Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants

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Abiotic factors are considered strong drivers of species distribution and assemblages. Yet these spatial patterns are also influenced by biotic interactions. Accounting for competitors or facilitators may improve both the fit and the predictive power of species distribution models (SDMs). We investigated the influence of a dominant species, *Empetrum nigrum* ssp. *hermaphroditum*, on the distribution of 34 subordinate species in the tundra of northern Norway. We related SDM parameters of those subordinate species to their functional traits and their co-occurrence patterns with *E. hermaphroditum* across three spatial scales. By combining both approaches, we sought to understand whether these species may be limited by competitive interactions and/or benefit from habitat conditions created by the dominant species. The model fit and predictive power increased for most species when the frequency of occurrence of *E. hermaphroditum* was included in the SDMs as a predictor. The largest increase was found for species that 1) co-occur most of the time with *E. hermaphroditum*, both at large (i.e. 750 m) and small spatial scale (i.e. 2 m) or co-occur with *E. hermaphroditum* at large scale but not at small scale and 2) have particularly low or high leaf dry matter content (LDMC). Species that do not co-occur with *E. hermaphroditum* at the smallest scale are generally palatable herbaceous species with low LDMC, thus showing a weak ability to tolerate resource depletion that is directly or indirectly induced by *E. hermaphroditum*. Species with high LDMC, showing a better aptitude to face resource depletion and grazing, are often found in the proximity of *E. hermaphroditum*. Our results are consistent with previous findings that both competition and facilitation structure plant distribution and assemblages in the Arctic tundra. The functional and co-occurrence approaches used were complementary and provided a deeper understanding of the observed patterns by refinement of the pool of potential direct and indirect ecological effects of *E. hermaphroditum* on the distribution of subordinate species. Our correlative study would benefit being complemented by experimental approaches.

Understanding the relative roles of climate and species interactions in shaping species ranges is among the oldest challenges in ecology and has now become a prerequisite for predicting species' responses to global change (Adler and HilleRisLambers 2008). A large number of studies have focused on abiotic drivers of species distributions, such as climatic or land-use factors (Randin et al. 2009; see Guisan and Zimmermann 2000). However, it is also recognised that the observed patterns of species occurrences are strongly influenced by source-sink dynamics, dispersal limitation and biotic interactions (Pulliam 2000, Lortie et al. 2004, Gotelli et al. 2010) which should be taken into consideration in species distribution studies (Guisan and Thuiller 2005). In particular, predation, competition or facilitation may restrict or inflate species ranges (Pulliam

2000). Therefore, species interactions shaping community assemblages should also be accounted for.

Recent analyses using species distribution models (SDMs) have shown that the inclusion of additional predictors that account for known competitors or facilitators may increase both our understanding of species range limits and the predictive power of models (Leathwick and Austin 2001, Anderson et al. 2002, Heikkinen et al. 2007, Meier et al. 2010). However, positive or negative relationships between species inferred from such empirical models only provide limited information. Deeper ecological insights regarding species relationships are likely to come from other approaches developed in community ecology. For instance, the analysis of species co-occurrence patterns has been used to assess the importance of biotic interactions

and to evaluate whether biotic assembly rules determine the structure of natural communities (i.e. if species co-occur less or more frequently than would be expected by chance alone; Weiher and Keddy 1999, Gotelli and McCabe 2002). However, the detection of co-occurrence patterns and the ecological processes behind them is scale dependent (Weiher and Keddy 1999), and thus, such analyses may be refined by measuring and comparing co-occurrences at different scales. Additionally, the study of co-occurrence alone might be meaningless when considering species altogether, irrespective of their ecological characteristics. That is, co-occurrence analyses and SDMs provide correlative inferences that do not necessarily relate to the causal effects of competition or facilitation on species ranges.

One proposed alternative is to use functionally relevant plant traits that provide means of analysing biotic interactions from trait similarities or differences between species (Lavorel et al. 1997, Kraft et al. 2008). Here we assume that trait patterns can provide useful insights about the role of interactions in shaping actual spatial associations between species (Keddy et al. 1998, Wardle et al. 1998); that is, the functional approach might provide complementary insights into the statistical relationships between species found in SDMs and/or within co-occurrence analyses. While this approach is also correlative in nature, we argue that combining SDMs with approaches inherited from community ecology can deepen our understanding of the relationships that shape species distributions.

Although competition was long considered to be the main type of biotic interaction driving species assemblages (Tilman 1994), during the last decade, numerous experimental studies demonstrated that positive interactions may also play an important role in these processes, particularly in severe environments (Choler et al. 2001, Callaway et al. 2002), which is also reflected in the stress-gradient hypothesis (Bertness and Callaway 1994). This hypothesis predicts that the frequency of facilitative and competitive interactions will vary inversely across abiotic stress gradients with facilitation being more common in conditions of high abiotic stress relative to more benign abiotic conditions (Michalet et al. 2006, Maestre et al. 2009). In the intermediate to severe environments found in the Arctic tundra, both facilitation and competition processes are expected to shape plant distributions and assemblages. However, this expectation remain to be tested with empirical data on species distributions along environmental gradients.

