

Contrasting effects of biotic interactions on richness and distribution of vascular plants, bryophytes and lichens in an arctic-alpine landscape

Heidi K. Mod¹, Risto K. Heikkinen², Peter C. le Roux^{1,3}, Henry Väre⁴ & Miska Luoto¹

¹ Department of Geosciences and Geography, University of Helsinki, P.O. Box 64, 00014 University of Helsinki, Finland.

² Natural Environment Centre, Finnish Environment Institute, P.O. Box 140, 00251 Helsinki, Finland.

³ Department of Plant Science, University of Pretoria, Private Bag X20, Pretoria 0002, South Africa.

⁴ Botanical Museum, Finnish Museum of Natural History, P.O. Box 7, 00014 University of Helsinki, Finland.

Corresponding author: Heidi K. Mod, heidi.mod@helsinki.fi, +358 (0) 408273212

ABSTRACT

Biotic interactions may strongly affect the distribution of individual species and the resulting patterns of species richness. However, the impacts can vary depending on the species or taxa examined, suggesting that the influences of interactions on species distributions and diversity are not always straightforward and can be taxon-contingent. The aim of this study was therefore to examine how the importance of biotic interactions varies within a community. We incorporated three biotic predictors (cover of the dominant vascular species) into two correlative species richness modelling frameworks to predict spatial variation in the number of vascular plants, bryophytes and lichens in arctic-alpine Fennoscandia, in N Europe. In addition, predictions based on single-species distribution models were used to determine the nature of the impact (negative vs. positive outcome) of the three dominant species on individual vascular plant, bryophyte and lichen species. Our results suggest that biotic variables can be as important as abiotic variables, but their relative contributions in explaining the richness of sub-dominant species varies among dominant species, species group and the modelling framework implemented. Similarly, the impacts of biotic interactions on individual species varied among the three species groups and dominant species, with the observed patterns partly reflecting species' biogeographic range. Our study provides additional support for the importance of biotic interactions in modifying arctic-alpine biodiversity patterns, and highlights that the impacts of interactions are not constant across taxa or biotic drivers. The influence of biotic interactions, including the taxon-contingency and range-based impacts, should therefore be accounted for when developing biodiversity forecasts.

Keywords: *Betula nana*, *Betula pubescens* ssp. *czerepanovii*, *Empetrum hermaphroditum*, species distribution model, species richness model, vegetation

INTRODUCTION

The considerable influence of biotic interactions on species assemblages has been demonstrated both in experimental (e.g. Shevtsova et al. 1995; Shevtsova et al. 1997; Liancourt et al. 2005; Aerts 2010; Bråthen and Lortie in press), and modelling studies (e.g. Araújo and Luoto 2007; Meier et al. 2010; Giannini et al. 2013; González-Salazar et al. 2013; le Roux et al. 2014; Mod et al. in press). However, in studies examining multiple species, the impacts of biotic interactions on individual species have often varied depending on the species or taxa examined (e.g. Shevtsova et al. 1995; Pellissier et al. 2010). This suggests that the impacts of biotic interactions on species richness and distribution are not always straightforward and that drawing generalisations from one species (or taxon) to another may be difficult (Löbel et al. 2006; Nylén et al. 2013). These limitations in the understanding of the role of biotic interactions in the assembly of communities may have important implications in terms of, for example, biodiversity conservation (Gilman et al. 2010) and climate change impact assessments (Pearson and Dawson 2003; Araújo and Luoto 2007).

Ecological experiments encompassing entire communities (or even just dominant species) are often logistically impractical and economically prohibitive. Thus, there has been an increasing interest to incorporate known, tentative or potential biotic interactions into species distribution and richness modelling (e.g. Araújo and Luoto 2007; Meier et al. 2010; Pellissier et al. 2010; Nylén et al. 2013; le Roux et al. 2014). Such correlative approaches enable us to infer the potential importance of biotic interactions across larger numbers of species and bigger areas (Kissling et al. 2012), allowing the assessment of the impacts of species interactions at the community level (Wisz et al. 2013). Studies simultaneously covering a larger array of species and environmental drivers could thus complement spatially-limited experimental studies that focus only on a very small subset of a community. When using modelling approaches, it is, however, essential to incorporate all the

influential predictors to the models to avoid a situation where species co-occurrence patterns only represent shared physiological tolerances and/or requirements of species (Ovaskainen et al. 2010). When studying biotic interactions, this means that in addition to biotic drivers, also the ecologically relevant abiotic factors, including temperature, water, nutrients and radiation related variables, must be accounted.

