

Biotic interactions in driving biodiversity: Insights into spatial modelling

HEIDI MOD

ACADEMIC DISSERTATION

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Abstract

The effects of co-occurring species, namely biotic interactions, govern performance and assemblages of species along with abiotic factors. They can emerge as positive or negative, with the outcome and magnitude of their impact depending on species and environmental conditions. However, no general conception of the role of biotic interactions in functioning of ecosystems exists. Implementing correlative spatial modelling approaches, combined with extensive data on species and environmental factors, would complement the understanding of biotic interactions and biodiversity. Moreover, the modelling frameworks themselves, conventionally based on abiotic predictors only, could benefit from incorporating biotic interactions and their context-dependency.

In this thesis, I study the influence of biotic interactions in ecosystems and examine whether their effects vary among species and environmental gradients (*sensu* stress gradient hypothesis = SGH), and consequently, across landscapes. Species traits are hypothesized to govern the species-specific outcomes, while the SGH postulates that the frequency of positive interactions is higher under harsh environmental conditions, whereas negative interactions dominate at benign and productive sites. The study applies correlative spatial models utilizing both regression models and machine-learning methods, and fine-scale (1 m²) data on vascular plant, bryophyte and lichen communities from Northern Finland and Norway (69°N, 21°E). In addition to conventional distribution models of

individual species (SDM), also species richness, traits and fitness are modelled to capture the community-level impacts of biotic interactions. The underlying methodology is to incorporate biotic predictors into the abiotic-only models and to examine the impacts of biotic interactions and their dependency on species traits and environmental conditions. Cover values of the dominant species of the study area are used as proxies for the intensity of their impact on other species.

The results show, firstly, that plant–plant interactions consistently and significantly affect species performance and richness patterns. Secondly, the results make evident that the impacts of biotic interactions vary between species, and, more importantly, that the guild, geographic range and traits of species can indicate the outcome and magnitude of the impact. For instance, vascular plant species, particularly competitive ones, respond mainly negatively to the dominant species, whereas lichens tend to show more positive responses. Thirdly, as proposed, the manifestation of biotic interactions also varies across environmental gradients. Support for the SGH is found as the effect of the dominant species is more negative under ameliorate conditions for most species and guilds. Finally, simulations of species richness, where the cover of the dominant species is modified, demonstrate that the biotic interactions exhibit a strong control over landscape-level biodiversity patterns. These simulations also show that even a moderate increase in the

cover of the dominant species can lead to drastic changes in biodiversity patterns. Overall, all analyses consistently demonstrate that taking into account biotic interactions improves the explanatory power and predicting accuracy of the models.

There are global demands to understand species-environment relationships to enable predictions of biodiversity changes with regard to a warming climate or altered land-use. However, uncertainties in such estimates exist, especially due to the precarious influence of biotic interactions. This thesis complements the understanding of biotic interactions in ecosystems by demonstrating their fundamental, yet species-specific and context-dependent, role in shaping species assemblages and performance across landscapes. From an applied point of view, our study highlights the importance of recognizing biotic interactions in future forecasts of biodiversity patterns.

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Publications I-IV

List of original publications

This thesis is based on the following publications:

- I Mod, H. K., P. C. le Roux, A. Guisan & M. Luoto (2015). Biotic interactions boost spatial models of species richness. *Ecography* 38: 9, 913-921.
- II Mod, H. K., R. K. Heikkinen, P. C. le Roux, H. Väre & M. Luoto (2016). Contrasting effects of biotic interactions on richness and distribution of vascular plants, bryophytes and lichens in an arctic-alpine landscape. *Polar Biology* 39: 4, 649-657.
- III Mod, H. K., P. C. le Roux & M. Luoto (2014). Outcomes of biotic interactions are dependent on multiple environmental variables. *Journal of Vegetation Science* 25: 4, 1024-1032.
- IV Mod, H. K., R. K. Heikkinen, P. C. le Roux, M. Wisz & M. Luoto (in press). Impact of biotic interactions on biodiversity varies across a landscape. *Journal of Biogeography*.

The publications are referred to in the text by their Roman numerals.

Author's contributions

- I The study was planned by M. Luoto and A. Guisan. Heidi K. Mod and M. Luoto prepared the data for the statistical analyses and P. C. le Roux and H. K. Mod conducted the analyses. Heidi K. Mod and P. C. le Roux were responsible on preparing the manuscript, with all authors commenting and contributing on writing.
- II The study was planned by M. Luoto and H. K. Mod. Heidi K. Mod was responsible on the analyses and preparation of the manuscript, with all authors commenting and contributing on writing.
- III The study was planned by H. K. Mod, P. C. le Roux and M. Luoto. Peter C. le Roux supervised the analyses performed by H. K. Mod. Heidi K. Mod and P. C. le Roux led the preparation of the manuscript, with all authors commenting and contributing on writing.
- IV The study was planned by M. Luoto and H. K. Mod. Heidi K. Mod was responsible on the analyses and preparation of the manuscript, with all authors commenting and contributing on writing.

Abbreviations

AIC	Akaike information criterion
AUC	area under receiver operating characteristics curve
BAM	biotic-abiotic-movement; model of species niche
CAL	calcareousness of soils; proportion of calcareous bedrock
DEM	digital elevation model
GAM	generalised additive model
GBM	generalised boosting method
GDD	growing degree days
GEE	generalised estimating equation
GIS	geographical information system
GLM	generalised linear model
m.a.s.l.	meters above sea level
MEM	macroecological modelling
R ²	coefficient of determination
RAD	radiation
SDM	species distribution model
SGH	stress-gradient hypothesis
SLA	specific leaf area
SSDM	stacked species distribution model
TCQ	temperature of coldest quarter
TSS	true skill statistics
TWI	topographic wetness index
WAB	water balance

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1 Introduction

Biodiversity is shaped by varying drivers, creating mosaic-like patterns across landscapes (Gaston 2000; Ricklefs 2004). While the effects of some of these drivers on distributions and assemblages of species are rather straightforward and well known (Whittaker et al. 2001; Sarr et al. 2005; Field et al. 2009), the role of co-occurring species, namely biotic interactions, is less understood and more complex (Götzenberger et al. 2012; Morales-Castilla et al. 2015). Biotic interactions can be negative or positive, with the outcome and magnitude of the effect varying among species and environmental conditions (Callaway et al. 2002; Liancourt et al. 2005; He et al. 2013; Chamberlain et al. 2014). Thus, ecological and biogeographical theories have struggled to form an all-embracing concept of how biotic interactions function among ecosystems (Whittaker et al. 2001; Bruno et al. 2003; Lortie et al. 2004; Michalet et al. 2006; Maestre et al. 2009). The limited understanding of biotic interactions and how their effects vary among species, environmental conditions and ecosystems hinders biodiversity estimates and conservation (Brooker et al. 2007; Tylianakis et al. 2008; Gilman et al. 2010; Walther 2010; Blois et al. 2013).

Biotic interactions have been mainly investigated using experimental study designs (Aarssen & Epp 1990; Dormann & Brooker 2002). These studies have demonstrated the influence of co-occurring species on governing species performance, and the connection between the environmental conditions and the manifestation of biotic interactions (Brooker & Callaghan 1998; Klanderud 2005; He et al. 2013; Chamberlain et al. 2014). However, while the ecological experiments are fundamental in evaluating the causal effects between co-

occurring species (Dormann & Brooker 2002), they are limited in the number of species and range of environmental conditions covered (Wardle et al. 1998). Thus, forming a comprehensive conception of biotic interactions within ecosystems using experiments alone might be unfeasible (Leathwick & Austin 2001). Correlative spatial models, such as species distribution modelling (SDM), are widely used observational approaches in biogeography and ecology to examine and predict biological responses in space and time (Guisan et al. 2013; Guo et al. 2015). The methods are based on associations between spatially explicit biological and environmental data, i.e. biotic measures are correlated to environmental conditions based on geographical positions (Guisan & Zimmermann 2000; Elith & Leathwick 2009; Franklin 2009; Peterson et al. 2011). Combining the models with appropriate datasets would enable examination of the role of biotic interactions simultaneously among multiple species and across a variety of environmental gradients (Wiszniewski et al. 2013; Leathwick & Austin 2001). Thus, applying modelling tools could complement understanding of the functioning of biotic interactions, especially at the ecosystem- and landscape-level where manipulative experiments are difficult to conduct.