The present study focuses on the tundra of northern Norway, which includes landscapes with varying topography and strong climatic gradients. Within the whole region, the evergreen dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* (hereafter referred to as *E. hermaphroditum*) is the most abundant plant species (Bråthen et al. 2007a). Its dominance is related to four attributes (Aerts 2010): 1) it is clonal and exhibits a dense pattern of growth and can, thus, pre-empt space locally; 2) it produces phenols that sequester nutrients in the soil and cause low nutrient availability; 3) it produces the allelopathic compound batatasin III, which potentially limits seedling growth and the survival of recruited species in its vicinity; and 4) its leaves are unpalatable to herbivores.

In this study, we investigated the influence of this dominant species on the distribution of subordinate species in plant communities at three spatial scales. Subordinate species may be strongly limited by competitive interactions in addition to climatic constraints and, thus, may exhibit a restricted distribution compared to ranges expected from abiotic factors alone. Conversely, some species may also benefit from the habitat conditions established by the dominant species (Callaway et al. 2002). If this is true, these two types of association (positive and negative) should be apparent in the observed data. We proceeded by comparing the modelled distribution of subordinate species, either including or not including the frequency of the dominant species as a biotic predictor.

Because both biotic and abiotic processes contribute to community assemblages (Adler and HilleRisLambers 2008), variance partitioning approaches can be useful to estimate the relative contributions of biotic interactions and environmental variables (Borcard et al. 1992). We related the proportion of variance explained by the biotic predictor in SDMs to indices used in community ecology: 1) a new index that can be used to compare co-occurrences between species across several scales and 2) values of traits that can describe the functional abilities of plant species during the phase of their life cycle once they are established in the community. To understand how spatial scale affects co-occurrence patterns between the dominant and subordinate species, we applied a study design in which the vegetation was sampled in small plots nested in larger plots (2×2 m, 100×100 m and 750×750 m plots). On this basis, we addressed the following hypotheses:

H_1: when included as an additional predictor into commonly-used topo-climatic SDMs, the frequency of occurrence of *E. hermaphroditum* improves the explained variance and predictive power of topo-climatic SDMs of subordinate tundra species.

H_2: because the response of species to their biotic and abiotic environment depends on their functional attributes, we expect that variation in the direction of the relationship between *E. hermaphroditum* and subordinate species will be related to plant functional traits. The functions associated with traits will provide substantial information on the role of ecological processes associated with the presence *E. hermaphroditum*, such as competition (canopy height, specific leaf area), tolerance to resource depletion (leaf dry matter content, woodiness), or tolerance to grazing (leaf dry matter content).

H_3: the variation in the direction of the statistical relationship between the subordinate tundra species and *E. hermaphroditum* is related to their pattern of diminishing co-occurrence from large to fine scales; that is, when co-occurrence is observed in large plots (750-m plots) but not in the smaller plots (100-m plots or 2-m plots) nested within the former. Because biotic interactions mostly take place at smaller scales, we assume that spatial aggregation or segregation at smaller scales in a homogenous physical environment can be considered as signals of the influence of biotic interactions induced by *E. hermaphroditum*.

Methods

Study area

Finnmark and Troms Counties in Norway form the northern frontier of the European continent, delineated by the Barents Sea towards the north and by birch forests and continuous taiga towards the south. In its western regions, this area is topographically characterised by steep hills running from peaks around 800–1800 m a.s.l., which are often surrounded by glaciers, deep valleys and narrow fjords or the open sea. In the eastern part of Finnmark, the mountain ranges gradually decrease in altitude towards the Barents Sea to plateaus of 300–500 m a.s.l. with abrupt edges interspersed with moderately sloped hills. The relief gradient from west to east has effects on the spatial variability of the local climate. Additionally, in this region there are climatically steep gradients from west to east, as well as from the coast to inland regions caused by the NE Atlantic current, the influence of which gradually declines from west to east. *Empetrum* heaths are widely distributed within this region (Haapasaari 1988), first occurrence dating back 12 500 (cal) yr (Alm 1993).

The current study focuses on the area where the average temperature of the warmest month is <11°C, corresponding to the beginning of the tundra in northern Norway (Fig. 1). The heaths dominated by *Empetrum nigrum* ssp. *hermaphroditum*, along with *Betula nana* and *Vaccinium* spp., are interspersed with patches of mesic and wet vegetation where herbs (such as *Bistorta vivipara, Alchemilla alpina, Thalictrum alpinum* and *Viola biflora*) and graminoids (such as *Avenella flexuosa, Nardus stricta, Carex bigelowii, Eriophorum angustifolium, Agrostis capillaris* and *Deschampsia cespitosa*) are common species, as is the dwarf shrub *Salix herbacea*.

Environmental predictors

We used monthly average temperature and precipitation grids from the WorldClim climatic maps (Hijmans et al. 2005) at a resolution of 30 arc-seconds (ca 750 m). We combined these grids with our own calculations to develop topo-climatic layers that have recognised strong biological meaning for plants (Zimmermann and Kienast 1999, Guisan and Zimmermann 2000, Zimmermann et al. 2009) and well-established environmental factors that have a clear ecophysiological significance for alpine and tundra flora (Körner 2003): degree-days (DDEG), averaged moisture index of the growth period (June to August, MIND), solar radiation (SRAD), average temperature of the coldest quarter (TCQ), average precipitation of the coldest quarter (PCQ) and intra-annual variation of precipitation (SDPREC).

