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Statistical and process-based models for understanding species distributions in changing environments

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Anett Schibalski

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Summary

Understanding the distribution of species is fundamental for biodiversity conservation, ecosystem management, and increasingly also for climate impact assessment. The presence of a species in a given site depends on physiological limitations (abiotic factors), interactions with other species (biotic factors), migratory or dispersal processes (site accessibility) as well as the continuing effects of past events, e.g. disturbances (site legacy). Existing approaches to predict species distributions either (i) correlate observed species occurrences with environmental variables describing abiotic limitations, thus ignoring biotic interactions, dispersal and legacy effects (statistical species distribution model, SDM); or (ii) mechanistically model the variety of processes determining species distributions (process-based model, PBM). SDMs are widely used due to their easy applicability and ability to handle varied data qualities. But they fail to reproduce the dynamic response of species distributions to changing conditions. PBMs are expected to be superior in this respect, but they need very specific data unavailable for many species, and are often more complex and require more computational effort. More recently, hybrid models link the two approaches to combine their respective strengths.

In this thesis, I apply and compare statistical and process-based approaches to predict species distributions, and I discuss their respective limitations, specifically for applications in changing environments. Detailed analyses of SDMs for boreal tree species in Finland reveal that non-climatic predictors - edaphic properties and biotic interactions - are important limitations at the treeline, contesting the assumption of unrestricted, climatically induced range expansion. While the estimated SDMs are successful within their training data range, spatial and temporal model transfer fails. Mapping and comparing sampled predictor space among data subsets identifies spurious extrapolation as the plausible explanation for limited model transferability. Using these findings, I analyze the limited success of an established PBM (LPJ-GUESS) applied to the same problem. Examination of process representation and parameterization in the PBM identifies implemented processes to adjust (competition between species, disturbance) and missing processes that are crucial in boreal forests (nutrient limitation, forest management). Based on climatic correlations shifting over time, I stress the restricted temporal transferability of bioclimatic limits used in LPJ-GUESS and similar PBMs. By critically assessing the performance of SDM and PBM in this application, I demonstrate the importance of understanding the limitations of the applied methods.

As a potential solution, I add a novel approach to the repertoire of existing hybrid models. By simulation experiments with an individual-based PBM which reproduces community dynamics resulting from biotic factors, dispersal and legacy effects, I assess the resilience of coastal vegetation to abrupt hydrological changes. According to the results of the resilience analysis, I then modify temporal SDM predictions, thereby transferring relevant process detail from PBM to SDM. The direction of knowledge transfer from PBM to SDM avoids disadvantages of current hybrid models and increases the applicability of the resulting model in long-term, large-scale applications. A further advantage of the proposed framework is its flexibility, as it is readily extended to other model types, disturbance definitions and response characteristics.

Concluding, I argue that we already have a diverse range of promising modelling tools at hand, which can be refined further. But most importantly, they need to be applied more thoughtfully. Bearing their limitations in mind, combining their strengths and openly reporting underlying assumptions and uncertainties is the way forward.

Zusammenfassung

Wissen über die Verbreitung von Arten ist fundamental für die Erhaltung von Biodiversität, das Management von Ökosystemen und zunehmend auch für die Abschätzung der Folgen des Klimawandels. Das Vorkommen einer Art an einem Standort hängt ab von: physiologischen Grenzwerten (abiotischen Faktoren), Interaktionen mit anderen Arten (biotischen Faktoren), Ausbreitungsprozessen (Erreichbarkeit des Standorts) sowie Nachwirkungen vergangener Ereignisse, z.B. Störungen (Standortgeschichte). Modellansätze zur Vorhersage von Artverbreitungen (i) korrelieren entweder beobachtete Artvorkommen mit abiotischen Umweltvariablen und ignorieren damit biotische Interaktionen, Ausbreitung und Nachwirkungen (statistische Artverbreitungsmodelle, SDM); oder (ii) sie modellieren mechanistisch, wie sich die verschiedenen Prozesse auf Arten auswirken (prozessbasierte Modelle, PBM). SDMs sind weitverbreitet, da sie einfach anzuwenden sind und verschiedenste Datenqualitäten akzeptieren. Aber sie beschreiben nicht korrekt, wie Arten dynamisch auf Umweltänderungen reagieren. PBMs sind ihnen in dieser Hinsicht überlegen. Allerdings benötigen diese sehr spezifische Daten, welche für viele Arten nicht verfügbar sind. Zudem sind sie oft komplexer und benötigen mehr Rechenkapazität. Relativ neu ist der Ansatz des Hybridmodells, welches statistische und prozessbasierte Modelle verknüpft und so ihre jeweiligen Stärken vereint.