Further, the applicability of the models should also benefit from consideration of biotic interactions (Thuiller et al. 2013). As these models aim to understand relationships among ecosystems by relating observed or measured biological responses to surrounding environmental conditions, all environmental variables having an impact on the studied biological phenomenon should be accounted for in the models (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Austin & Van Niel 2011). However, despite their ecological significance and demonstrated importance for the SMDs (e.g.

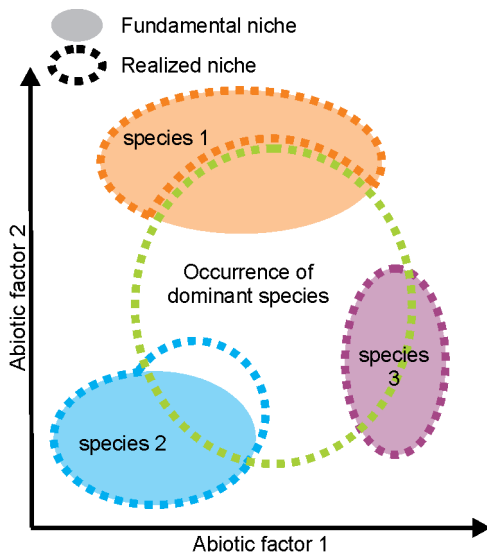


Figure 1. Biotic interactions affect the distribution of species. Negative influence of co-occurring dominant species (i.e. competition, interference) may decrease species distribution (species 1). Positive impact via modifying abiotic conditions may enhance species distribution (species 2). Nevertheless, not all species are affected by the dominant species (species 3).

Araújo & Luoto 2007; Heikkinen et al. 2007; Pellissier et al. 2010; González-Salazar et al. 2013; le Roux et al. 2014; Bueno de Mesquita et al. in press), biotic interactions are often neglected in spatial modelling (Zimmermann et al. 2010; Thuiller et al. 2013). Disregarding biotic interactions in the models may hinder distinguishing actual connections between biodiversity and environmental conditions, and it can also result in biased predictions and poor conservation decisions (Davis et al. 1998; Godsoe et al. 2015). Elucidating the role of biotic interactions in both ecosystems and models is therefore crucial.

1.1 Biotic interactions

Biotic interactions are the effects that one organism of a community has on another (Begon et al. 2006). These effects can be direct, i.e. one species affects the growth or reproduction of another species (Nilsson et al. 2000), or secondary,

i.e. one species modifies the suitability of the environment for another species (Jones et al. 1994, 1997). Biotic interactions can thus emerge as negative (e.g. competition, Klausmeier & Tilman 2002; Passarge & Huisman 2002) or positive (e.g. facilitation, Stachowicz 2001; Bruno et al. 2003; Brooker et al. 2008), and enhance or inhibit species performance (e.g. growth, abundance). As a result, biotic interactions affect species distribution (Goldberg & Barton 1992; Tilman 1994; le Roux et al. 2012 and Fig. 1) together with abiotic factors (see e.g. Fig. 2 and Soberón 2007). Usually biotic interactions are considered between species (interspecific), but they also occur between individuals of the same species (intra-specific). In addition, the effect of biotic interactions scales from individual and species level to other biological measures such as species richness and trait composition (Michalet et al. 2006, 2015; McIntire & Fajardo 2014; Olsen & Klanderud 2014; Morales-Castilla et al. 2015).

There are at least two prevailing perceptions of the role of biotic interactions along with abiotic factors in constraining species assemblages. The first one, namely the BAM model, acknowledges the roles of both abiotic and biotic conditions combined with dispersal and argues that a species can exist only where its abiotic and biotic requirements are met and where it can move (Soberón & Peterson 2005; Soberón 2007; see also Fig. 3). The second viewpoint relates

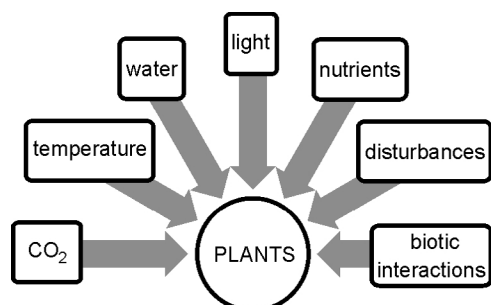


Figure 2. Factors governing performance (e.g. occurrence, growth, fitness) of vascular plants (Nobel 2005) and similar sessile terrestrial guilds (i.e. lichens, bryophytes).

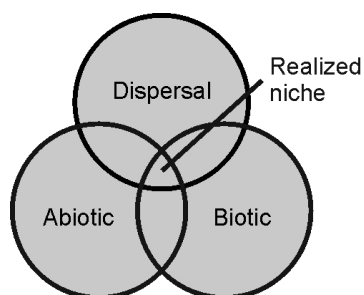


Figure 3. Factors governing realized niche, i.e. occurrences, of a species. A species is able to occur where both suitable abiotic and biotic conditions are met and no dispersal barriers inhibit movement (modified from BAM model by Soberón & Peterson 2005 and Soberón 2007).

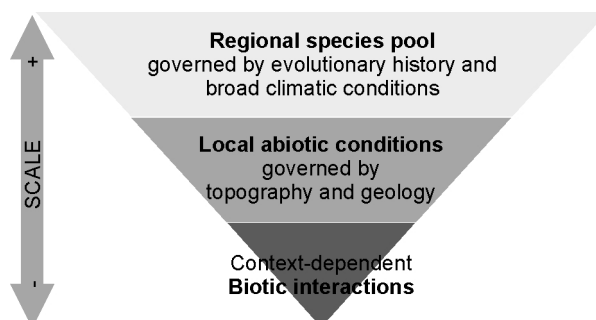
the factors constraining species assemblages to spatial scale (Fig. 4), where the large-scale species pool is defined by broad climatic patterns and evolutionary history. At finer scales, abiotic factors governed by topography and geology define the species assemblages, and finally, at the local scale, biotic interactions dictate species occurring at the site. Both viewpoints have their origins in Hutchinson's (1957) view of niche-concept, where the species' realized niche, i.e. observed occurrence, is the space constrained by abiotic factors (i.e. fundamental niche) further defined by biotic interactions (Pulliam 2000; Soberón 2007; Soberón & Nakamura 2009; Wiens 2011).

Interestingly, the impact of one species on another, i.e. outcome and magnitude of the biotic interaction, has been demonstrated to be both species-specific and conditional on environmental stress (Choler et al. 2001;

Chamberlain et al. 2014). Thus, the impact of one species is not constant, but varies according to the species being affected and the environmental conditions present (Elmendorf & Moore 2007). Species traits (i.e. such properties as productivity, resource capturing ability and stress tolerance) have been suggested to govern the outcome of biotic interactions between species pairs and along environmental gradients, but no unanimous conclusions about the dominant trait have been reached yet (Wardle et al. 1998; Liancourt et al. 2005; Maestre et al. 2009; Pellissier et al. 2010; Adler et al. 2013; Butterfield & Callaway 2013; Kunstler et al. 2016).

The environment-dependence of the outcome of biotic interaction is formalized as the stress-gradient hypothesis (SGH, Bertness & Callaway 1994; Brooker & Callaghan 1998; He et al. 2013), and it relates to the productivity-diversity paradigm (Michalet et al. 2006; Virtanen et al. 2013 and Fig. 5). The SGH postulates that under benign conditions with high productivity the negative (i.e. competition) interactions prevail thus potentially decreasing species range and diversity. In contrast, under high environmental stress and disturbance, and thus, low productivity, the presence of dominant species has a positive (or less negative) effect due to the amelioration of harsh conditions, such as winds. This, in turn, could enlarge ranges with also a positive influence on species richness. Most studies of the SGH are conducted using only one type of environmental (stress) gradient (although see Kawai & Tokeshi

Figure 4. Hierarchical representation of the factors confining species distribution to geographical scale (following the ideas presented in Hutchinson 1957; Pulliam 2000; Pearson & Dawson 2003; Pearson et al. 2004; Guisan & Thuiller 2005; Sarr et al. 2005).