Systems with relatively simple interaction networks, such as arctic and alpine environments, provide an ideal setting to study biotic interactions (Olofsson 2004; Wisz et al. 2013). In arctic-alpine tundra of high-latitude Europe, three species have previously been identified to have strong impacts on the distribution, performance and/or richness of other species (i.e. ecological engineers as defined in Jones et al. (1994) and (1997)): *Empetrum hermaphroditum* Hagerup, *Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti, and *Betula nana* L. (Jonasson 1992; Eränen and Kozlov 2007; Aerts 2010; le Roux et al. 2013a). The impacts of these three dominant species can be both negative (e.g. allelopathy and competition for resources) and positive interactions (e.g. ameliorating micro-climatic conditions). However, despite a good ecological understanding of these species and their interactions with some co-occurring species, their net influence across entire communities remains difficult to predict due to the differing impacts among species. Therefore, as biotic interactions can have a strong impact on species assemblage, estimation of their relative contribution and influence at the community level is essential.

Here we examine the importance and impact of key biotic interactions on ecologically dissimilar and evolutionary distant species, namely vascular plants, bryophytes and lichens, in arctic-alpine Fennoscandia (Fig.1). This is achieved by incorporating the cover of the three dominant plant species (as a proxy for the frequency and intensity of their interaction with co-occurring species) on species richness and distribution modelling frameworks, following le Roux et al. (2012); (2014) and

Mod et al. (in press), which allows us to assess the role of biotic interactions across the whole community. Specifically, we aim to (i) examine the importance of dominant species interactions for species richness of different taxa, and (ii) assess the variability in the responses of sub-dominant species to these biotic interactions. Further, we test if differences in species responses to the dominant plants are related to their biogeographic range (i.e. distribution in relation to altitude and latitude, a correlate for their broad climatic tolerances) and taxon (a correlate for their evolutionary history and some functional traits). Here, the three species groups (i.e. vascular plants, bryophytes, lichens) are used as substitutes for taxa, although phylogenetically they are not at the same taxonomic level.

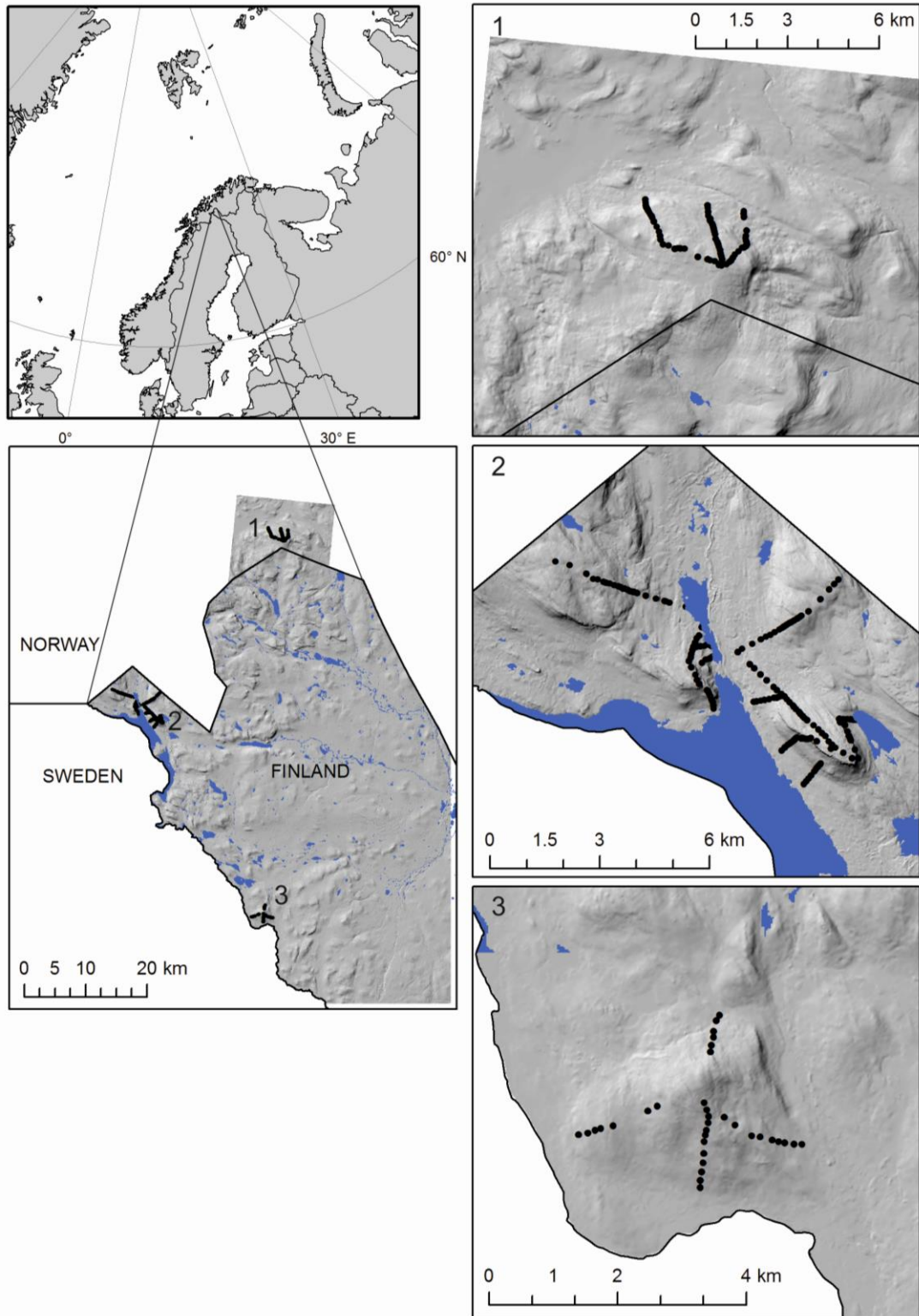


Fig 1 Study sites (black dots; $n=270$) were located along 18 altitudinal transects on 6 massifs in northern Fennoscandia.