First, we generated monthly potential global radiation grids (SRAD) consisting of both direct and diffuse components using Kumar's approach (Kumar et al. 1997). Next, we calculated degree-days (DDEG) from monthly average temperatures according to Zimmermann and Kienast (1999). We also calculated potential evapotranspiration grids (Zimmermann and Kienast 1999). The moisture index was calculated as the difference between monthly precipitation and potential evapotranspiration (MIND). Finally, the standard deviation of the monthly precipitation values was calculated (SDPREC). More details on the derivation of topo-climatic predictors can be found in Zimmermann et al. (2007). These environmental predictors were first used to design the environmentally
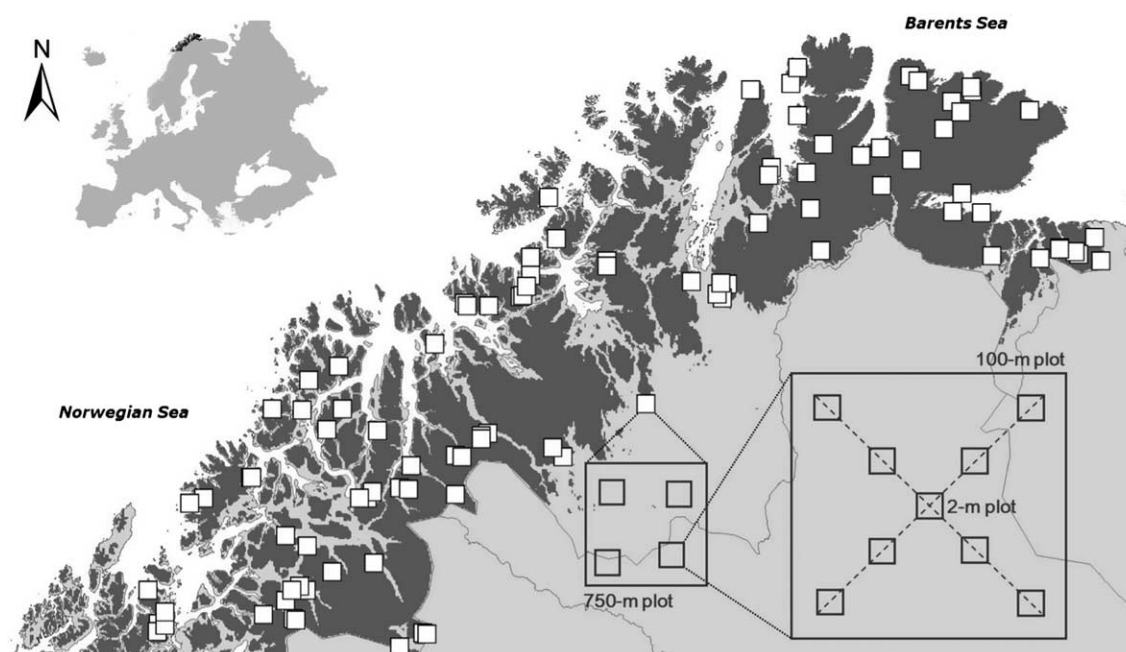

Figure 1. Geographical location of the study area (dark grey) in northern Norway and illustration of the method used to sample vegetation in small plots nested in larger plots (2 × 2 m, 100 × 100 m and 750 × 750 m plots). For better illustration, the plot size on the map has been magnified.

stratified sampling procedures and were then used in the statistical analyses of the SDMs.

Vegetation sampling

Because an inventory of all vascular plant species would have been too time consuming to conduct, we selected 39 plant species representing several growth forms and rarity levels occurring in the low alpine zone of Finnmark. For sampling these species, we stratified our study area using three climatic variables selected for their importance for structuring tundra vegetation: DDEG, MIND and PCQ. All three variables were classified into three equal categories. By combining these three layers, we generated a map representing 25 realised climatic combinations (from the 27 possible) occurring in the alpine zone in the region. We then randomly selected 750×750 m plots (hereafter referred to as 750-m plots) from the map according to an equal-stratified sampling design (Hirzel and Guisan 2002). Each random plot was sub-sampled by randomly selecting four 100×100 m plots (hereafter, 100-m plots), separated from one another by at least 200 m. Within each 100-m plot, we visited 9 plots of 2×2 m (hereafter, 2-m plots) and inventoried the species along a planned route. We set a first 2-m plot at the centre of a 100-m plot (located using a high quality GPS) and recorded all of the target species present. We then moved 25 m to the northeast to sample the second 2-m plot and another 25 m further to the northeast to sample the third 2-m plot before returning to the central point. We performed similar sampling procedures for the three other directions, i.e. northwest, southeast and southwest (Fig. 1). Additionally, we recorded whether the 39 target species were present in the routes between the 2-m plots. During the summer 2008, we visited 98 750-m plots within the inventoried climatic strata. For the following analyses, we considered only those species for which the number of occurrences in the 750-m plots was > 20, yielding 34 species plus *E. hermaphroditum* (Supplementary material Table S1).

Testing the importance of a biotic predictor in species distribution models

To address our first hypothesis (H_1), species distribution models were fitted for each species against the set of topo-climatic predictors, with and without the frequency of *E. hermaphroditum* as additional biotic predictor. We calculated the frequency of *E. hermaphroditum* as the number of 2-m plots occupied by the species within the 750-m plots, i.e. a count variable ranging from 0 to 36. This frequency reflects the coverage of *E. hermaphroditum* and, therefore, quantifies the impact this species might have on the presence of other plant species within the 750-m plots. Note that *E. hermaphroditum* occurred within all but two of the 750-m plots, but with varying coverage between plots, which demonstrates its wide distribution in Finnmark.