In dieser Arbeit, nutze ich sowohl statistische als auch prozessbasierte Modelle, um die Verbreitung von Arten vorherzusagen, und ich diskutiere ihre jeweiligen Schwächen, besonders für die Anwendung im Klimawandelkontext. Eine detaillierte Analyse der SDMs für boreale Baumarten in Finnland zeigt, dass nicht-klimatische Variablen - Bodeneigenschaften und biotische Interaktionen - wichtige Faktoren an der Baumgrenze sind und daher die Reaktion von Arten auf Klimaänderungen beeinflussen. Während die SDMs innerhalb der Wertebereiche ihrer Trainingsdatensätze erfolgreich sind, scheitern Versuche, die Modelle auf andere Regionen oder in die Zukunft zu übertragen. Die Visualisierung und der Vergleich des abgedeckten Umweltraums zwischen den Teildatensätzen liefert eine plausible Erklärung: Extrapolation. Basierend auf diesen Ergebnissen, analysiere ich den bedingten Erfolg eines etablierten PBMs (LPJ-GUESS), das ich auf dieselbe Fragestellung anwende. Die Untersuchung der Prozessbeschreibungen im Modell sowie der Parametrisierung zeigen, dass bereits implementierte Prozesse angepasst werden müssen (Konkurrenz, Störungen) und dass für boreale Wälder entscheidende Prozesse fehlen (Nährstoffe, Bewirtschaftung). Mithilfe von klimatischen Schwellenwerten, die sich über die Zeit verschieben, betone ich die eingeschränkte Übertragbarkeit von bioklimatischen Grenzwerten in LPJ-GUESS und ähnlichen PBMs. Indem ich die Performance beider Methoden in dieser Anwendung kritisch beleuchte, zeige ich, wie wichtig es ist, sich der Grenzen jedes Modellansatzes bewusst zu sein.

Als Lösungsmöglichkeit füge ich dem bestehenden Repertoire der Hybridmodelle einen neuen Ansatz hinzu. Mithilfe von Simulationsexperimenten mit einem individuenbasierten PBM, das erfolgreich die Dynamik von Artgemeinschaften beschreibt (resultierend aus biotischen Faktoren, Ausbreitung und Nachwirkungen), untersuche ich die Resilienz von Küstenvegetation auf abrupte Änderungen der Hydrologie. Entsprechend der Ergebnisse dieser Resilienzanalyse passe ich die zeitlichen Vorhersagen eines SDMs an und übertrage so das nötige Prozesswissen von PBM zu SDM. Die Übertragungsrichtung von PBM zu SDM umgeht die Nachteile bestehender Hybridmodelle und verbessert die Anwendbarkeit für langfristige, großflächige Berechnungen. Ein weiterer Vorteil des vorgestellten Konzepts ist seine Flexibilität, denn es lässt sich einfach auf andere

Modellarten, andere Definitionen von Umweltstörungen sowie andere Vorhersagegrößen anwenden.