Our work builds on the earlier studies conducted in the same region, particularly studies of le Roux et al. (2012); (2013a; 2014); and Mod et al. (in press), which demonstrated the general importance and impact of biotic interactions in arctic-alpine vegetation. However, the present work provides an important extension to the earlier studies by examining the level of contribution and net-impact of biotic interactions in communities of three species groups, thereby tackling research questions hitherto rarely addressed.

MATERIAL AND METHODS

Data collection

Our study area is located in north-western Finland and Norway *c.* 69° N 20°50' E and has an oceanic arctic climate with an annual mean temperature of -1.9 °C (January -12.9 °C, July 11.2 °C), as measured at the nearby Kilpisjärvi meteorological station (484 m a.s.l. 1981 – 2010; Pirinen et al. (2012)). Vegetation of the area consist of arctic-alpine tundra with boreal features at lower elevations (Virtanen et al. 2010). Species data were collected from 270 sites established along 18 altitudinal transects on six massifs. The sites were located at 20 altitudinal meter intervals, with the maximum distance between sites being 80 km, and altitude ranging from 460 to 1360 m a.s.l.. At each site, four 1 m² plots were placed five meters from the centre of the site resulting in 1080 survey plots. In each plot, the identity and cover of all vascular plant, bryophyte and lichen species were recorded (i.e. foliar cover estimation), with an exception of few groups that could not be distinguished reliably on species level or have unresolved taxonomy. These were only identified at the family or genus level (~3.5% of records; including *Taraxacum* spp. and some *Bryum* and *Stereocaulon* spp.; see Virtanen et al. (2010); and le Roux et al. (2012) for more details). For analyses of individual species, observed cover values were transformed to presence-absence values (species was recorded as present when cover > 0 %). For richness analyses, all species present per species group were summed to derive a species richness values.

For predicting species richness and distribution, we used the same nine environmental predictors (6 abiotic and 3 biotic variables) in all models. Abiotic predictors, downscaled using a digital elevation model with resolution of 5 x 5 meters, were: mean air temperature of the coldest quarter (TCQ; °C December-February), growing degree days (GDD; d, sum of the days when air temperature >3 °C),

water balance (WAB; ratio of precipitation to evaporation), soil wetness (estimated by the topographic wetness index = TWI), solar radiation (RAD; MJ/cm²/a⁻¹) and soil quality (SQ; proportion of nutrient-rich calcareous and nutrient-poor siliceous bedrock). The abiotic predictors were selected based on previous studies in our study area (Sormunen et al. 2011; le Roux et al. 2012; le Roux et al. 2013b) and their ecological relevance (see e.g. Guisan and Zimmermann 2000; Austin and Van Niel 2011). For further details on the methods for extracting and calculating the abiotic predictors and the reasoning for their selection, see the detailed description of how environmental predictors were derived in Online Resource 1 and Mod et al. (in press).

The three dominant species (*E. hermaphroditum*, *B. pubescens* and *B. nana*) employed in this study as biotic predictors have previously been identified as influential on vegetation patterns by a number of both experimental (e.g. Edvardsen et al. 1988; Shevtsova et al. 1995; Nilsson et al. 2000; Aerts 2010) and observational studies (e.g. Pellissier et al. 2010; le Roux et al. 2013a; Mod et al. in press). These species are considered to suppress other species via competition, e.g. *E. hermaphroditum* and *B. nana* are the most dominant species in the study area, with *E. hermaphroditum* also being allelopathic and *B. pubescens* forming the treeline (c. 600-700 m.a.s.l.) which inhibits alpine species from growing at lower elevations (see Nilsson 1994; Tybirk et al. 2000; Eskelinen et al. 2009; Aerts 2010; Eskelinen 2010; Pellissier et al. 2010; González et al. 2014). As tall and/or densely-growing species under certain circumstances, these three dominant species may also facilitate other species (expanding their local distribution and increasing fine-scale species richness) by providing shelter, ameliorating micro-climatic conditions, trapping protective snow in winter or inhibiting soil movement. In addition, *B. pubescens* sustains boreal habitat at lower elevations, creating favourable conditions for boreal species in areas that would otherwise be unsuitable (see Olofsson 2004; Grytnes et al. 2006). Our three biotic predictors were incorporated into the models as the percentage cover of the species in each plot.