Modelling methods differ not only based on their performance but also with respect to the biological explanation they can provide. In particular, generalised linear models (GLM, McCullagh and Nelder 1989)

provide parameter estimates that are easier to interpret and compare among species than are many other modelling algorithms. We modelled the distribution of the 34 species first with the five topo-climatic predictors alone and then including the frequency of *E. hermaphroditum* as a biotic predictor, using GLMs with a binomial variance function and a logit function as implemented in the R environment (R Development Core Team 2010, Table 1). In addition to linear relationships, we allowed up to second-order polynomials (i.e. quadratic terms) for each predictor. To evaluate the predictive performance of our species distribution models, we used 10-fold cross-validation measured based on the area under the receiver operating characteristic (ROC) curve (AUC, Fielding and Bell 1997). In addition to the AUC, we compared the model fit estimated with the adjusted geometric mean squared improvement R^2 (Cox and Snell 1989, Nagelkerke 1991). This R^2 is rescaled to a maximum of 1 and adjusted for both the number of observations and predictors in the model. We computed the R^2 of the global fit and the AUC both with and without the biotic predictor.

We projected the models over the entire study area. However, because the data on the frequency of *E. hermaphroditum* was available only for the inventoried pixel, we modelled the frequency of *E. hermaphroditum* with a generalised additive model (GAM; Hastie and Tibishirani 1986) with a smoothing function allowing four degrees of freedom and a Poisson distribution using the topo-climatic predictors mentioned earlier. GAMs are sometimes referred to as being data rather than model driven because the data determine the nature of the relationship between the response and the set of explanatory variables, rather than assuming some form of parametric relationship (Guisan et al. 2002). Because our aim was to establish a spatially explicit variable reflecting the spatial frequency of *E. hermaphroditum* as close as possible to the observed frequencies throughout our study area, a GAM was preferred to a GLM for this analysis.

To quantify the respective proportions of the variance explained by the biotic and topo-climatic predictors in the GLMs of each species, we used a variance partitioning approach based on partial regression analyses. This approach allows variance partitioning into four fractions (Borcard et al. 1992; see Randin et al. 2009 for implementation): 1) pure topo-climatic (TC), 2) shared topo-climatic and biotic (TC+BIO), 3) pure biotic (BIO) and 4) unexplained variance. The use of a GLM is required to apply this framework. The adjusted geometric mean squared improvement R^2 was used as an estimator of the explained variance, without adjustment for the number of observations and predictors (see also Zimmermann et al. 2007). Additionally, we extracted from linear GLMs with a binomial variance function and a logit function the sign (positive or negative) of the coefficient of the relationship between the occurrences of each of the 34 species and the biotic predictor alone as well as the associated p-value (from a Wald-z test, Supplementary material Table S2). This allows investigation of the direction of the relationship between the frequency of the dominant species and the occurrence of the subordinate species.

Table 1. Summary of the results regarding the total fit (Tot. R²), the predictive power (AUC) for the topo-climatic (TC) and biotic (BIO) models and the improvement expressed in percent (Tot. R² Imp., AUC Imp.) of the 10 species for which the total fit is the most improved by the frequency of *E. hermaphroditum* (five with a negative relationship in the linear regression with the biotic predictor and five with a positive one). The values of partitioned variance (topo-climatic: R² TC, biotic: R² BIO, shared: R² Sh., and unexplained: R² Un.) are also tabulated.

	Sign	R² TC	R² BIO	R² Sh.	R² Un.	Tot. R² TC	Tot. R² BIO	Tot. R² Imp.(%)	AUC TC	AUC BIO	AUC Imp.(%)
Veronica alpina	−	0.181	0.165	0.054	0.600	0.228	0.307	34	0.716	0.733	2
Potentilla crantzii	−	0.019	0.131	0.049	0.801	0.116	0.238	105	0.558	0.684	23
Silene acaulis	−	0.208	0.172	0.007	0.614	0.184	0.349	90	0.687	0.732	7
Ranunculus glacialis	−	0.123	0.250	0.273	0.355	0.350	0.574	64	0.775	0.805	4
Arabis alpina	−	0.104	0.382	0.175	0.340	0.287	0.525	83	0.759	0.840	11
Loiseleura procumbens	+	0.194	0.180	0.080	0.546	0.222	0.470	112	0.653	0.738	13
Vaccinium uliginosum	+	0.083	0.161	0.114	0.643	0.363	0.621	71	0.711	0.837	18
Rubus chamaemorus	+	0.044	0.316	0.143	0.497	0.199	0.484	143	0.660	0.815	23
Juncus trifidus	+	0.336	0.186	−0.048	0.526	0.243	0.554	128	0.656	0.840	28
Arctostaphylos alpina	+	0.103	0.216	0.129	0.551	0.257	0.569	122	0.712	0.821	15