Zusammenfassend argumentiere ich, dass uns bereits vielfältige, erfolgversprechende Modellansätze zur Verfügung stehen, die noch weiterentwickelt werden können. Vor allem aber müssen sie mit mehr Bedacht angewendet werden. Voran kommen wir, indem wir die Schwächen der Ansätze berücksichtigen, ihre Stärken in Hybridmodellen kombinieren und die zugrunde liegenden Annahmen und damit verbundene Unsicherheiten deutlich machen.

1. Introduction

1.1. Species distributions in a changing world

Understanding the distribution of species is fundamental for biodiversity conservation (Pěknicová and Berchová-Bímová 2016, Guisan et al. 2013, Rodríguez et al. 2007), ecosystem management (Folke et al. 2004), and increasingly also for climate impact assessment (Rowland et al. 2011, Thuiller et al. 2004). Whether a species occurs in a site depends on three main factors (cf. BAM-diagram, Peterson et al. 2015). Firstly, physiological limitations (e.g. temperature, water availability, light and nutrients for plant species) describe the abiotic (**A**) boundaries of the fundamental ecological niche of an organism (Grinnellian niche, Soberón 2007). Secondly, biotic (**B**) interactions (e.g. competition, facilitation, predation, and parasitism) reduce the fundamental niche, as species are out-competed on otherwise favourable sites within their fundamental niche by stronger competitors (Grime 1973, Zaret and Rand 1971). And thirdly, migratory (**M**) processes further limit species on abiotically and biotically favourable sites, if species are unable to reach suitable sites due to dispersal barriers, or if they fail to successfully establish, survive and reproduce on sites outside their current range (Svenning and Skov 2007, Ozinga et al. 2005, Ehrlén and Eriksson 2000). In addition to these three factors (**BAM**) influencing species distribution, I explicitly add temporal (**T**) aspects to underline their importance (‘the legacy of history’, Zimmermann et al. 2010). For example, species are absent from a currently favourable site because they have become locally extinct during a disturbance event in the past and need to re-establish from neighbouring populations (source-sink dynamics of metapopulations, Boughton 1999, Eriksson 1996, Harrison 1991). Alternatively, long-living species are present in currently unfavourable sites because they have established successfully during a favourable period in the past and persist under now unfavourable conditions (extinction debt, Hylander and Ehrlén 2013, Hanski 2000). In conclusion, species are constrained by factors **B**, **M** and **T**, and thus occupy only part of their fundamental niche, the realized niche (Hutchinsonian niche, Holt 2009).

Observing, describing and documenting where species occur started with naturalists like Charles Darwin, Alfred Russel Wallace and Alexander von Humboldt who returned from their adventurous journeys with countless specimens and notes which are preserved and exhibited in Natural History Museums around the world. This wealth of data can now be analyzed by recently developed methods (Maldonado et al. 2015, Elith et al. 2006), and even today hitherto undescribed species are discovered in old museum collections (Yong 2016). Understanding the underlying processes of observed patterns is the aim of field and laboratory experiments (Pearcy et al. 1989) which systematically manipulate abiotic and biotic growing conditions (e.g. Lau et al. 2008, Greulich et al. 2000). Eventually, collected observations and ecological knowledge are jointly applied to map species distributions across space which is one focus of species distribution modelling (Elith and Leathwick 2009). Species distribution models have been applied with considerable success to predict current species distributions (e.g. Elith et al. 2006).

In recent decades, however, anthropogenic climate change has triggered phenological, range and community shifts (Parmesan 2006, Walther et al. 2002). Climate change affects all of the factors determining species distributions (**BAMT**): Due to climate warming (**A**), plants flower earlier in spring (Menzel et al. 2006), possibly resulting in (**B**) phenological asynchrony of plant-pollinator relationships (Memmott et al. 2007). Treelines have shifted towards higher latitudes and altitudes (Harsch et al. 2009) where they are (**A**) mainly climatically-driven (Holtmeier and Broll 2007) and (**M**) no dispersal barrier constrains range expansion (Rupp et al. 2001). Altered disturbance regimes (**T**) likely increase the pressure on e.g. tree species by pests and pathogens (Dale et al. 2009, Ayres and Lombardero 2000). Modelling the impact of climate change on species distribution is, thus, a new challenge which requires the inclusion of not only (**A**) climatic (Pearson and Dawson 2003) and other abiotic factors such as edaphic characteristics (Dubuis et al. 2013), but also (**B**) biotic interactions (Anderson 2017, Wisz et al. 2013), (**M**) dispersal and (**T**) metapopulation dynamics (Fordham et al. 2013, Araújo and Luoto 2007, Guisan and Thuiller 2005, Davis et al. 1998).