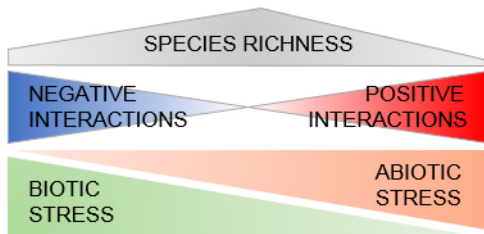


Figure 5. Productivity-diversity paradigm postulates that species richness decreases with both increasing biotic and abiotic stress due to competition and harsh environmental conditions, respectively, regulating species assemblages (modified from Michalet et al. 2006). In addition to the biotic stress (i.e. negative biotic interactions) being more pronounced under productive conditions, the SGH adds that positive interactions would dominate in areas of high environmental stress (Bertness & Callaway 1994).

2007; Maalouf et al. 2012), or combining stress gradients (i.e. using elevation as a surrogate for multiple parallel gradients, Callaway et al. 2002). However, scaling the results of such studies to actual ecosystems, where the basis for biological patterns and processes is formed of multiple co-varying environmental gradients, is difficult (Kawai & Tokeshi 2007; Maalouf et al. 2012).

While evidence to support the essential role of co-occurring species in the ecosystem exists (Chapin III et al. 1997; Götzenberger et al. 2012), and context-dependency of biotic interactions has been demonstrated (He et al. 2013), the generality of the hypotheses is still under discussion. A general consensus on the role of biotic interactions across all ecosystems (Schemske et al. 2009), species, guilds and taxa (Giannini et al. 2013), environmental conditions (Chamberlain et al. 2014) and spatial scales (Chase & Leibold 2002) should be formed. The absence of such a consensus impedes predictions of the manifestation of biotic interactions across landscapes comprising a multitude of different habitats.

1.2 Modelling of biodiversity

Correlative spatial modelling, such as SDM and species richness modelling, is widely used in biogeography and ecology (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Algar et al. 2009; Peterson et al. 2011; Pottier et al. 2013; D'Amen et al. 2015) both to examine the relationships between response and predictor variables (i.e. explanatory model) and to predict the response variable in space or time (i.e. predictive model, Mac Nally 2000, 2002). The models exploit mathematical functions to relate the response variable to explanatory ones and use the fitted model for prediction (Elith & Leathwick 2009). Understanding and forecasting biodiversity responses to environmental fluctuations are topical due to the expected changes in the environment (e.g. warming climate and land-use modification, Guisan et al. 2013; Ehrlén & Morris 2015). While these models are useable in determining even complex and non-linear relationships between multiple factors (Guo et al. 2015), their predictive ability, in particular, makes them practical tools for environmental change impact assessments (Mouquet et al. 2015).

Models can be fitted using a variety of algorithms (Guisan & Thuiller 2005; Elith et al. 2006; Elith & Graham 2009; Franklin 2009). Performance of different algorithms vary in relation to data, mathematical functions and chosen parameters and settings (Segurado & Araújo 2004; Heikkinen et al. 2006; Wisz et al. 2008; Marmion et al. 2009a; Nenzén & Araújo 2011; Aguirre-Gutiérrez et al. 2013). Thus, a suitable algorithm and its parameters should be selected based on the data and question at hand. However, choosing the best method beforehand can be difficult. Also, when modelling multiple response variables, assigning individual settings for each model might not

be feasible (Gotelli et al. 2009). Under such circumstances, one solution is to use multiple algorithms with different parameters and through a model validation choose the best performing modelling method (Guisan & Zimmermann 2000; Thuiller 2003). Another way to overcome the varying predictions of different algorithms is to use ensemble modelling (Araújo & New 2007), where results of different algorithms are averaged. This approach can increase the robustness and accuracy of predictions (Grenouillet et al. 2011), which, however, are dependent on the performance of individual models (Marmion et al. 2009b).

As a technical detail, the terminology used in this thesis must be addressed. There are a myriad of terms referring to correlative spatial models of biodiversity, including ecological niche modelling (Peterson et al. 2011), predictive habitat distribution modelling (Guisan & Zimmermann 2000), macroecological modelling (Dubuis et al. 2011), correlative modelling in predictive vegetation mapping (Franklin 1995; Tarkesh & Jetschke 2012), predictive spatial modelling of biodiversity (Ferrier & Guisan 2006) and predictive geographical modelling in ecology (Guisan & Zimmermann 2000). Some of these terms refer to a specific response variable, like the most commonly used term of species distribution modelling, SDM, literally meaning the distribution models of individual species (although some literature sources apply the term to cover also other biological response variables such as species abundance and richness, e.g. Franklin 2009). Nonetheless, all of these terms share a correlative and spatial nature and the goal of explaining and/or predicting biological responses. In this thesis, the terminology for modelling refers to the above-mentioned type of modelling and covers all response variables (i.e. species distributions, richness, traits and reproductive effort), unless otherwise specified.

1.3 Increasing the realism of biodiversity models

Variable selection in correlative spatial models of biodiversity should be guided by biogeographical and ecological theories (Araújo & Guisan 2006; Austin & Van Niel 2011; Thuiller et al. 2013), meaning that as the models aim to understand the relationships between biological responses and surrounding environment, all explanatory variables having a causal impact on the studied biological phenomenon should be considered (Guisan & Zimmermann 2000). In ecophysiological terms, these variables would thus include both the resources required by species (e.g. water, nutrients) and non-resource variables (e.g. temperature, competition) constraining species performance (see e.g. Fig. 2). Some other factors, such as topographic variables, may also influence species assemblages. However, their effects are not causal, but indirect (Austin 2002, 2007). For example, elevation governs species richness (Bruun et al. 2006; Grytnes et al. 2006), but the detected effect results from the impact that elevation has on temperature, which in turn affects species (Moeslund et al. 2013). There is also an ongoing discussion about how evolutionary history and dispersal influence local biological patterns found in the ecosystems (Huston 1999 and Fig. 3). However, under the current conception, these processes do not operate on the scale (both local extent and fine-resolution) utilized in this thesis (Cornell & Lawton 1992; Sarr et al. 2005; Soberón & Peterson 2005, see also Barve et al. 2011).

While the impact and recognition of causal abiotic constraints in these models are relatively straightforward and widespread, the conception of the role of biotic interactions and the ways off incorporating them are complex (Boulangéat et al. 2012; Kissling et al. 2012; Giannini et al. 2013; Wisz et al. 2013). Thus,

biotic interactions are rarely incorporated into spatial models, despite the response variables used (e.g. species occurrence, abundance, species richness) usually being related to the realized niches of species. Consequently, without incorporating information on biotic interactions, the models can only insufficiently represent the relationship of species ranges to the surrounding environment (Davis et al. 1998; Thuiller et al. 2013; Godsoe et al. 2015, see also Gotelli & McCabe 2002). Indeed, SDMs of individual species have demonstrated improved explanatory and predictive power when incorporating (a proxy of) biotic interactions (e.g. Pellissier et al. 2010; Meier et al. 2011; González-Salazar et al. 2013). Accordingly, spatial models of other biological measures (e.g. fitness, morphology and abundance, Tielbörger & Kadmon 2000; Leathwick & Austin 2001) should also benefit from including biotic interactions (le Roux et al. 2014, although see Mitchell et al. 2009)

Applying spatial models to evaluate biological measures other than species distributions is also interesting from an ecological point of view. Most of the studies aiming to explain and predict biodiversity with correlative models have concentrated on individual species and their distributions (Ehrlén & Morris 2015). Although valuable as such, concentrating on multiple species or other entities of ecosystems, communities and biodiversity, such as species richness or composition, may provide a more comprehensive understanding of the functioning of ecosystems and biodiversity (Gotelli & Colwell 2001; Ferrier & Guisan 2006; Certain et al. 2014). Further, including species' properties (i.e. traits) could enable generalizations to be made regarding discrepant responses of different species to explanatory variables (McGill et al. 2006; Adler et al. 2013). Therefore, incorporating biotic interactions into the models of species richness and traits should not only increase the

realism of models, but might also provide a deeper understanding of their functioning at the ecosystem level.