Analysing the role of species traits

To address our second hypothesis (H$_2$), we collected for each of the 34 studied species data on four biological traits from the LEDA database (Knevel et al. 2003) and other sources in the literature (Wijk et al. 2005, Caccianiga et al. 2006, Baptist et al. 2010). We selected leaf dry matter content (LDMC [mg g^{-1}]), woodiness or stem specific density (SSD [g cm^{-3}]), specific leaf area (SLA [mm^2 mg^{-1}]) and canopy height (CH [mm]). These traits can be seen as syndromes of plant species performance related to the phase of the plant life cycle when they are becoming established in the vegetation (Weiher et al. 1999). In particular, under rich nutrient conditions, fast growth is a prerequisite for competitive ability, which is reflected by high SLA and CH values (Weiher et al. 1999, Lavorel et al. 2007). In contrast, under nutrient poor conditions, success can be achieved through resource sequestration ability, which is reflected by a higher LDMC and SSD (Weiher et al. 1999, Lavorel et al. 2007). LDMC is also recognised as being related to environmental stress tolerance, for example, to grazing by large herbivores (Rusch et al. 2009). The analyses were performed on 29 species because trait values were missing for five species. The species were classified into three categories: species that showed a significant positive linear relationship with the biotic predictor (i.e. the frequency of *E. hermaphroditum* see above, +), those that showed a significant negative relationship (−) and finally the species that showed no significant relationship (0). Then we compared the trait values between these three groups using a logistic regression. We also graphically related the variance explained by the biotic predictor to the values of LDMC.

Co-occurrence pattern

To address our third hypothesis (H$_3$), we calculated the co-occurrence between *E. hermaphroditum* and the 34 subordinate species across our system of nested plots at different scales: 750-m, 100-m and 2-m plots. For each pair of species (S1, S2), we divided the number (N) of plots where both species were present by the number of plots where the rarest of the two species was present. This index ranges from 0 (no co-occurrence) to 1 (always in co-occurrence) as given in eq. 1.

$$\mathrm{Ind}_{coo} = \frac{N_{(S1 \cap S2)}}{Min(N_{S1}, N_{S2})}, \tag{1}$$

where $N_{(S1 \cap S2)}$ is the number of times species S1 and S2 co-occur, while $Min(N_{S1}, N_{S2})$ is the occurrence frequency of the rarest of the two species.

Because the scale is crucial when analysing co-occurrence patterns, we calculated the reduction in co-occurrences as the spatial scale decreased by taking the difference of the co-occurrence values between the 750-m and 100-m plots and also between the 750-m and 2-m plots. This difference reflects the spatial segregation of the subordinate species and *E. hermaphroditum* within the 750-m plots. If a species frequently co-occurs with the dominant species in the 750-m plot, but not in the nested 100-m or 2-m plot, which is assumed to have similar climatic conditions, we

consider this result to be consistent with a biotic effect (hypothesis 3), although causality can formally only be demonstrated through experiments. If the decrease of co-occurrence is close to average, a biotic effect is less likely. We compared the reduction in co-occurrences between the three groups of species defined above ($+$, $-$ and 0) using a Kruskal-Wallis test. We also graphically related the variance explained by the biotic predictor to the reduction in co-occurrences.

Results

Testing SDM improvement (H_1)

The SDMs based on topo-climatic variables were improved for most species by including *E. hermaphroditum* as a biotic predictor, but the strength of the improvement was highly variable among the subordinate species. By accounting for the frequency of *E. hermaphroditum*, both the predictive power (on average, $+0.04$ in the AUC, corresponding to $+7\%$, and up to $+0.18$, i.e. an increase of 28%, for *Juncus trifidus*, Table 1) and the fit (on average, $+0.10$ in R^2, corresponding to $+50\%$, and up to $+0.31$, i.e. an increase of 122% for *Arctostaphylos alpina*, Table 1) were improved. However, for three species, the fit and the predictive power of the model were not improved and were even slightly reduced, and for 9 species, the fit slightly improved, while the predictive power decreased (Supplementary material Table S1). The variance partitioning method indicated that the total explained variance was shared between the topo-climatic and biotic predictors. Twenty-three species had a negative sign, while 11 had a positive sign in the linear relationship between the occurrence of the species and the biotic predictor (Table 1, Supplementary material Table S2 and S3, S4 for details on full models). The GAM based on the frequency of *E. hermaphroditum* explained 39% of the variance. The projections of the models for those species that are highly influenced by the dominant species changed when the frequency of *E. hermaphroditum* was accounted for (Fig. 2).

Testing SDM improvement and subordinate species trait relationships (H_2)

Logistic regression showed that LDMC was the only trait significantly discriminating between the three groups of species, showing either a positive, a negative sign or no significant relationship ($+$, $-$ and 0) in the linear relationship with the frequency of *E. hermaphroditum* (Table 2). The species with a positive sign had higher LDMCs than species with a negative sign. Also, species for which the variance explained by the biotic predictor was the highest had particularly high or low values of LDMC (Fig. 3). Note that *Rubus chamaemorus* is an outlier of this relationship.

Testing co-occurrence patterns across scales (H_3)

We compared the loss of co-occurrence toward smaller scales between the three groups of species ($+$, $-$ and 0),

but only the reduction from large to small scale showed significant results (Kruskal-Wallis test, 750-m–100-m: $H = 1.91$, $DF = 2$, $p = 0.38$; 750-m–2-m: $H = 19.67$, $DF = 2$, $p < 0.001$; Fig. 3, Supplementary material Fig. S1). The species with a positive sign in the relationship with the biotic predictor co-occurred with *E. hermaphroditum* independent of scale, while the species with a negative sign decreased in co-occurrence from the 750-m to the 2-m plots. Species that either tended to co-occur with *E. hermaphroditum*, or decreased in co-occurrence from the 750-m to the 2-m plots were also those for which the variance explained by the biotic predictor was the highest (Fig. 3).