Statistical analysis

Our species richness modelling includes both basic macroecological modelling (MEM) tools and stacked species distribution modelling (SSDM) (Ferrier and Guisan 2006; Mod et al. in press). In MEM, species richness is modelled directly, whereas in SSDM, occurrence of each species is first predicted separately with single species distribution models (SDMs), and these individual occurrence predictions are then stacked to construct species richness values. Both species richness and species' distribution were modelled using all nine predictors and applying generalized boosting regression models (GBM) in R (Elith et al. 2008; Dubuis et al. 2011; Guisan and Rahbek 2011). GBMs were fitted using functions from the *gbm* and *dismo* packages (Ridgeway 2005; Elith et al. 2008; R Core Team 2013), setting interaction depth to six, learning rate to 0.001 (reduced for species where inadequate trees were calculated) and bagging fraction to 0.75. In the models, a logarithmic link function was applied assuming a Poisson distribution of errors for MEM and a Bernoulli distribution for SDMs. Predicted probabilities of occurrence from single SDMs were converted to presence/absence predictions using the threshold value maximizing sensitivity and specificity (Liu et al. 2005; Levinsky et al. 2013), and these occurrence values were used for stacking species richness values (SSDM).

Only species with at least 12 presence records in each calibration dataset and 8 presence records in each validation dataset were included in analyses (excluding *E. hermaphroditum*, *B. nana* and *B. pubescens*). This resulted in 91 vascular plant species, 67 bryophyte species and 54 lichen species being modelled, with species richness of these species groups in the study plots varying from zero to 32, 17 and 23, respectively. The selected study species were then categorized as boreal or arctic-alpine based on their biogeographic range (Hämet-Ahti et al. 1998), resulting in 42 boreal and 49

arctic-alpine vascular plant, 25 boreal and 42 arctic-alpine bryophyte and 14 boreal and 40 arctic-alpine lichen species.

For both MEM and SSDM and for all taxa, the importance (i.e. relative influence; (sensu Elith et al. 2008) of all abiotic and biotic predictors was extracted from the models. Variable importance is determined both by the frequency of a variable being selected as a predictor in a model and the improvement resulting from the inclusion of the variable (Friedman 2001). For SSDM, variable importance was averaged across individual SDMs. Species response curves (from SDMs) and species richness response curves (from MEM) for each biotic predictor variable were visually categorized as positive, negative, neutral (i.e. response curve horizontal) or complex (e.g. parabola-shaped). For model evaluation, all models were rerun using four-fold cross-validation with randomly assigning three quarters of the data as calibration dataset and remaining data as validation dataset (Fielding and Bell 1997). Variable importance and response curves are based on models fitted with all data. The relationship between the outcome of biotic interaction (positive vs. negative vs. neutral & complex) and biogeographic range of species (arctic-alpine vs. boreal) was assessed using log-likelihood test (G^2 -test from *Deducer* package in R).

RESULTS

The importance of the biotic interactions varied among the species groups, three biotic predictors, and the modelling framework utilized. Nonetheless, in some cases a biotic variable was estimated to be the second most influential predictor (Fig. 2; see variable importance values for each species and predictor in Tables 1-3 in Online resource 2). Among the three dominant species, *E. hermaphroditum* showed the highest predictive power across the three species groups modelled (mean variable importance across taxa 9.5 %) followed by *B. pubescens* (mean variable importance across species groups 5.4 %). For MEMs the importance of biotic predictors varied between 0.36 % and 18.0 %, whereas in SSDMs this variation was lower, ranging from 2.1 % to 10.3 %. In comparison, the mean variable importance of abiotic predictors was 13.6 %, with maximum variable importance being growing degree days (51.3 %) for bryophytes in the MEM model. Overall, vascular plants and lichens were more strongly related to the dominant species than bryophytes (Fig. 2; mean variable importance of biotic predictors was 7.4 %, 3.3 % and 7.6 % on vascular plant, bryophyte and lichen species, respectively). In general, all models performed satisfactorily; for MEM based models correlations between observed and predicted species richness values were 0.86, 0.67 and 0.83, for vascular plants, bryophytes and lichens, respectively. For SSDM mean area under the receiver operating characteristic curve (AUC) values across single species distribution models were 0.889, 0.815 and 0.811 for vascular plants, bryophytes and lichens, respectively.