There are multiple ways of incorporating biotic interactions into spatial models (Kissling et al. 2012; Giannini et al. 2013; Wisz et al. 2013). In this study, one of the most straightforward approaches, “*Adding an interacting species as an additional predictor*” (sensu Kissling et al. 2012), was chosen. This approach is applicable in the ecosystems where only a few potential species, with abilities to dictate other species, exist (le Roux et al. 2014). When using this kind of approach to account for biotic interactions, abiotic predictors must be selected carefully. With an insufficient set of abiotic predictors, the effect of unaccounted abiotic factors might appear as a pseudo-effect of biotic interactions, i.e. the biotic predictor is shown to be significant due to shared environmental preferences (Ovaskainen et al. 2010; le Roux et al. 2013b). Preferably, also the impact of dominant species should be (experimentally) validated to ensure causal impacts (Dormann et al. 2012; Giannini et al. 2013). Further, such species must be widespread with a known (or easily interpretable) distribution in the study area to allow predictions.

1.4 Arctic-alpine environments

Arctic-alpine landscapes provide a suitable setting for studying biotic interactions for multiple reasons. First, these cold environments are relatively simple, with a low number of interacting species, vegetation layers and trophic levels (Billings & Mooney 1968; Wisz et al. 2013). While accounting for interactions can be a challenging task (Morales-Castilla et al. 2015), in species-poor environments the few interacting species and layers decrease the complexity. Second, mountainous areas have varying topography, creating heterogeneous environmental conditions covering broad

gradients (Billings & Mooney 1968), therefore enabling spatially effective field-work. Third, arctic-alpine species and environments are currently under intense research, allowing comparison and validation of results between studies (Dormann & Brooker 2002; Dormann & Woodin 2002). Fourth, as remote areas, arctic and alpine ecosystems usually encounter little human interference, and thus, the measured biological and environmental properties represent natural conditions (Hannah et al. 1994).

In addition, it is important to study arctic and alpine ecosystems, as they are highly sensitive to changes in climate and land-use (Parmesan 2006; Post et al. 2009). The melting of ice and snow increases the warming experienced in these environments relative to other parts of the world. Moreover, the possibilities of arctic and alpine species to follow isotherms to higher latitudes or altitudes are limited (Parmesan 2006), with the dispersal of species from lower latitudes and altitudes further seizing space from arctic and alpine ecosystems (Sturm et al. 2001; Elmendorf et al. 2012). Due to the susceptibility of these ecosystems to environmental changes, it is essential to understand the factors and processes affecting arctic and alpine biodiversity and how the potential responses to changes in one part of the ecosystem affect the other parts (Post et al. 2009; Elmendorf et al. 2012). Studies of biotic interactions in the ecotone between the boreal zone and arctic provide a valuable means for assessing climate change impacts.

1.5 Objectives of the thesis

The main aim of this thesis is to examine the role of biotic interaction in ecosystems by exploiting correlative spatial modelling frameworks and fine-resolution data on vascular plant, bryophyte and lichen communities. Attention is especially paid to two issues: 1) species-specific outcomes of biotic interactions and their dependence

on species' guild, traits and biogeographic ranges; and 2) how the manifestation of biotic interactions is related to environmental conditions. Understanding the functioning of biotic interactions across species, guilds, environmental conditions and ecosystems enables a more comprehensive view of how biodiversity takes shape across landscapes. An applied aim of the thesis is to promote the implementation of spatial modelling and predictions of biodiversity. Analyses are conducted using data on vascular plants, bryophytes and lichens from the ecotone between mountain birch forest zone and tundra, including boreal and arctic-alpine species and conditions, but the findings are not restricted only to these guilds or ecosystems.

More specifically, this thesis seeks answers to these five study questions:

1. Do biotic interactions impact high-latitude ecosystems? (all Papers)
2. Does the effect of biotic interactions vary between guilds, species and species traits? (Papers II-IV)
3. Is the outcome of biotic interactions contingent on environmental conditions? (Papers III and IV)
4. How do biotic interactions manifest across the landscape, in relation to environmental conditions and guilds? (Papers I and IV)
5. Do biotic interactions improve spatial models of biodiversity? (all Papers)

2 Materials and methods

2.1 Study area

The data derive from Northern Finland and Norway (69°N, 21°E; Fig. 6). The study area represents the ecotone between the boreal forest zone and the arctic tundra, with alpine features at high altitudes (Bliss 1971; Billings 1973;

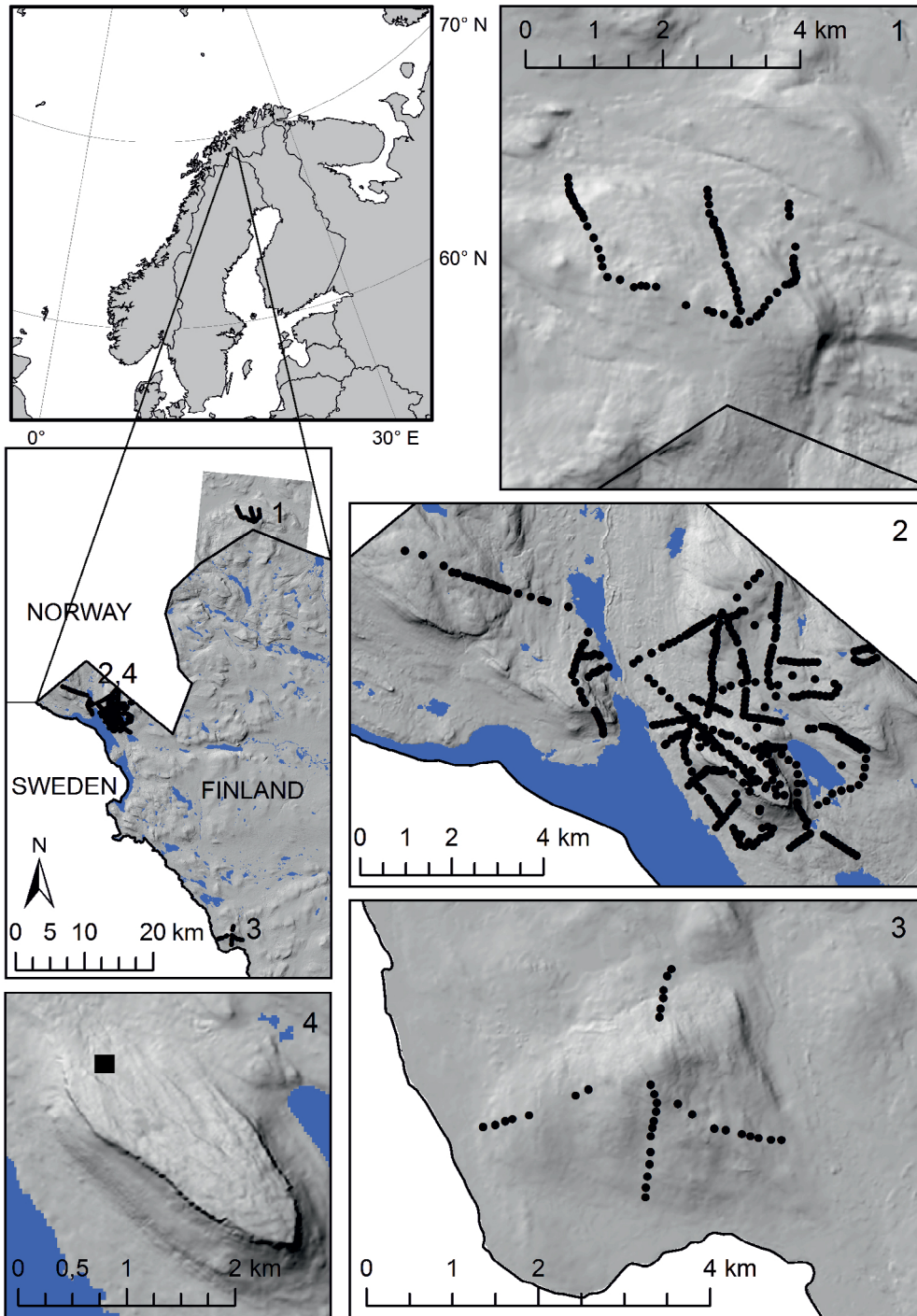


Figure 6. Data are gathered from 3084 plots (1 m²) in Northern Finland and Norway (69°N, 21°E). Altogether 2124 plots are organized along transects on the slopes of seven massifs (black dots; sub-areas 1-3), and 960 plots are organized in six grids on the northern slope (700 m.a.s.l.) of Saana massif (black square; sub-area 4). Hillshade (ESRI 2015), based on the 10 m resolution digital elevation model, demonstrates the topographic conditions of the study area. Elevation of the study area varies from 400 to 1360 m.a.s.l.