Discussion

In this study, we used species distribution models (SDM) associated with approaches used in community ecology to improve our understanding of interspecific relationships and their possible inclusion in models. While positive interactions (i.e. facilitation) have been assumed to be more common under harsh conditions (e.g. at high elevations or latitudes) recent experimental studies indicated that co-existing plant species may have both positive and negative effects on each other in cold environments (Choler et al. 2001, Dormann and Brooker 2002). However, drawing similar inferences from single correlative modelling studies is difficult because it is not possible to analyse which of the two interacting species exerts what influence on another (Meier et al. in press), and the potential role of unaccounted environmental factors is difficult to assess. Here, to overcome this problem, we assessed the influence of one largely dominant plant species, *Empetrum hermaphroditum*, on 34 other species in an Arctic tundra ecosystem more specifically. We expected the frequency of *E. hermaphroditum* to improve the explained variance and predictive power of topo-climatic SDMs and to be related to the distribution of most other species (hypothesis 1, H_1), primarily through negative impacts on their distribution. However, we also expected to observe some positive relationships because facilitation is also known to structure plant communities in the Arctic tundra (Dormann and Brooker 2002). Furthermore, the directions of the relationships was expected to be related to functional traits (hypothesis 2, H_2) and co-occurrence patterns (hypothesis 3, H_3) of these species.

In accordance with H_1, the fit and predictive power were improved when *E. hermaphroditum* was added as predictor in the models. Additionally, variation in the direction (i.e. whether negative or positive) of the relationship between *E. hermaphroditum* and subordinate species were linked to one of the functional traits (H_2) and to the co-occurrences patterns (H_3). In the latter case, co-occurrences with *E. hermaphroditum* strongly decreased from the 750-m to the 2-m plots only for subordinate species that were negatively associated with *E. hermaphroditum*. These species typically have LDMC values indicating lower competitive sequestering abilities and higher palatability to herbivores. In contrast, subordinate species for which the co-occurrence was unaffected by the scale were typically positively
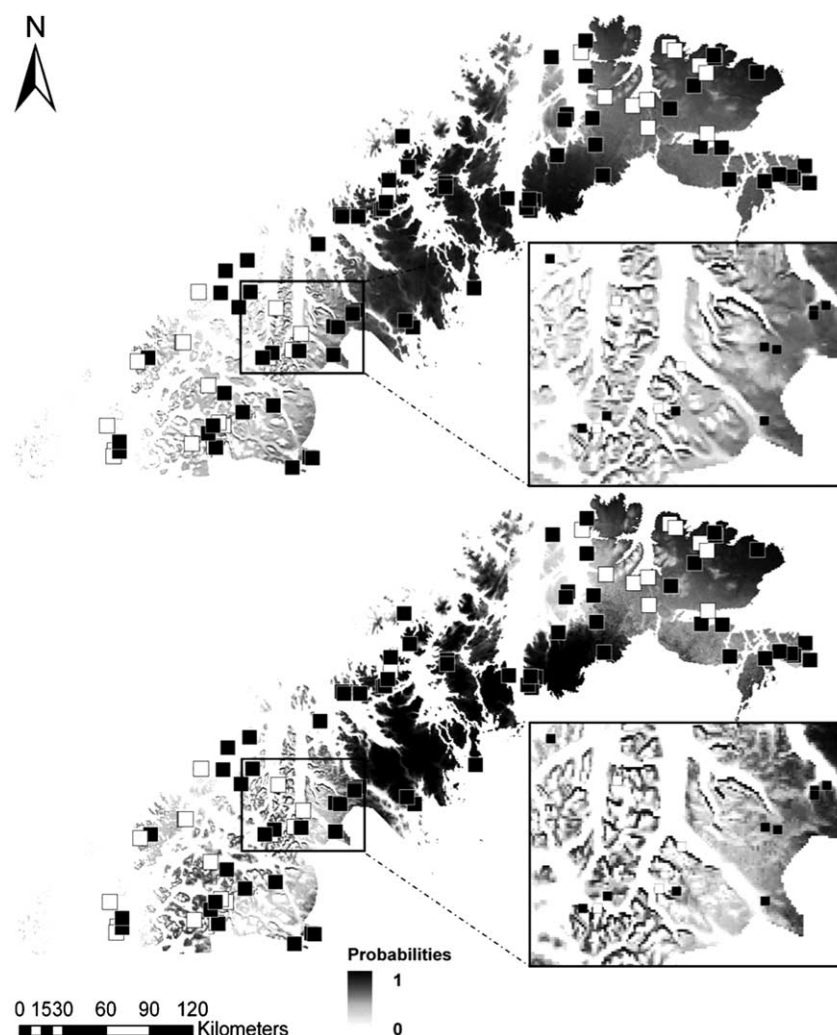
Figure 2. Potential habitat maps of probabilities of occurrence for *Carex bigelowii*, which is positively influenced by *E. hermaphroditum* through a nurse effect. Compared to the projection using only topo-climatic predictors (upper), the fit of the model is improved when the frequency of *E. hermaphroditum* is incorporated (lower). The dark squares indicate observed presences, while the white squares indicate observed absences.

associated with *E. hermaphroditum* and had higher LDMC values. Hence, it appears that *E. hermaphroditum* influences the distributions of other tundra species through both competitive and facilitative effects (as discussed below). This represents a new finding obtained by combining approaches in community ecology with species distribution modelling.

Table 2. Summary of the logistic regression used to discriminate species with a positive relationship with the frequency of *E. hermaphroditum* in the linear regression from the species with a negative relationship, with the p-values (p) highlighted in bold when significant. The leaf dry matter content (LDMC) shows a significant trend, while woodiness (SSD), canopy height (CH) and specific leaf area (SLA) do not.