1.2. Species distribution modelling

1.2.1. Statistical vs. process-based approaches

In ecological modelling, two fundamentally different approaches may be applied to model species distributions: statistical (empirical, correlative, phenomenological) models and process-based (mechanistic) models. Dormann et al. (2012) compared the two approaches in a comprehensive review (see also Peterson et al. (2015) and Kearney and Porter (2009), Table 1) which I will not attempt to recreate here. Instead, I will only briefly introduce the most important characteristics of the two approaches and refer to relevant reviews (**Table 1.1**).

Statistical species distribution models (SDMs) relate observed species occurrence (presence-absence) or abundance (= response variable) to environmental factors that are assumed to be determinants, often proxies for physiological limitations (= predictor variables). The form of the described relationship differs greatly between statistical approaches (Segurado and Araújo 2004), ranging from relatively simple bioclimatic envelopes (e.g. BIOCLIM, Busby 1991), based on species presences and climate proxies alone, to more sophisticated regression models including non-climatic predictors as well as interactions between predictors, to even more complex machine learning methods (see examples in **Table 1.1**). Applying SDMs to maps of predictors yields habitat suitability maps which is one main focus of species distribution modelling (alongside ecological explanation, Mac Nally 2000). SDMs have been successfully and widely applied to model species distributions (e.g. Elith et al. 2006, Thuiller 2003) due to their easy application using open-source statistical software (e.g. R Core Team 2016) as well as their flexibility concerning input data. For example, SDMs allow distal predictors (Austin 2002), climate proxies (Heikkinen et al. 2006) and presence-only data (Pearce and Boyce 2006). This enables the utilization of readily available species data from e.g. natural history collections (Graham et al. 2004) as well as publicly available current climate (e.g. WorldClim, Hijmans et al. 2005), climate scenario (e.g. ALARM, Fronzek et al. 2012) and land cover datasets (e.g. CORINE, http://land.copernicus.eu/pan-european/corine-land-cover).

Table 1.1. Comparison of statistical and process-based modelling approaches (see also Peterson et al. (2015), Dormann et al. (2012) and Kearney and Porter (2009), Table 1).

	statistical model (SDM)	**process-based model (PBM)**
synonyms	ecological niche model, habitat suitability model	mechanistic model
nature	correlative; static	causal; dynamic
process representation	implicitly by selection of predictors and form of relationship	explicitly by e.g. mathematical equations
model parameters	have no ecological meaning	have ecological meaning; measurable
species distribution	modelled directly as response variable	emerges as a by-product
specificity – generality trade-off	high specificity (good prediction results), low generality (limited transferability)	low(er) specificity, greater generality and transferability
computational effort / complexity	low / low (higher for machine learning)	often high (depends on resolution) / simple to very complex
data requirements	accepts various data qualities (e.g. presence-only, proxies, distal predictors)	requires very specific data on the species' ecology
reviews	Guisan and Zimmermann (2000), Austin (2002), Araújo and Guisan (2006), Elith and Leathwick (2009), Franklin (2010b), Sillero (2011), Araújo and Peterson (2012)	individual-based models, IBM (Grimm and Railsback 2005); matrix population models (Caswell 2006); metapopulation models (Hanski 1994); mechanistic niche models, e.g. NicheMapper (Kearney and Porter 2009), PHENOFIT (Chuine 2000); dynamic global vegetation models, DGVM, e.g. LPJ (Smith et al. 2001), IBIS (Foley et al. 1996), ORCHIDEE (Krinner et al. 2005); gap models (Bugmann 2001)
examples	regression: LM, GLM, GAM, MARS; machine learning: CART, boosting (BRT, RF), ANN, MaxEnt; ►BIOMOD; bioclimatic envelopes: BIOCLIM (Busby 1991), HABITAT (Walker and Cocks 1991), DOMAIN (Carpenter et al. 1993)	