Haapasaari 1988; Virtanen et al. 2016). The vegetation and climatic conditions are influenced by the northern location and the border between continental and oceanic zones crossing the study area. Mean annual temperature of the area is -1.9°C (January: -12.9°C , July: 11.2°C), and the annual precipitation sum is 487 mm (1981-2010 averages for Kilpisjärvi Meteorological Station, Pirinen et al. 2012). However, large spatial variations exist in temperature and moisture conditions due to the geographical extent and, especially, the heterogeneous topography of the area (Aalto et al. 2013, 2014); the maximum distance between sampled sites is 65 km, and elevation of the studied sites varies from 400 to 1360 m.a.s.l. The geographical location and topography affect also the spatial and temporal distribution of energy; solar radiation varies in relation to azimuth, slope and time of year, creating a mosaic of shade and light (Caldwell et al. 1980). Also geology in the area increases the heterogeneity of the abiotic, and thus, biotic environment (Eurola et al. 2003, 2004). The tail of the Scandinavian Caledonides extends to the study area, adding calcareous rock to otherwise acidic bedrock (granite and gneiss) of the Baltic shield (Lehtovaara 1995). Soil properties of the cold environments are also indirectly affected by geomorphological disturbances (e.g. frost-related cryoturbation and solifluction) in the area (le Roux et al. 2013a; le Roux & Luoto 2014).

Vegetation in the area comprises dwarf-shrub-dominated heath and tundra vegetation (Kaplan et al. 2003), with boreal features at the lower altitudes (below 600-650 m.a.s.l.) dominated by *Betula pubescens* ssp. *czerepanovii*, which also forms the tree line in the area (Eurola & Virtanen 1991; Oksanen & Virtanen 1995; Virtanen et al. 2010). *Empetrum hermaphroditum* (also known as *Empetrum nigrum* ssp. *hermaphroditum*; hereafter *Empetrum*) is the most abundant species in the area, followed by *Betula nana*,

Juniperus communis and species from the Ericaceae family. The most common graminoids are *Calamagrostis lapponica*, *Carex bigelowii*, *Deschampsia flexuosa* and *Festuca ovina*, and the most common forbs are *Bistorta vivipara* and *Solidago virgaurea*. The field layer is rich with forbs and graminoids under the tree line, whereas the sparse vegetation at the highest altitudes is dominated by, for example, a few graminoid species from the *Luzula* and *Juncus* genera. At drier sites, lichens are abundant (Eurola & Virtanen 1991), with genus *Cladonia* being the most common, whereas under greater moisture conditions, bryophytes dominate over lichens. Vegetation is organized into zones following primarily the altitude and latitude, i.e. climatic constraints (Haapasaari 1988). From south/low altitudes to north/high altitudes, the vegetation zones are northern boreal/upper oroboreal, hemiarctic/orohemiarctic and southern arctic/lower oroarctic. The highest peaks of the study area represent the middle oroarctic zone. However, the ranges of these zones vary due to azimuth, with heterogeneous topography and geology creating mosaic patterns.

2.2 Materials

The two datasets exploited in the thesis comprise fine-resolution, spatially explicit information on vascular plant, bryophyte and lichen species and environmental conditions, allowing spatial modelling of biological responses for multiple guilds. Both datasets consist of 1 m² study plots ($n = 3084$), with field-quantified and remotely sensed data, and geographic information system (GIS) and digital elevation model (DEM) derivatives and interpolations. Data on geology were also derived using geological maps (Korsman 1997), and species traits were gathered from databases (e.g. the LEDA-Traitbase, Kleyer et al. 2008) and literature sources (e.g. Austrheim et al. 2005). Temperature- and precipitation-related

predictors are based on climate station data processed following Aalto et al. (2014). In the first dataset, the plots are organized into 531 sites, each consisting of four plots, with 5 m distances to the centre of the site (Virtanen et al. 2010). The second dataset is organized in six 8 x 20 m grids (le Roux et al. 2013b). Data gathering and analyses were chosen to be performed with fine scales to allow a more accurate understanding of the ecosystems studied and more precise predictions (Gottschalk et al. 2011). This is also an appropriate resolution to study biotic interactions, which presumably operate mainly at finer scales (Huston 1999; Pearson & Dawson 2003; Sarr et al. 2005; McGill 2010, although see Araújo & Luoto 2007 and Araújo & Rozenfeld 2014). The field data were collected during 2008-2013.

In each 1 m² plot studied, the identity and cover of vascular plant species were recorded following Hämet-Ahti et al. (1998). Additionally, in subsets of study plots, the identity and cover of lichen and bryophyte species were recorded ($n = 1080$; identified following Hallingbäck et al. 2008 and Stenroos et al. 2011, respectively), and number of flowers and berries per vascular plant species counted (i.e. reproductive effort; $n = 960$). For the analyses, the cover values were transformed to presence-absence values or to richness values to represent the total species richness or the richness of a certain trait. Totals of 218, 209 and 98 vascular plant, bryophyte and lichen species, respectively, were identified in study plots. Plot-level species richness of vascular plants, bryophytes and lichens varied from 0 to 40, 23 and 23, respectively.

Abiotic explanatory variables represent ecophysiological essential factors for plant and lichen species, such as temperature, moisture, nutrients and radiation, which should be included as a comprehensive set in models (Guisan & Zimmermann 2000; Austin & Van Niel 2011).

Temperature conditions are represented by temperature of the coldest quarter (TCQ; Dec-Feb) and growing degree days (GDD; daily sums of temperatures when mean temperature is above 3°C). Moisture conditions are represented by water balance (WAB; a ratio of precipitation to evaporation), topographic wetness index (TWI; wetness index based on DEM) and field-measured soil moisture (volumetric water content). Proportion of calcareous bedrock (CAL) was used as a proxy for nutrient content, i.e. soil fertility. Radiation (RAD) was calculated using DEM and GIS-algorithms. Some analyses (Paper III) included also the geomorphological disturbance variable as a predictor regulating species performance (le Roux et al. 2013a). It is a visually estimated proportion of topsoil under active geomorphological disturbances (e.g. cryoturbation, solifluction, fluvial erosion) per plot. CO₂ was excluded from the analysis, as its current levels are not assumed to limit species performances (Inauen et al. 2012; Bader et al. 2013).

2.3 Proxy for biotic interactions

The dominant species of the study area, namely Nordic crowberry (*Empetrum*), Dwarf birch (*B. nana*) and Mountain birch (*B. pubescens*), were chosen as surrogates for biotic predictors (following e.g. Meier et al. 2010; Pellissier et al. 2010; le Roux et al. 2012). *Empetrum* and *B. nana* are dwarf shrubs, with the former being evergreen and the latter deciduous. *Empetrum* is known to affect other species by spreading allelopathic compounds to soil (Nilsson 1994; Gallet et al. 1999; Nilsson et al. 2000; González et al. 2014). However, it does sustain ericoid mycorrhiza in the soils, thus potentially favouring species forming symbiosis with the same mycorrhiza (mainly Ericaceae-species, Tybirk et al. 2000). *Betula nana* is an ectomycorrhizal species (Väre et al. 1997). *Betula pubescens* is a subspecies of

moor birch, and it forms birch forests at the lower altitudes (Eurola & Virtanen 1991).