	Estimate	p
Intercept	−8.266	
SSD	4.120	0.175
CH	5.499	0.632
LDMC	0.015	**0.045**
SLA	0.209	0.166

Species negatively associated with *E. hermaphroditum*

The distributions of most species considered in this study were negatively related to the frequency of *E. hermaphroditum* but were also characterised both by low LDMC and strongly decreased co-occurrences from large to small scales. Therefore, even if these species generally occur under similar climatic conditions (i.e. in the same 750-m plot), they rarely occur in close proximity to *E. hermaphroditum* (i.e. in the same 2-m plot). This result can be interpreted as a competitive effect of *E. hermaphroditum,* either due to exploitation or interference. Additionally, LDMC is a trait that is well recognised as being symptomatic of a plant species' resource use strategy, i.e. the strategy it employs in the fundamental trade-off between rapid assimilation and growth and the efficient conservation of resources within well-protected tissues (Wilson et al. 1999, Garnier et al. 2001, Diaz et al. 2004). By comparing species uptake patterns of soil nitrogen, McKane et al. (2002) showed that the dominance of a species can be related to the species'
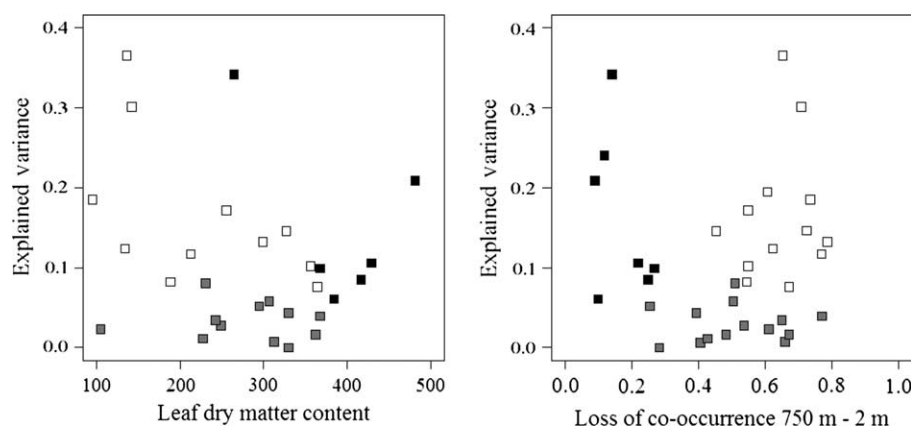
Figure 3. Partial variance of the model explained by the biotic predictor for each of the species plotted against the values of leaf dry matter content (LDMC) (left) and the loss of co-occurrence between the 750 and 2-m plots (right). The small squares represent the three groups of species: species with a significant positive linear relationship with the biotic predictor (black), with a significant negative relationship (white) and finally the species that showed no significant relationship (grey). The black outlier in the upper middle of the left graph is *Rubus chamaemorus*.

ability to exploit the most abundant resource more efficiently. Because nitrogen is a strongly limiting factor in Arctic environments (Parsons et al. 1994) and *E. hermaphroditum* immobilises nutrients (Nilsson 1994), competition for this resource may limit the growth of less competitive species. Species that do not co-occur with *E. hermaphroditum* at the smallest scale investigated are generally palatable grasses and herbaceous dicotyledons. These species have a low LDMC and, thus, do not share with *E. hermaphroditum* the ability to sequester nutrients in their leaves. Rather, they can quickly exploit and release resources, which becomes an advantage in more productive environments. In turn, these species might be considered as weak competitors in nutrient-poor systems. Additionally, *E. hermaphroditum* secretes allelopathic compounds into the soil, which can negatively affect the growth of herbaceous plants (Bråthen et al. 2010). The effects of allelopathic compounds can either be direct or indirect, through a negative influence on soil microbial (Wardle and Nilsson 1997) or mycorrhizal activity (Nilsson 1994), but such allelopathic effects may also lead to humus accumulation and reduced nitrogen availability, in turn negatively impacting plant growth.

We also found that several species with a negative relationship with *E. hermaphroditum* typically grow on rocky outcrops (*Cryptogramma crispa*, *Oxyria digyna*, *Arabis alpina*, *Saxifraga oppositifolia*), which represent a microhabitat rarely inhabited by *E. hermaphroditum*. These species might be very weak competitors and may, therefore, be outcompeted in areas occupied by *E. hermaphroditum* or other species, thus being restricted to less productive rocky outcrop. Alternatively, the frequency of *E. hermaphroditum* might provide indirect information about the frequency of rocks and boulders, which might be required for the establishment of these species.

Species positively associated with *E. hermaphroditum*

Conversely, woody species and sedges with a high LDMC, which are species that typically adapt to nutrient-poor

systems (Stark 2007), had distributions that were positively related to the frequency of *E. hermaphroditum* and co-occurred with *E. hermaphroditum* independent of scale, following our third hypothesis. This limited loss of co-occurrence might be the result of indirect facilitation (Brooker et al. 2008) by *E. hermaphroditum* or of shared environmental filters with *E. hermaphroditum*. That is, the dense cover of *E. hermaphroditum* might influence other species by a nursing effect. Particularly, our results corroborate the facilitative effect observed for *E. hermaphroditum* on *Carex bigelowii* that was shown by Carlsson and Callaghan (1991). However, species co-occurring with *E. hermaphroditum* also have a higher LDMC in general. In this context, it is possible that only species sharing traits reflecting adaptation to nutrient sequestration can tolerate the potential competitive effects of *E. hermaphroditum* through soil resource depletion. Additionally, the vegetative matrix built by *E. hermaphroditum* might also provide other kinds of positive feedback to co-occurring plants, including protection from disturbances, such as desiccation or cold temperatures (Callaway 1995).