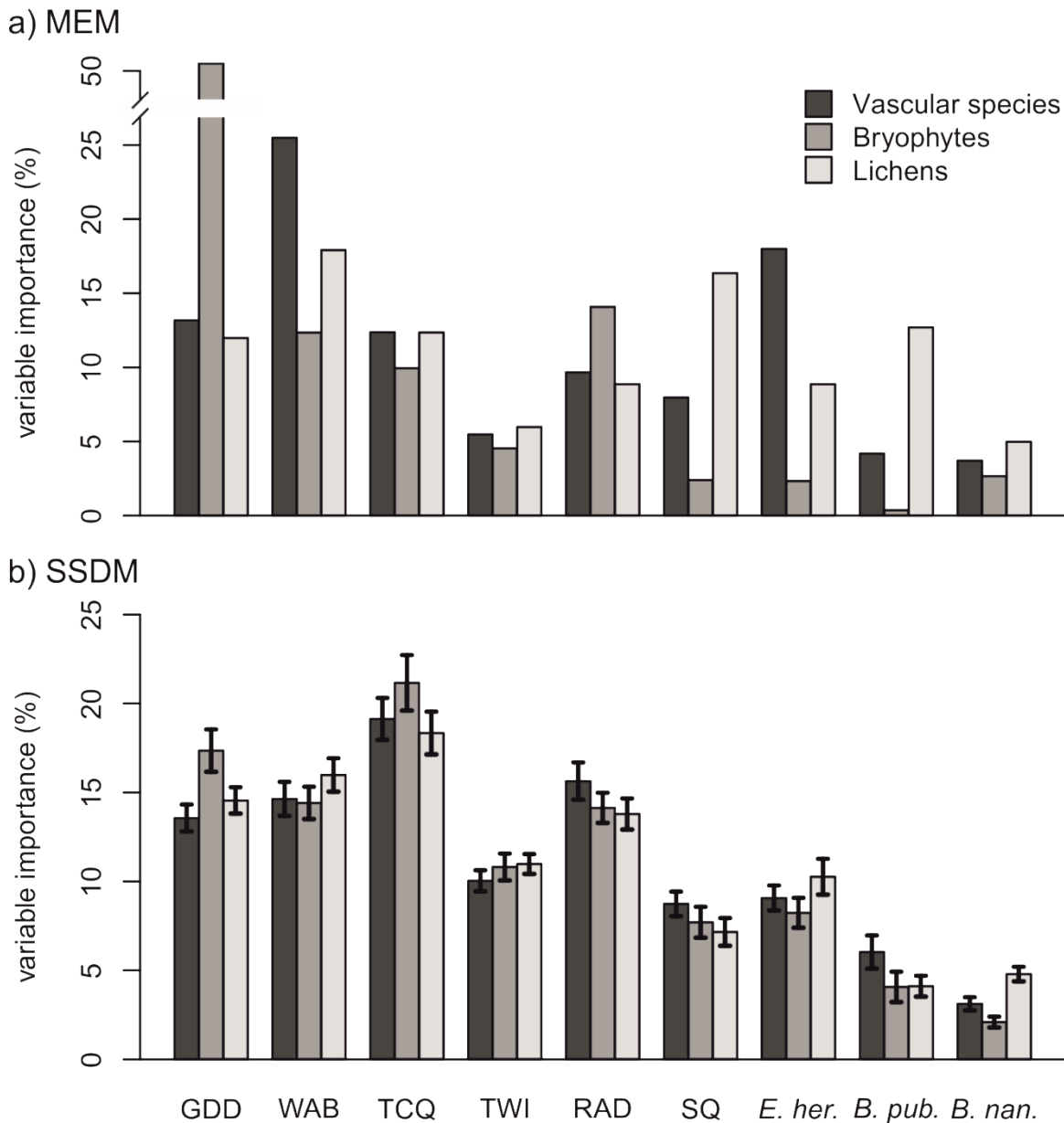


Fig. 2 Importance of each predictor variable when modelling the species richness of vascular plants, bryophytes and lichens using a) macroecological modelling (MEM), and b) stacked species distribution modelling (SSDM). For SSDM, the values are the means (\pm SE) of individual species distribution models (SDMs). Each model comprised six abiotic predictors (GDD = Growing degree days, WAB = Water balance, TCQ = Temperature of coldest quarter, TWI = Topographic wetness index, RAD = Solar radiation, SQ = Soil quality) and three biotic predictors (*E. her.* = *Empetrum hermaphroditum*, *B. pub.* = *Betula pubescens* ssp. *czerepanovii*, *B. nan.* = *Betula nana*)

The influence of the three dominant plant species differed strongly among the three taxa (Fig. 3). The occurrence of most vascular plant species was negatively related to the cover of *E. hermaphroditum*, with the inverse observed for lichen species. In contrast, vascular plants were positively related to the cover of *B. pubescens*, whereas for lichen species this relationship was reversed. The impact of *B. nana* on the occurrence of all species groups was equally often negative as it was positive. Overall, the occurrence of bryophyte species was only weakly related to the cover of any of the three dominant plant species, with a relatively high proportion of bryophytes showing a neutral or complex response to dominant plant cover (35.8 %, 43.3 % and 44.8 % for *E. hermaphroditum*, *B. pubescens* and *B. nana*, respectively). For vascular plant species and lichens corresponding numbers were 8.8 %, 22.0 % and 24.2 %; and 16.7%, 18.5 % and 27.8 %, respectively.

The biogeographic range of sub-dominant species explained only some of the negative and positive responses (Fig. 3). For example, a larger proportion of arctic-alpine species responded negatively to *B. pubescens*, whereas boreal species more often responded positively to the same dominant species. However, these patterns were statistically weak, with a significant effect ($p < 0.01$) only for *E. hermaphroditum* and bryophytes and *B. pubescens* and lichens (see Tables 1-3 in Online Resource 3).