These species are known to influence co-occurring species (Tybirk et al. 2000; Grytnes et al. 2006; Aerts 2010; Pellissier et al. 2010; le Roux et al. 2013b, 2014), with, however, species-specific outcomes (Shevtsova et al. 1995; Pellissier et al. 2010). Specifically, their percentage cover values per plot were used as proxies for intensity of biotic interactions (le Roux et al. 2012). High cover values are assumed to represent competitive effects (Pajunen et al. 2011). However, as relatively tall species with dense growth, these species could function as facilitators for other species by ameliorating environmental conditions (Brooker et al. 2008). Some evidence from experimental studies exists on switching impact of *Empetrum* (Carlsson & Callaghan 1991; Olofsson 2004), while *B. pubescens*, especially, could pose species-specific impacts: positive influence on boreal species and negative on arctic-alpine (Grytnes et al. 2006; Nieto-Lugilde et al. 2015).

2.4 Methods

The methodology implemented in the thesis is based on correlative spatial modelling frameworks (Guisan & Zimmermann 2000; Elith & Leathwick 2009; Franklin 2009). The general idea was to examine the impact of inclusion of biotic predictors in the models, i.e. the effect of biotic interactions in explaining the species richness, distribution or reproductive effort (following Meier et al. 2010; le Roux et al. 2012, 2014; Meineri et al. 2012), and how the effect depends on species, guilds, traits or environmental conditions. Species richness models were run using two types of frameworks (Ferrier & Guisan 2006; Dubuis et al. 2011): stacked species distribution modelling (SSDM) and macroecological modelling (MEM). For the SSDM, first the distributions of individual species

are modelled and then the species richness value is formed by summing the predicted occurrences. In the MEM-based approach, the observed species richness value is modelled directly. Species traits were examined both as response variables (number of species with a certain trait in a plot) and against detected relationships (to determine whether the responses of species with different traits vary). The measures of reproductive effort were used solely as response variables in the models. Species distributions were mainly used as response variables, but when modelling fitness, cover value of the species were included to control size-related variation in fruit and/or flower production.

The models were run using various algorithms. For the analyses in Paper I, ensemble modelling using generalized linear modelling (GLM), generalized additive modelling (GAM) and generalized boosting method (GBM; also known as boosted regression trees = BRT) was exploited. Here, for the two different kinds of modelling frameworks implemented, the ensembles of the three algorithms were formed by majority vote approach for the SSDM and by counting an arithmetic mean of the predictions for the MEM (Araújo & New 2007). In the majority vote approach, a phenomenon is recorded as true/false if the majority (here two out of three) of algorithms predicts true/false. In Papers II and IV, the analyses were run utilizing GBM. In Paper III, the analyses were primarily conducted using GLM, but repeated with generalized estimating equation (GEE) models to account for possible spatial autocorrelation (Kraan et al. 2010).

GLM (Nelder & Wedderburn 1972) and GAM (Hastie & Tibshirani 1986) are regression models based on linear models, but they can fit non-normally distributed response variables through link functions, and thus, they are suitable for modelling species distributions and richness (Guisan et al. 2002). GMB is a machine learning

method that fits multiple models by dividing data into homogeneous subsets to optimize predictive performance (Elith et al. 2008). In contrast to regression models, machine learning methods are data-driven, with multiple non-parametric trees fitted to detect rules for how the response variable is related to explanatory variables. The strength of GBM is especially in its ability to handle non-linearity and high-order statistical interactions between predictors (De'ath & Fabricius 2000). GEEs are used in biogeography to account for spatial autocorrelation (Carl & Kühn 2007), a common problem of spatially structured datasets (Legendre & Fortin 1989; Legendre 1993). They are based on GLM, but factor in potential non-independency of predictors.

Determining the accuracy of the models is necessary before interpreting the results (Fielding & Bell 1997; Araújo et al. 2005). A commonly used approach is to examine the explanatory power (i.e. deviance explained) of the model. Explanatory power (or any measure of model performance) can also be used in model selection (a form of explanatory modelling approach used in Paper III), where a hypothesis is tested by choosing the best-performing set of predictors from competing models (Johnson & Omland 2004). For predictive purposes, the prediction accuracy of a model must also be assessed. Approaches such as cross-validation and bootstrapping are used when no independent evaluation dataset exists (Steyerberg et al. 2001). In this thesis, four-fold cross-validation was used with data randomly divided into four parts. Models with binary response variables were evaluated by adjusted R^2 , area under curve (AUC) and true skills statistics (TSS) values (Manel et al. 2001; Allouche et al. 2006). Richness models based on MEM were evaluated based on correlation between observed and predicted species richness. For Paper III, Akaike information criterion (AIC) values were inspected to choose the best-fitting

models (Akaike 1974; Ward 2008). To assess the influence of predictors, their response coefficients and variable importance values were derived (Friedman 2001; Papers II and III).

In Papers I and II, both species richness (implementing SSDM and MEM) and species distribution of vascular plants, bryophytes and lichens were modelled using three climate variables (TCQ, GDD, WAB), three abiotic variables (TWI, CAL, RAD) and three biotic variables (cover estimates of *Empetrum*, *B. nana* and *B. pubescens*), with 1080 cells of transect-dataset. In Paper III, both species reproductive effort (i.e. number of flowers/berries per species per cell) and species distribution of 17 vascular plant species were modelled using soil moisture, geomorphological disturbance, cover of *Empetrum* and their statistical interactions ($n = 960$). In Paper IV, species richness of vascular plants ($n = 2292$), bryophytes, lichens ($n = 1080$) and different specific leaf area classes (SLA; a trait representing species competitiveness–stress tolerance, Wilson et al. 1999) were modelled implementing MEM and using the same climatic and abiotic predictors as in Papers I and II, with addition of only one biotic predictor: cover of *Empetrum*.

3 Results

Influence of biotic interactions in governing species performance and assemblages

Biotic interactions were shown to be important in explaining species distribution (Papers I and II), species richness (Papers I, II and IV), richness of traits (Paper IV) and reproductive effort (Paper III). The findings were robust for all guilds examined. Explanatory power (Papers I and IV) and the best-subset model approach (Paper III) showed that biotic interactions (here cover of dominant species) are important in

explaining these biodiversity properties. For example, including biotic predictors in the GLM of vascular plant species richness improved adjusted R^2 from 38% to 55% (Paper I). Indeed, the importance of biotic interactions exceeded the variable importance of some abiotic variables in explaining species richness (Paper II). Cover of *Empetrum* was the second most important predictor to explain the richness of vascular plants, and to explain richness of lichen species, *B. pubescens* ranked third.

Species-specific impacts of biotic interactions and relation to traits, guild and geographic range

In addition to the magnitude of biotic interactions varying between guilds, also the outcomes of interactions differed among guilds, species and biotic predictors (Papers II and IV). For example, 77% of vascular plant species, especially competitive ones (as measured with SLA), respond mainly negatively to *Empetrum*, whereas its relationships with lichen species were mainly positive (60% of the species). In contrast, *B. pubescens* had mainly positive relationships with vascular plant species (59% of species), but negative relationships with lichens (67% of species). Bryophytes showed only weak responses to biotic predictors. Also *B. nana* had only a weak influence on species distributions or richness of any guilds. When examining the reproductive effort of the 17 species, eight showed negative and six positive responses, whereas three species showed no effect on *Empetrum* (Paper III). In addition to guild and SLA, geographic range of species can indicate species responses to biotic interactions (Paper II). For example, although not statistically significant, arctic-alpine species tended to show more negative responses to dominant species than boreal species.

Context-dependency of the impacts of biotic interactions

The outcome of biotic interactions was dependent on environmental conditions. The analyses in Paper IV showed that the dominant species had the strongest statistical interaction with GDD, meaning that the impact of *Empetrum* varied along the temperature gradient. Based on the best-subset model approach, outcome of biotic interactions was dependent on environmental conditions for all but one species (Paper III). In addition, for most species, the outcome was not only dependent on a single environmental gradient, but multiple gradients simultaneously (soil moisture and geomorphological disturbance; Paper III). Most of the detected relationships gave support for the SGH (Papers III and IV). For example, more positive interactions occur under intense geomorphological disturbance, and the dominant species had more negative influence on species richness of vascular plants under benign and productive conditions.