Alternatively, the pattern observed for the LDMC values might result from a common environmental filter, such as grazing. Rusch et al. (2009) showed that the most intensely grazed sites on fertile soils possessed plant communities with highly aggregated LDMCs, indicating some environmental filtering through herbivores. The region of Troms and Finnmark is grazed to a considerable extent by reindeer, and species with a high LDMC are less palatable and, thus, will be less affected by grazing (Bråthen et al. 2007). For example, *E. hermaphroditum* is systematically avoided by herbivores (Grime et al. 1988). Other plant characteristics might also be important in this context. For example, even though the LDMC of *Rubus chamaemorus* is not particularly high, the amount of phenolic compounds in its leaves is important (Quested et al. 2005), as this character also limits the effects of grazing (Alonso et al. 2001) and might explain the persistence of this species in the vicinity of *E. hermaphroditum*. Finally, the frequency of *E. hermaphroditum* may affect substrate acidity, so that it facilitates the establishment of some species as for example *Nardus stricta*

or *Juncus trifidus*. A similar pattern was shown for *Vaccinium myrtillus* by Coudun and Gégout (2007). Interestingly, the relationships found in the model were only related to the pattern of a loss of co-occurrence from large to small scales (750 m–2 m), but not from a large to an intermediate scale (750 m–100 m). This finding suggests that the biotic processes leading to facilitation or exclusion occur at a very small scale. Hence, it is only when the coverage of *E. hermaphroditum* extends over a major proportion of the local environment that the species not tolerating *E. hermaphroditum* are excluded (i.e. from the 750-m plot).

Limitations to the approach

One caveat of our approach is that, to limit model complexity and allow proper variance partitioning, we did not account for interactions between variables. On the other hand several studies have documented a change in the direction of interaction from negative to positive between plant species depending on climatic conditions (Brooker and Callaghan 1998, Meier et al. 2010). Hence, even though we found strong relationships in this study, the interactions between plants in a community might, in fact, be more complex. For example, some of the species showing no trend related to the frequency of *E. hermaphroditum* might be positively influenced under certain abiotic conditions, but negatively under others. Furthermore, even though *E. hermaphroditum* as a dominant species is expected to occupy most of the suitable environment, this species appears to also be displaced by other species under some conditions. For example, Nilsson (1994) observed that when the availability of nutrients increases, *E. hermaphroditum* is outcompeted by *Avenella flexuosa*. Other biotic variables, such as the density of reindeer, could also be important in accounting for the frequency of *E. hermaphroditum* through, e.g. grazing (Bråthen et al. 2007) and could improve the fit of the model based on the frequency of *E. hermaphroditum*. Nevertheless, despite the fact that our results are correlative, they suggest new research areas related to the inclusion of biotic interactions in studies of species distributions, which may serve to initiate experimental studies aimed at confirming our results.

Community-based modelling approaches have been proposed to assess interactions between more than one species at a time (Ferrier and Guisan 2006), which could yield further insight about ecological processes underlying SDMs. Comparing individual SDMs incorporating biotic interactions with community-based models accounting for co-occurrence patterns along environmental gradients (Ferrier et al. 2002a, b, Ferrier and Guisan 2006) is one possibility, while making predictions for single species to be assembled later into communities is another (Ferrier and Guisan 2006). However, studies assessing the performance of such community-based models are scarce, and the results are often inconclusive (Baselga and Araújo 2010).

Alternatively, recent studies on functional characteristics of plants have led to the idea that these traits may be linked to the ability of species to face biotic interactions (Gross et al. 2009), especially when distinguishing between species abilities related to rapid acquisition of resources (i.e. exploitative or acquisitive strategy) and long conservation of resources in well protected tissues (i.e. conservative strategy) (Diaz et al. 2004). This study indicates that such traits may help in inferring the role of interactions based on the spatial distribution of species observed in a statistical model. This finding suggests that a functional approach is potentially useful in improving community predictions from single niche-based SDMs, as proposed by the "predict first, assemble later" concept of Ferrier and Guisan (2006).

Conclusion

The results of this study are consistent with the existence of both positive and negative interactions taking place between a dominant species and 34 subordinate species. Hence, although competition experiments in the Arctic have generally documented a greater importance of facilitation compared to competition in plant communities, our results suggest that both competition and facilitation may play an important role. Moreover, trait values and co-occurrence patterns observed at small scales suggested processes acting behind the fitted statistical relationships. Hence, by assembling the predictions of subordinate species according to their traits or co-occurrence values, we might improve our predictions of tundra communities compared to a simple stacking of individual species predictions based on environmental predictors alone (Guisan and Rahbek unpubl.). This study highlights the promising results of integrating approaches from community ecology into models of species distribution.

As the Arctic is expected to suffer the greatest degree of warming on the Earth of more than 4°C over the next decades (IPCC 2007), it is essential to develop accurate predictions of the response of species and communities in this region and, therefore, to account for the types of apparent biotic interactions found in this study.

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