LM = linear model; GLM = generalized linear model; GAM = generalized additive model; MARS = multi-variate adaptive regression splines; CART = classification and regression trees; BRT = boosted regression trees; RF = random forests; ANN = artificial neural networks; MaxEnt (Elith et al. 2011, Phillips et al. 2006) originates from statistical mechanics (Dewar and Porte 2008); BIOMOD (Thuiller et al. 2009) uses a weighted ensemble of nine regression and machine learning methods (see Heikkinen et al. (2006) for an overview of the different methods)

Methodological issues to be considered when estimating SDMs (see also Zuur et al. 2010) include model and predictor selection (Symonds and Moussalli 2011, Austin and Niel 2011, Segurado and Araújo 2004), spatial autocorrelation (Warren et al. 2014, Dormann et al. 2007, Segurado et al. 2006) and non-stationarity (Hothorn et al. 2011, Austin 2007, Brunsdon et al. 1998) as well as collinearity (Dormann et al. 2013) and overfitting (Merow et al. 2014). Major uncertainty sources in SDMs are data deficiencies (e.g. missing predictors and small sample size) and model specification (Buisson et al. 2010, Dormann et al. 2008, Barry and Elith 2006, Heikkinen et al. 2006).

More importantly, several underlying assumptions on which SDMs are based limit their applicability in studies of environmental change as discussed in depth by Guisan and Thuiller (2005) and Heikkinen et al. (2006). First, SDMs assume that the data collected and used to estimate the model represent equilibrium conditions (Guisan and Theurillat 2000). This assumption is violated by definition when studying responses to climate change or the spread of invasive species (Elith et al. 2010, Kleinbauer et al. 2010). Second, they assume the stationarity of estimated statistical relationships across space and time (Pearman et al. 2008, Austin 2007, Osborne et al. 2007). Third, SDMs are not intended for extrapolation to novel environments, i.e. beyond the training data range (Zurell et al. 2012a, Elith and Leathwick 2009). Violation of the stationarity assumption and extrapolation to novel environments reduce the transferability of SDMs across space (i.e. to other regions, Randin et al. 2006) and time (e.g. to future conditions, Dobrowski et al. 2011) which we will demonstrate in **chapter 2**. Unfortunately, despite awareness of these critical issues of SDM application especially in the context of environmental change, the easy applicability has led to numerous studies of e.g. the very popular MaxEnt approach (**Table 1.1**), often without the required methodological understanding to create meaningful results (Anderson 2015, Guillera-Arroita et al. 2015, Yackulic et al. 2013).

As biotic interactions, spatial dispersal processes and transient dynamics are usually not represented in SDMs, they fail to distinguish between observed absences due to (**A**) physiological limitation (fundamental niche) and those due to (**B**) biotic pressure from other species, (**M**) dispersal limitation or (**T**) ongoing effects of past disturbances and population dynamics (realized niche). Process-based models (PBMs), on the other hand, do allow the explicit representation of any of these processes causally influencing species distribution, e.g. via differential equations, physiological thresholds or rule-based simulations. For example, transient dynamics, such as succession or recovery from a disturbance, emerge from simulations over time in models with a memory, i.e. in which previous time steps impact on the present and future time step. Dynamics of populations can be captured by simple differential equations (e.g. Lotka-Volterra model), by more complex stage- or age-structured matrix population models (Caswell 2006) or as emergent outcome of individual-based models (Grimm and Railsback 2005) and gap models (Bugmann 2001). Metapopulation models (Hanski 1994) explicitly consider colonization of new habitat patches by dispersal and extinction of local populations, e.g. due to disturbances. On a global scale, dynamic global vegetation models (DGVM, Peng 2000) predict the distribution of plant functional types or species, often linked to a global circulation model (GCM).