Manifestation of biotic interactions across landscapes

Biotic interactions govern the spatial patterns of species richness (Paper I). In addition, the context-dependency of the outcomes of interactions was apparent also across the landscape (Paper IV). The effect of the dominant species on species richness of vascular plants was most negative under benign conditions at low altitudes, with high GDD. At higher altitudes the effect was less negative or even positive. For lichens, the findings were the opposite: *Empetrum* had the most positive influence at low altitudes, with the effect diminishing with increasing elevation and environmental stress. The weak effect of dominant species on bryophytes (Paper II) is apparent also at landscape level: biotic interactions have marginal effects on spatial patterns of species richness of bryophytes (Paper IV).

Importance of biotic interactions in spatial modelling of biodiversity

For all frameworks and guilds, the models trained with abiotic only and abiotic + biotic predictors were compared. Incorporating biotic interactions improved the SDMs for individual species (Paper I). This resulted also in improvement in SSDM, i.e. decreased overprediction of species richness. For MEM, including biotic interactions as predictors removed bias at both ends of the species richness gradient. These improvements were shown for all guilds (vascular plants, bryophytes, lichens and three SLA classes; Papers I and IV). In addition, in most models (Paper III), the cover of a dominant species was found to be an important factor in explaining the reproductive effort of the species. Improvement in the species richness models affected spatial predictions accordingly. While the SSDM and MEM, based on climatic and abiotic predictors, produced spatially highly varying predictions of species richness, the inclusion of biotic interactions converged the predictions of the two frameworks (Paper I).

4 Discussion

4.1 Role of biotic interactions in ecosystems

This thesis contributes to elucidation of the roles of biotic vs. abiotic factors in governing species performance, niches and richness (Grinnell 1924; Hutchinson 1957; Menge & Sutherland 1976; Martin 2001; Wiens 2011; Klanderud et al. 2015). By using multiple approaches, species, guilds and predictors, this study shows that biotic interactions have as high, or even higher, significance in driving species' performance and assemblages as abiotic drivers. In addition to demonstrating how biotic interactions determine ecosystems along with abiotic factors, the biotic

interactions were revealed to affect ecosystems dependent on abiotic conditions (Fig. 7). Thus, although this study does not explicitly examine the scale-dependence of biotic interactions (see Fig. 4 and e.g. Sarr et al. 2005; McGill 2010, Araújo & Rozenfeld 2014), the results show that, at least partly, biotic interactions are conditional on environmental factors and their variability in space.

In addition, the results support species-specific outcomes of biotic interactions (Papers II and IV). Studies of individual species have shown that the outcome of biotic interactions are species-pair-specific (Pellissier et al. 2010; Nylén et al. 2013; Bueno de Mesquita et al. in press). Moreover, species- and guild-specific outcomes would only be reasonable since responses of different species and guilds to abiotic predictors vary as well (Bruun et al. 2006; Grytnes et al. 2006; Löbel et al. 2006). Yet, more importantly, and as proposed earlier (e.g. McGill et al. 2006; Soliveres et al. 2012), these analyses indicate that species traits drive the magnitude and outcome of biotic interactions (see e.g. Kunstler et al. 2016). Here, species' competitiveness – stress tolerance, geographic range and guild were found to be decisive traits (see e.g. Fig. 8).

Moreover, the results reveal that species- and individual-level effects can also be seen at the landscape level (Fig. 9). The multiple

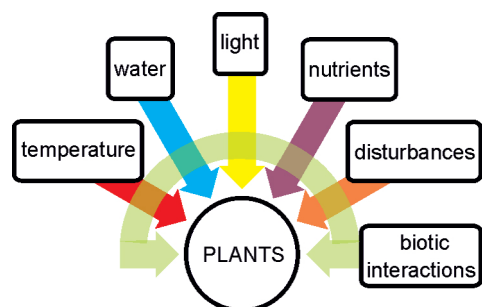


Figure 7. Biotic interactions play a part in defining biodiversity along with abiotic factors. In addition to the direct impacts, their effects are partly dependent on environmental conditions.

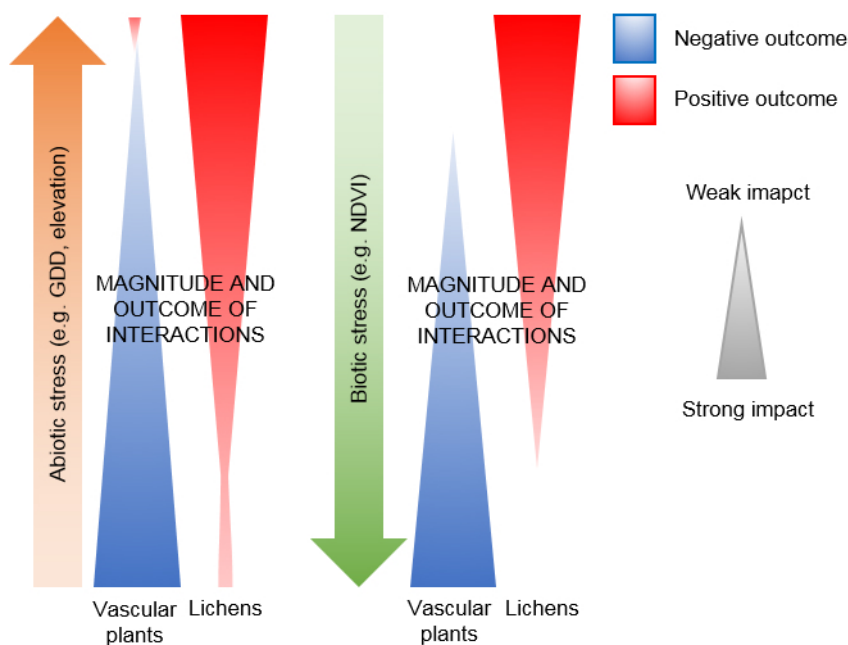


Figure 8. Magnitude and outcome of biotic interactions (i.e. the effect of *Empetrum hermaphroditum*) varied along both abiotic and biotic stress gradients and between guilds (here vascular plants and lichens).

predictions demonstrate how biotic interactions can have equally important influences on spatial biodiversity patterns as abiotic drivers. Hypotheses, like the SGH, and species traits are demonstrated to be useful in predicting the spatial manifestation of biotic interactions. In conclusion, biotic interactions are both ecologically and biogeographically significant in determining ecosystems and biodiversity (Wiens 2011).

Two applied conclusions can also be drawn. Firstly, the demonstrated complex manifestation of biotic interactions indicates that scaling the results of studies concerning only a few species, one taxa or snapshots of environmental conditions to cover whole ecosystems might result in incomplete conceptions. This finding should especially be acknowledged in conservation targeted research (Cornelissen et al. 2001; Gilman et al. 2010). Secondly, the magnitude of the impact of the dominant species was unexpectedly strong.

In a set of model simulations where the cover of the dominant species was slightly increased, vascular plant richness was decreased by up to half. The most negative impacts occur under productive conditions. Paper II also cautions that arctic-alpine species are particularly sensitive to dominant species. These findings are alarming with regard to the future of cold environments (Klanderud et al. 2015). Under potentially warmer conditions, negative interactions would be more intense and widespread, and an increase in the abundance of the dominant species could affect particularly the arctic-alpine species.

4.2 Role of biotic interactions in spatial modelling

As biotic interactions are shown to be important both ecologically and biogeographically, it is critical to account for them in spatial models. Indeed, here, all utilized modelling frameworks showed improved explanatory and predictive

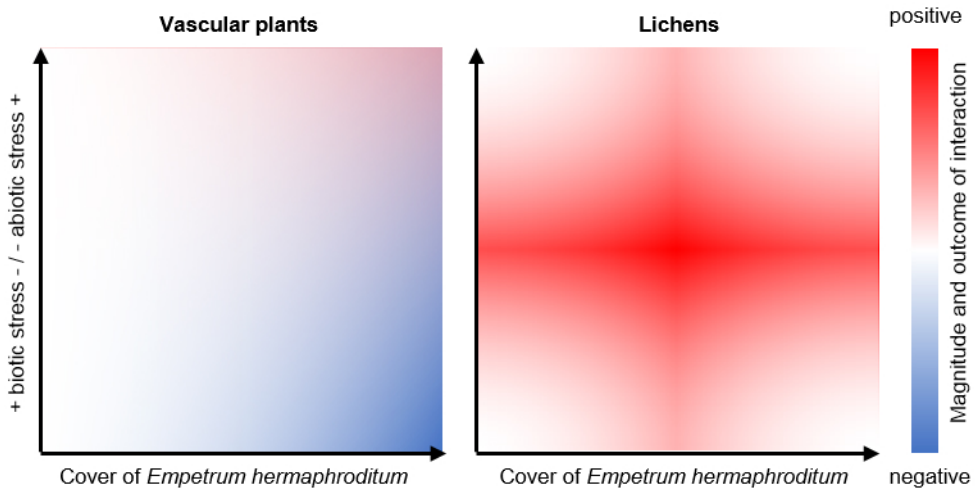


Figure 9. High cover of *Empetrum hermaphroditum* has a negative impact on vascular plant species richness under benign conditions (e.g. at low altitudes), whereas the negative effect decreases and becomes slightly positive with increasing environmental stress. For lichens, the effect of *Empetrum* is constantly positive, with the impact being the strongest with intermediate stress and cover of the dominant species. In the figure, red indicates positive and blue negative interactions, with the intensity of the colour reflecting the magnitude of the interaction.

