely decoupled (Devictor et al. 2010; Monnet et al. 2014). With this result, we call attention to the necessity of describing biodiversity changes in all their facets and at different spatial scales, to get a more precise

picture of the long-term responses of species and communities to human activity.

Patterns in phylogenetic diversity largely mimicked those observed in terms of species richness, i.e. no change in average diversity between the historical and contemporary surveys, even if we used an index of phylogenetic diversity that is corrected by the number of species observed. Moreover,

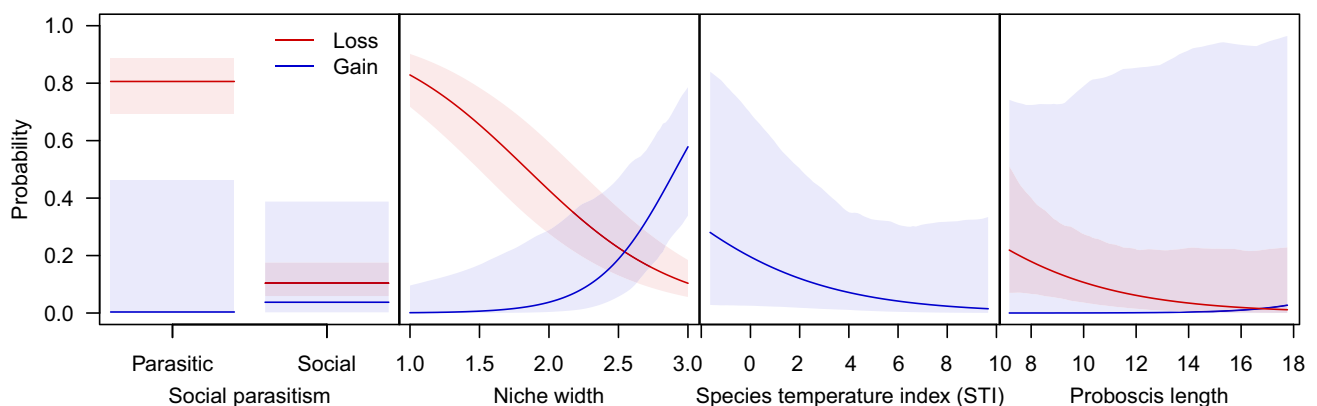


Fig. 5 Partial regression plots showing the effect of the significant factors explaining probabilities of species gains and losses (shown as blue and red lines, respectively) between the historical and contemporary surveys.

Confidence intervals around mean partial trends were estimated using a bootstrap procedure. Full model results are shown in Table 3

although this effect was not strictly significant at the $\alpha=0.05$ level, low-elevation sites seemed to harbour on average a larger phylogenetic diversity than their high-elevation counterparts, similar to what we observed for species richness. Elevational gradients in species diversity are fairly ubiquitous, even if often nonlinear (Sanders and Rahbek 2012). Since our standardized measure of phylogenetic diversity (PD_{ses}) is actually an index of phylogenetic clustering/dispersal, if the effect of elevation on PD_{ses} we observe is real, it means that high-elevation assemblages are on average composed of species that are more phylogenetically close to each other than expected given their level of species richness. Because there is often a strong phylogenetic signal in important physiological traits (Webb et al. 2002)—as it is likely the case here with several alpine species belonging to the subgenus *Alpinobombus* it may represent selective pressure for some specific traits that make high-elevation species adapted to their environmental conditions. Here, as an illustration of phylogenetic clustering, high-elevation communities were composed of seven subgenera only, which was a subset of the ten subgenera found at low elevation (*Subterraneobombus*, *Thoracobombus* and *Melanobombus* were missing from the high-elevation sites). Interestingly, Hoiss et al. (2012) and Pellissier et al. (2013) also found that phylogenetic clustering of bumblebee communities was associated with higher elevation and lower temperature. Contrary to species richness and (standardized) phylogenetic diversity, we observed a severe decline (-30%) in the functional diversity of bumblebee communities between historical and contemporary surveys. Bumblebees are pollinators of a wide range of plant species in sub-alpine ecosystems (Marshall et al. 2020); such decline in their functional diversity may thus have unexpected consequences for the maintenance of plant communities in mountainous regions.