Despite their structural diversity, PBMs generally share certain limitations which set them apart from statistical models. First, PBMs generally require more detailed ecological information about the modelled species and processes which usually limits their application to well-studied species. Second, they are often more complex and, thus, require more computational effort than SDMs, as they e.g. track the fate of individuals in a population, require spin-up periods in time-series simulation or replicate model runs due to stochasticity in the model. On the other hand, if the relevant processes are implemented with sufficient detail and accuracy, PBMs are expected to be superior to purely statistical models when applied to new environments (Gustafson 2013, Dormann et al. 2012, Bossel 1992).

In this regard, Dormann et al. (2012) make the important distinction between 'forward' and 'fitted' process-based models (cf. Bossel's (1992) distinction between real-structure and elementary-structure models) which they defended (Schymanski et al. 2013) against criticism by Kriticos et al. (2013). In 'forward' PBMs, model parameters are process parameters such as threshold temperatures or growth rates which can be measured. In contrast, parameters in 'fitted' PBMs are aggregations without real-world counterpart and have to be fitted statistically. 'Fitted' PBMs are, thus, closer to statistical models and share their assumptions and limitations concerning e.g. model transferability. This distinction will be revisited in **chapter 3** of this thesis, in which we analyze the limited success of a 'fitted' process-based model, LPJ-GUESS (Smith et al. 2001).

In summary, statistical and process-based model approaches differ in many respects, each having their own strengths and limitations, and neither being inherently superior over the other. Limitations of process-based approaches seem to be not as abundantly or as critically published as the various methodological issues with SDM (but see Bachelet et al. 2015 for more critical views on e.g. DGVMs, Fisher et al. 2010, Quillet et al. 2010). Limitations of SDMs, on the other hand, have been discussed in depth (Jarnevich et al. 2015, Araújo and Peterson 2012, Franklin 2010a, Heikkinen et al. 2006, Guisan and Thuiller 2005) and many have cautioned their use in conservation planning and climate impact studies (Gustafson 2013, McPherson et al. 2004), although differences are made between various statistical approaches (Hijmans and Graham 2006). To improve purely statistical species distribution models, there has been a call to link them with process-based models (Swab et al. 2012, Mokany and Ferrier 2011, Franklin 2010a, Gallien et al. 2010, Huntley et al. 2010, Thuiller et al. 2008, Guisan and Thuiller 2005).

1.2.2. Linking statistical and process-based approaches

A first step to combining the strengths of both modelling approaches is to compare the predicttions of statistical and process-based approaches (Gritti et al. 2013), which many studies attempted with varied results (**Table 1.2**). Most comparative studies found good agreement of SDMs and PBMs under current conditions, while yielding diverging, even contrasting predictions under projected conditions (either future climate or new regions). Differences between approaches could be explained, in part, by missing processes, thus, confirming the need for more process detail in SDMs. For example, the effect of CO_2 fertilization led to increased productivity in PBMs, while it was missing in SDMs, where instead the effect of warming (not offset by CO_2 fertilization) resulted in decreased habitat suitability (Estes et al. 2013, Cheaib et al. 2012, Keenan et al. 2011). In **chapter 3**, we do not directly compare predictions of SDMs and PBMs, but we allow results from statistical modelling in **chapter 2** to stimulate our analysis of PBM results in **chapter 3**.