power when incorporating biotic interactions along with abiotic predictors into the models of all three guilds examined. Especially, Paper I shows that the previously reported importance of biotic interactions in SDMs of individual species (e.g. Araújo & Luoto 2007; Pellissier et al. 2010) also applies to two fundamentally different species richness modelling frameworks.

Stacked species distribution models are demonstrated to suffer from overprediction (Newbold et al. 2009; Dubuis et al. 2011; Mateo et al. 2012; Pottier et al. 2013; Cord et al. 2014). This is presumably due to the omission of biotic interactions and environmental carrying capacity in the models, thus allowing enlarged predictions of ranges of species, therefore also overpredicting species richness (Guisan & Rahbek 2011). In contrast, the MEM-based species richness models are found to overpredict species richness in species-poor areas, whereas underprediction occurs in species-rich areas (Newbold et al. 2009; Dubuis et al. 2011). These biases are presumably due to the MEM not being able to distinguish between sites that have similar abiotic conditions,

but varying biotic composition. Thus, in both SSDM and MEM frameworks, the demonstrated decreases in prediction biases were presumably a result of increased realism in the models by incorporating biotic interactions (Paper I and Guisan & Rahbek 2011; Thuiller et al. 2013; D’Amen et al. 2015). Further, analyses in Paper II demonstrate the importance of biotic interactions in the models to exceed that of abiotic predictors, while the analyses in Papers III and IV show the significance of biotic interactions in the spatial models for other biological measures, namely reproductive effort and community traits, as well. Taken together, biotic interactions play a critical role in governing biodiversity at multiple levels, and omitting their effect in the models may result in unrealistic forecasts.

4.3 Methodological issues

While correlative models have many advantages, some methodological caveats also exist (e.g. Barry & Elith 2006). The most criticized weakness is their correlative nature (Gotelli et al. 2009; Kearney & Porter 2009; Kearney et

al. 2010; Dormann et al. 2012). Relationships detected by models are based on statistical correlations between response and predictor variables, and presuming causality based on the detected relationships could lead to precarious assumptions. To overcome this issue, models must rely on strong theory when choosing covariates, and preferably, also on experimental studies to demonstrate causality between the variables (Austin 2002). Here, the variable selection was based on ecophysiological necessities of vegetation, meaning that the set of explanatory variables comprises factors with known causal effects on terrestrial plant and lichen species (i.e. temperature, water, nutrients, light, disturbances, biotic interactions). However, despite the experimentally demonstrated impacts and mechanisms of these dominant species on other species (e.g. Carlsson & Callaghan 1991; Nilsson et al. 2000; Aerts 2010), it is justifiable to question whether the proxy used for biotic interactions represents the influence of the dominant species or only shared environmental preferences between species (Giannini et al. 2013). In addition, while the percentage cover of the dominant species represents a proxy of volume of species, some other measures might provide more accurate approximations of volume (Suvanto et al. 2014), and thus, intensity of interactions. It is, for example, possible that the demonstrated reduction of competition with increasing environmental stress might result from the parallel decrease in dominant species height, which was not considered here. Moreover, allelopathic effects of *Empetrum* might be mitigated by disturbance (Bråthen et al. 2010).

One of the implicit problems with location-based correlative models is spatial autocorrelation, which is typical of spatially-structured datasets (de Oliveira et al. 2014). Neighbouring data points are more similar than distant ones, causing

non-independence of observations (Legendre & Fortin 1989; Legendre 1993), which in turn hinders the accuracy of models. Multiple methods for testing the data for spatial autocorrelation and for taking it into account in the analyses have been proposed (Carl & Kühn 2007; Dormann et al. 2007). Here, in addition to the use of GEE (Paper III), Moran's I correlograms (Moran 1950) were used to examine the similarity of data points (raw data and model residuals) against the distance between them. Only very weak spatial autocorrelation was found, and thus, it was not considered in subsequent analyses (see Paper I).

4.4 Future perspectives

This thesis contributes to the understanding of the functioning of biotic interactions in ecosystems. Nevertheless, many gaps remain, some of which are presented below. Firstly, the chosen proxy for biotic interactions might not be applicable outside the communities of the study area. To apply similar models to other ecosystems, their influential species must be known. In more complex systems, identifying dominant species might not be possible. Further, to make predictions for a new area or time, grid-type data of all predictors covering the whole area of interest are required. This is rarely the case for individual (even dominant) species. Thus, to effectively account for biotic interactions in spatial models of biodiversity, a more general proxy should be developed. Remotely sensed, high-resolution vegetation or productivity indices might be a solution here (Virtanen et al. 2010; Johansen & Tømmervik 2014).

Secondly, the effects of biotic interactions were studied only among sessile species. Studies covering a variety of species, guilds and environmental conditions should be repeated for animals, where additional (across-trophic level) interactions, such as prey-predation and parasitic or host-plant interactions, exist (Wiszniewski et al. 2013).

Plants (and similar taxa) can also experience interactions other than intra-taxa interactions. For example, interactions between soil microbes and plants and between herbivores and plants have been demonstrated (Olofsson et al. 2013; Bueno de Mesquita et al. in press). Here, only the relationships between above-ground species and guilds were tested, but presumably interactions between, for example, above- and below-ground organisms could also be detected (Van Der Heijden et al. 2008), probably influencing biodiversity predictions (Van Der Putten et al. 2010; However, in a study using the same data as here, inclusion of herbivory had only a weak effect on the predictive power of the species distribution models of 41 plants). Nevertheless, all types of biotic interactions can be assumed to affect the models (with the type of interactions [negative competition, positive mutualism, etc.] governing the effect in models), and thus, the predictions of future biodiversity (see e. g. Araújo & Luoto 2007 for the impact of host plants on a distribution model of butterfly). For instance, positive interactions presumably enlarge the ranges of species with a positive impact on species richness, while negative interactions would have the opposite effect.

Thirdly, for applied purposes, both future climatic and biotic conditions should be simultaneously incorporated for realistic approximations of future biodiversity. Dominant species were shown to strongly influence biodiversity, and alterations in their abundance and distribution are probable in warming conditions (Shevtsova et al. 1997; Sturm et al. 2001). Therefore, predictions of future biodiversity should be conducted acknowledging both future climatic conditions and predicted abundance of dominant species. This approach should provide more realistic predictions of changes in biodiversity.

5 Conclusions

This study demonstrates how the co-occurring dominant species affect species performance and assemblages, with their effect in some cases even exceeding that of abiotic factors. Further, the multiple modelling frameworks used found these effects to vary among species, guilds and traits and also in relation to environmental conditions. In conclusion, the magnitude and outcome of biotic interactions vary across landscapes due to the different assemblages of species and environmental conditions. Nevertheless, species traits and the SGH provide indications to predict the manifestation of biotic interactions. These are ecologically valuable findings, with especially important implications for biogeographical studies. Biotic interactions also drive the spatial biodiversity, and thus, abiotic factors alone cannot be used to explain these patterns.

Biotic interactions proved to be a critical part of not only the ecosystems but also the spatial models of biodiversity. This was evident in the improved explanatory power and predictive accuracy of the models with the inclusion of biotic predictors. Acknowledging biotic interactions in models increases the realism of predictions of biodiversity.

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