Different analyses converged to show a strong homogenisation of bumblebee communities, but suggesting different underlying processes at low and high elevations. The decomposition of β -diversity revealed a decrease in the nestedness of assemblages, both between elevations and among low- and high-elevation sites. Decline in nestedness among sites might reflect the loss of a few historically rare species that lead to a shift of communities towards a more restricted pool of common species. Interestingly, this pattern still holds when the rarest species were excluded from the dataset. In contrast, decline in between-elevation nestedness is consistent with the hypothesis that species shifted their altitudinal distribution uphill and colonised new sites at higher elevation. Several studies conducted in different areas showed an elevational shift of bumblebee distributions (Ploquin et al. 2013; Kerr et al. 2015; Pyke et al. 2016; Biella et al. 2017; Marshall et al. 2020). Here as well we observed that the majority of species losses occurred at low elevation, resulting in a decrease in species richness, while trends in species

richness tended to be positive on average at high-elevation sites (Fourcade et al. 2019). In addition, the spatial turnover of species increased at low elevation while it remained constant among high-elevation sites. It maintained stable the total β -diversity of low-elevation communities by balancing the decrease in nestedness and made spatial turnover now similar across elevations. As a consequence of these processes, not only did bumblebee communities become more similar overall, species assemblages also homogenised along the altitudinal gradient. Specifically, high-elevation assemblages that used to be less species-rich and to have a higher β -diversity now resemble communities at low elevations.

In agreement to the observed decline in functional β -diversity, the homogenisation of communities and decrease of regional species richness appeared to be mainly driven by a loss or decline of parasitic and specialised species. We could not test if this result was robust to the exclusion of rare species because they also represent most of the parasitic or narrow-niche species. However, the patterns we identified match what was observed elsewhere. For example, among the eight species that were lost compared to the historical data, three are listed as vulnerable in the Norwegian (*B. distinguendus* and *B. ruderarius*) or European (*B. pyrrhopygus*) Red Lists (Nieto et al. 2014). Generally, parasitic bees have been shown to be more sensitive to environmental disturbance than non-parasitic species (Sheffield et al. 2013). This is usually driven by the co-extinction of parasites following the extinction of their host (Koh et al. 2004), an effect that can be exacerbated when climate change drives spatial or temporal mismatch between hosts and parasites (Roberts et al. 2011). Moreover, a decline of diet-specialist bumblebees has been frequently observed (see for example Goulson et al. 2005). Here, we defined specialisation according to the range of different habitats that species can occupy. Even if this factor was based on a very coarse classification, it was the main driver of occupancy change and apparent species gains and losses. Typically, habitat specialists and rare species are more prone to decline and extinction, because they are less resilient to habitat loss or fragmentation and have often smaller population sizes (Foufopoulos and Ives 1999; Davies et al. 2004). Habitat- or diet-specialist species are also generally rarer and exhibit narrower climatic niches, making them particularly at risk of extinction in a context of rapid climate and land-use change (Williams et al. 2007).

Surprisingly, we observed a negative relationship between the probability of gaining a new species in a site and species' STI. Although counterintuitive at first glance, this result can be explained by the fact that we observe a lot more often gains of new species in high elevation sites than in low-elevation sites, which suggested that species adapted to alpine habitats, which are also those with a low STI (see Online resource, Figure S1), were more likely to colonize new sites. This is consistent with the hypothesis of altitudinal shifts

due to climate change, favouring species adapted to alpine environments, while higher human disturbance at low elevation prevented colonisations of new sites by lowland and forest species.