The overall impacts of *E. hermaphroditum* and *B. nana* on the species richness of vascular plants and bryophytes were negative and those of *B. pubescens* positive (Fig. 4). In contrast, species richness of lichens was negatively related to *B. pubescens* and *B. nana*, and the relationship between lichen richness and *E. hermaphroditum* cover was hump-shaped.

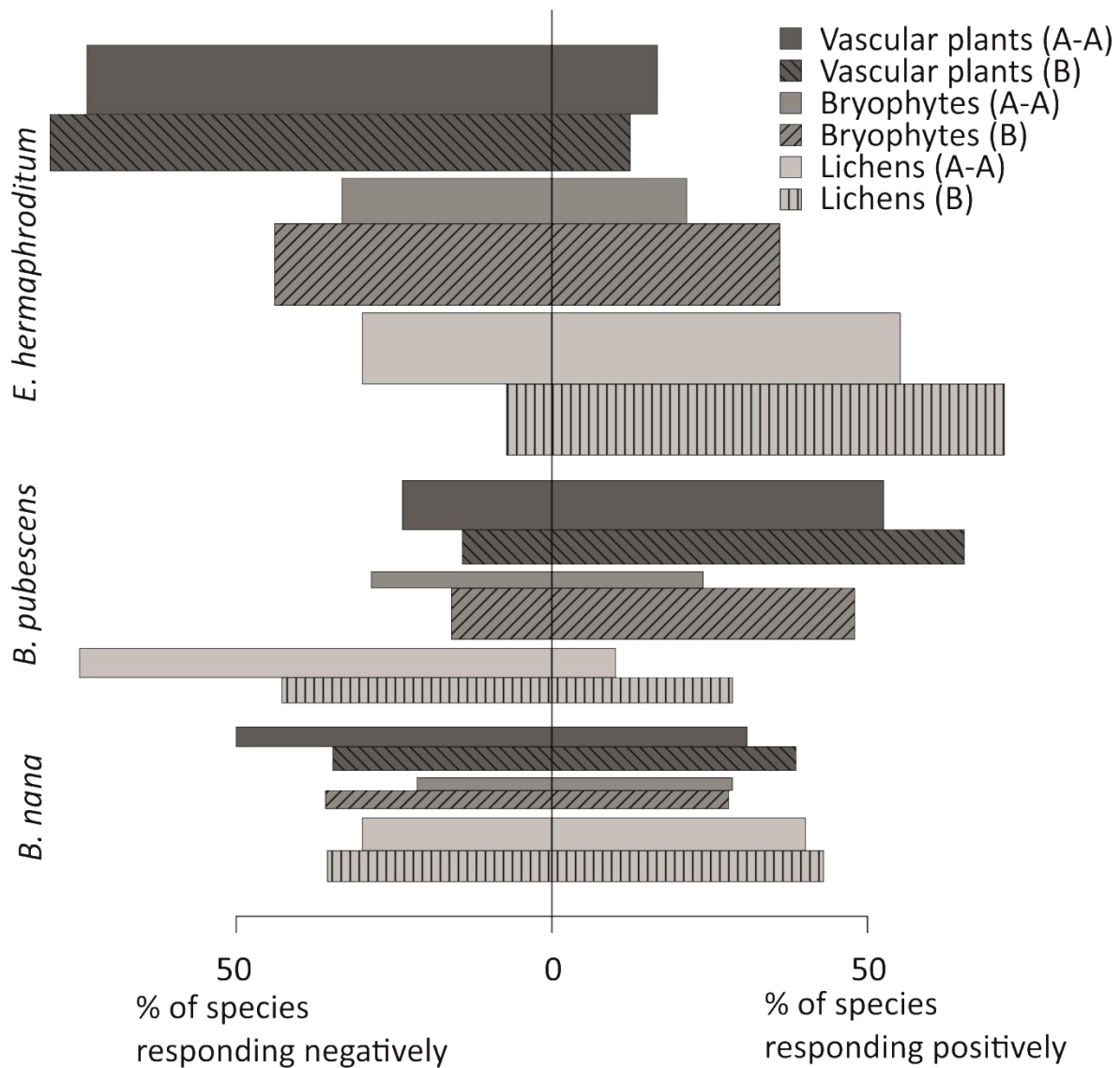


Fig. 3 Proportion of arctic-alpine (A-A) and boreal (B) vascular plant, bryophyte and lichen species responding positively and negatively to *Empetrum hermaphroditum*, *Betula pubescens* ssp. *czerepanovii* and *Betula nana*. Width of the bar indicates the mean variable importance of the biotic factor