In spite of convergent evidence for drastic shifts in bumblebee communities towards a stronger dominance of short-tongued generalist species (Dupont et al. 2011; Bommarco et al. 2012), we did not find such result here. In fact, we even observed the opposite trend, namely a probability of short-tongued species being lost, while species with a longer tongue were more likely to occur at new sites. This may be because studies that documented shifts in tongue size were conducted in very different settings, i.e. in regions of intensive agriculture. In sub-alpine environments as in our study, land use is generally extensively managed such that we expect different drivers, such as climate change, to be responsible for long-term community changes. Shifts in plant communities may also have been drastically different than those observed in lowland habitats, favouring different species. In alpine regions, proboscis length has also been shown to be linked to temperature gradients and floral resources, with a dominance of short-tongued species in colder conditions where resources are scarce and plant communities have a low diversity (Pellissier et al. 2013). Therefore, a warming climate may have increased plant diversity at higher elevations, allowing specialised species with long proboscis to occupy new sites. Generally, this finding highlights the need for more studies of biodiversity change across a wide range of ecoregions, since trends observed in well-studied regions under intensive lands use might not be universally representative.

Using a large set of convergent analyses, we documented a strong homogenisation of bumblebee assemblages across a large environmental gradient, presumably caused by the altitudinal shift of species and the loss of specialist species. It should be noted that we draw these conclusions based on data from two different time points only. Hence, there is a risk that, if interannual species turnover is larger than long-term trends in community composition, our results are an artefact of fast-changing factors that occurred at our sampling sites at the times of survey (e.g. stochastic extinctions, extreme climate event, random dispersion, etc.). However, our observations are consistent to what is expected under climate change (see Fourcade et al., 2019), and match other patterns observed in different contexts. For instance, similar homogenisation of bumblebee communities in montane areas has been found (Ploquin et al. 2013) or predicted (Pradervand et al. 2014) in other regions. Analyses of temporal trends in multiple facets of biodiversity have frequently pointed out a mismatch between taxonomic, phylogenetic and functional diversity (Devictor et al. 2010; Monnet et al. 2014; De Palma et al. 2017). Although this mismatch exists when investigating mean diversity per site, in contrast, our

main results were consistent when considering taxonomic, phylogenetic and functional β -diversity, showing that current species assemblages are composed of more closely related and more functionally similar species than they were ca. 50 years earlier. The underlying processes, however, slightly differed. We did not detect any change in phylogenetic and functional β -diversity between elevations, and there was no change in the functional β -diversity of high-elevation sites, the latter remaining more functionally diverse than low-elevation sites. Generally, a reduction of phylogenetic diversity implies that communities may have lost the evolutionary potential that would have helped them adapt to global changes (Lavergne et al. 2010). Moreover, knowing how it can affect ecosystem functioning is of crucial importance for pollinators. Functional homogenisation has been shown to be detrimental for pollination service in agroecosystems (Hoehn et al. 2008); whether a similar response to functional homogenisation of pollinators exists in (semi-) natural ecosystems remains an open, but important, question. In a context where a crucial challenge of global change science is to identify the complex interaction between species traits, climate change and land-use change, and how it affects ecosystems, using multifaceted descriptors of biodiversity change at various scales may prove to be an essential strategy.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-021-04970-3>.

Acknowledgements We thank S. Fröberg, M. Johansson, S. Larsson and M. W. Pettersson for their assistance in the field.

Author contribution statement EÖ and SÅ conceived and designed the fieldwork, YF analysed the data and wrote the manuscript under the supervision of EÖ. All authors conceived the original ideas and contributed to the final version of the manuscript.

Funding This study was funded by the Swedish Research Council Vetenskapsrådet, Grant Number 621-2010-5589. Y.F. was additionally funded by the Swedish Research Council FORMAS, Grant Number 2016-00667.

Availability of data and materials This manuscript reuses data from Fourcade et al (2019), available from the Figshare repository: <https://doi.org/10.6084/m9.figshare.6833531.v1>. All new data (e.g.: species' traits) are available in electronic supplemental material.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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