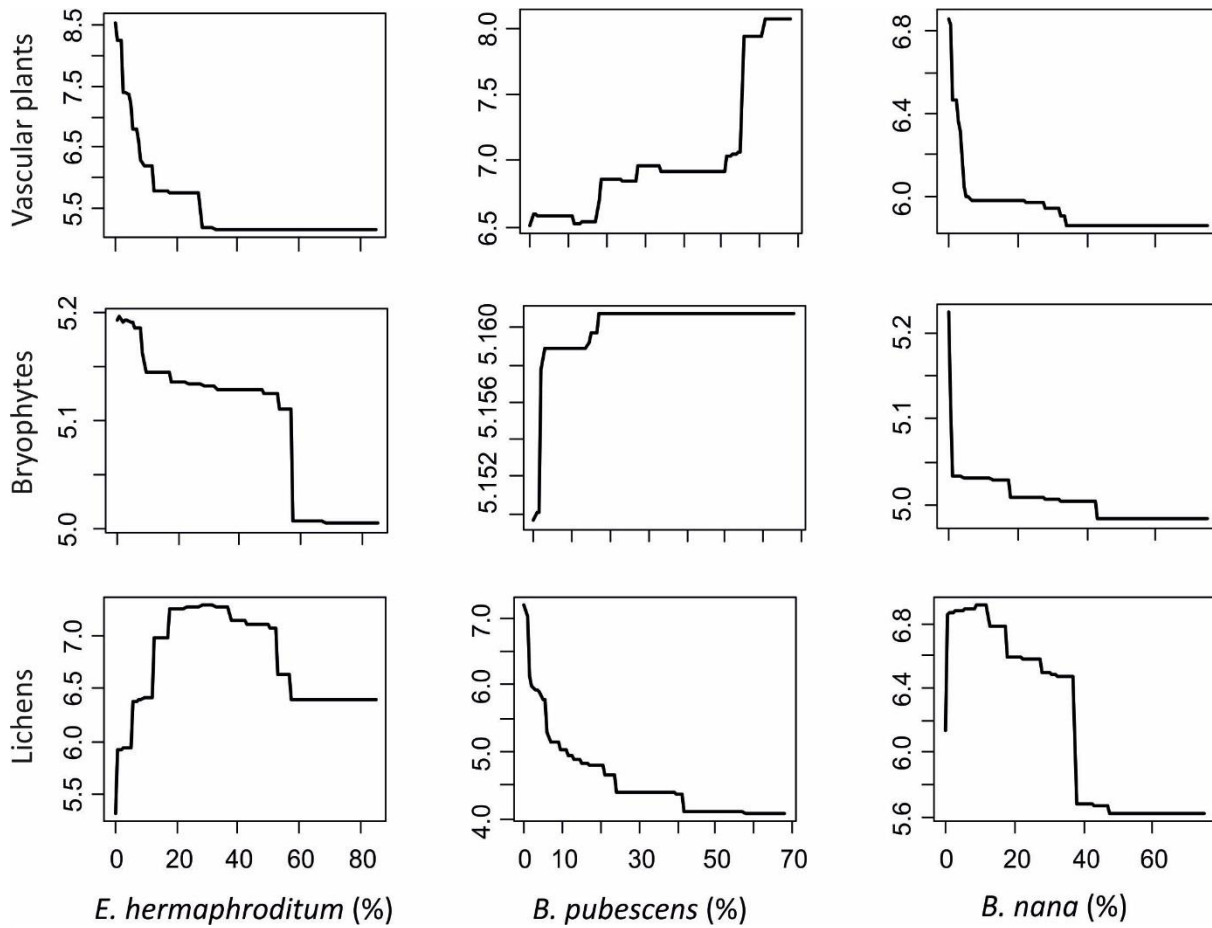


Fig. 4 Response curves (i.e. partial dependency plots from the generalized boosted regression tree method) of the species richness of vascular plants, bryophytes and lichens to the three biotic variables (the cover of *Empetrum hermaphroditum*, *Betula pubescens* ssp. *czerepanovii*, *Betula nana*)

DISCUSSION

The contributions of the cover of dominant plant species in the models of species richness were often as high as contributions of abiotic predictors, highlighting the importance of biotic interactions in high-latitude communities. Improvement in predictions of species richness of vascular plants, bryophytes and lichens by the explicit consideration of biotic interactions (Mod et al. in press) and the importance of biotic interactions in determining fine-scale distribution of vascular plant species (le Roux et al. 2013a) have previously been demonstrated in this same community. However, here we show that the importance and impact of biotic interactions for species richness and distribution models vary among species groups and the dominant plant species considered. Our results therefore provide a valuable insight into taxon-contingent influences of biotic interactions.

Of the three biotic predictors examined, the cover of *E. hermaphroditum* was most influential, irrespective of the species group being modelled and regardless of the modelling framework used. This finding is in line with previous studies showing *E. hermaphroditum*'s strong impact on the performance (e.g. Nilsson and Zackrisson 1992; Aerts 2010) and distribution of individual species (le Roux et al. 2013a), and on community composition (le Roux et al. 2014). These effects are driven via the negative impacts stemming from *E. hermaphroditum*'s intense resource competition and allelopathy (Tybirk et al. 2000; Bråthen et al. 2010), but also via positive effects related to amelioration of harsh environmental conditions (Carlsson and Callaghan 1991). However, the mainly positive relationships in individual SDMs between lichens and *E. hermaphroditum* were unexpected, particularly given the general negative impact of vascular plants on lichen performance (Cornelissen et al. 2001). This might partly be caused by facilitation of lichens by *E. hermaphroditum* at higher altitude sites under harsh conditions (as predicted by the stress-gradient

hypothesis; (Bertness and Callaway 1994; Brooker and Callaghan 1998). Alternatively, the relationship does not necessarily represent direct facilitation between *E. hermaphroditum* and lichens, but indirect effect of *E. hermaphroditum* outcompeting vascular plant species, thus creating habitat patches more suitable for lichens due to less intense competition for light and space from taller vascular species. Further, the allelopathic effect of *E. hermaphroditum* might have a weaker impact on rootless lichens inhabiting these patches. The unimodal relationship between lichen richness and cover of *E. hermaphroditum* (Fig. 4) slightly contradicts the mainly positive effect of *E. hermaphroditum* on individual lichen species. We consider three potential reasons for these differences: (i) the scarcity of plots with high *E. hermaphroditum* cover in our data (allowing outliers to have a strong influence in that portion of the data), and more importantly, (ii) the majority of lichen records come from (semi)dry mountain heath and forest stands where increasing (but not too dense) *E. hermaphroditum* cover coincides with increasingly favourable environmental conditions for lichens, (iii) in the areas of high cover of *E. hermaphroditum*, the negative impact of competition for space and light exceeds facilitative effects and depresses the number of lichen species.

Unexpectedly, the estimated impacts of the two *Betula* species were low when compared to the abiotic predictors and *E. hermaphroditum*. In particular, the generally weak importance of *B. pubescens* (apart from its influence on lichens when using MEM) was surprising, since this species forms the treeline in the study area. Thus this tree is expected to exert considerable control on the distribution of arctic-alpine (excluding them from forested areas) and boreal species (creating microclimatically suitable habitat under its canopy) (Grytnes et al. 2006; Eränen and Kozlov 2007). To some extent, our results nevertheless provide support to these expectations as within each species group the studied boreal species are more often positively related to *B. pubescens* whereas arctic-alpine species in each species group tend to show negative responses to *B. pubescens*. In

general, vascular plant species were positively related to the cover of *B. pubescens*, very likely reflecting the sheltering effect that *B. pubescens* provides (Eränen and Kozlov 2007). The opposite pattern shown by lichens (i.e. negatively related to *B. pubescens* cover), reflects how most lichens avoid heavy shade. The impact of *B. nana* on species richness of the three species groups was relatively weak, with a fairly even number of species being positively and negatively related to its cover. This indicates that its role as a biotic driver may be somewhat weaker than earlier suggested (le Roux et al. 2013a).

Bryophyte species were equally often positively and negatively related to the three dominant species. The main driver of their richness was growing degree days (>50 % importance), followed by other climatic predictors and radiation. The apparently weak interaction between vascular plants and bryophytes has also been demonstrated by Löbel et al. (2006). However, neither their results, nor ours, suggest that bryophytes are independent of biotic interactions, but may instead indicate that influential interactions are found within bryophytes and lichens or become apparent at a different (possibly finer) spatial scale.

Although no consistent relationships between outcome of biotic interactions and species biogeographic range were found, responses to *B. pubescens* (mainly positive for boreal and negative for arctic-alpine species within each species group) suggest that other classifications (e.g. CSR-strategies; Liencourt et al. (2005), leaf dry matter content; Pellissier et al. (2010)) might provide a more detailed understanding of how biotic interactions differentially impact species distribution and richness. Further, as species from different species groups show different responses to biotic interactions, using species traits could provide a more relevant explanation for this pattern. Such trait-focused approaches to understanding the impacts of biotic interactions have had

promising success (e.g. Schöb et al. 2012), but there is a clear need for further studies to examine whether species traits can predict how and why species responses to biotic interactions differ.

There were some differences in variable importance between MEM and SSDM, probably reflecting methodological differences between the two frameworks (Dubuis et al. 2011). For instance, for lichen species, *B. pubescens* was a highly important predictor based on MEM predictions, but its contribution was much weaker based on SSDM. In contrast, SSDM estimated greater variable importance for *B. pubescens* and *E. hermaphroditum* than MEM when modelling bryophyte richness. For SSDM, the variable importance of environmental predictors was more similar across the taxa, probably reflecting how variable importance is averaged across all individual species. However, neither modelling approach showed consistently higher (or lower) variable importance for the three dominant species, suggesting that our main findings are robust to methodological differences, with both frameworks showing support for the importance of biotic interactions.

CONCLUSIONS

Our study provides further evidence for the importance of biotic interactions in defining vegetation properties, measured here as the species richness and distribution of three different species groups. Importantly, we report contrasting responses to biotic interactions among taxa and biotic predictor species, highlighting an additional level of complexity to be considered when examining the influence of biotic interactions at the community level. These results provide valuable knowledge for future biodiversity forecasts as recognizing all key biotic drivers within an ecosystem, and accounting for them and the variation in their impacts, is critical for developing more realistic predictions of how communities will change under future conditions.

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