A further tentative step towards including more process detail into statistical SDMs, and thereby improving their transferability, is including more proximal (i.e. closer to the described process, Austin 2002), more meaningful predictor variables (Petitpierre et al. 2017, Mod et al. 2016). Examples of this approach, which some already call 'hybrid model approach' (Buckley et al. 2011), include: ecophysiological temperature thresholds as thermal constraints (Buckley et al. 2011), number of tourists and trade volumes as proxies for dispersal opportunities (Thuiller et al. 2005), or co-occurrence of species as proxy for biotic interaction (e.g. Giannini et al. (2013), Araújo et al.

(2014) and Schibalski et al. (2014) or **chapter 2** of this thesis). However, the co-occurrence of other species may equally be a proxy for a bundle of abiotic conditions, not biotic interactions (Austin 2002). Thus, more sophisticated ways to integrate statistical and process-based models are required.

Table 1.2. Studies comparing predictions by statistical and process-based modelling approaches.

Species, location	Statistical (SDM)	Process-based (PBM)	Notes	Study by
agreement of both model approaches for observed and projected conditions				
invasive moth, global	MaxEnt	CLIMEX [1]	accurate	Lozier and Mills (2011)
possum, Australia	MaxEnt, BIOCLIM	NicheMapper [1]	accurate	Kearney et al. (2010)
100 plant species, Americas	MaxEnt, BIOCLIM GAM, DOMAIN	EcoCrop [1]	only GAM accurate	Hijmans and Graham (2006)
agreement of both model approaches for observed conditions, disagreement for projected conditions				
koala, Australia	MaxEnt	NicheMapper [1]	agree on refugia	Briscoe et al. (2016)
maize and wheat, South Africa	GAM	CERES [2]	CO_2 increase: contrasting SDM/ PBM predictions	Estes et al. (2013)
three tree species, Spain	BIOMOD	GOTILWA+ [2]		Keenan et al. (2011)
butterfly and lizard, United States	MaxEnt, GLM	e.g. biophysical threshold [1]	greater range shifts (PBMs)	Buckley et al. (2010)
invasive toad, Australia	MaxEnt, GLM, GAM, BRT	biophysical model [1]		Elith et al. (2010)
15 tree species, North America	BIOCLIM	PHENOFIT [1]	higher extinction/ colonization (SDM)	Morin and Thuiller (2009)
disagreement of both model approaches for observed and projected conditions				
five tree species, France	N-NBM, BIOMOD	STASH [1*], PHENOFIT [1], Castanea [2], LPJ [2], IBIS [2], ORCHIDEE [2]	very species- and model-specific; CO_2 effect	Cheaib et al. (2012)
two invasive *Acacia* ssp., South Africa	MaxEnt, BRT	CLIMEX [1]	SDMs over-estimate ranges	Webber et al. (2011)

N-NBM = logistic regression model (Badeau et al. 2010); [1] ecophysiological, mechanistic niche models; [2] growth simulators, e.g. DGVMs; * Gritti et al. (2013) classified STASH as correlative model

Dormann et al. (2012) distinguish between ‘hybrid’ models (Gallien et al. 2010), in which statistical and process-based models are run sequentially, and ‘integrated’ models, when statistical and process-based approaches are dynamically linked and run simultaneously (see also Ehrlén and Morris 2015). An example for an ‘integrated’ approach is the statistical fitting of parameters in process-based models (Merow et al. 2011) by pattern-oriented or inverse modelling (Grimm et al. 2005). Recent approaches include the Bayesian framework (e.g. Hartig et al. 2012, Arhonditsis et al. 2007, van Oijen et al. 2005) and model-data fusion (Peng et al. 2011). Using a hierarchical Bayesian framework, Pagel and Schurr (2012) statistically estimated process-based dynamic range models (DRMs), specifically including population dynamics (Schurr et al. 2012). DRMs outperformed SDMs and 'hybrid' models in a comparison using virtual species (Zurell et al. 2016). The 'virtual ecologist approach' (Zurell et al. 2010, Zurell et al. 2009) itself may be seen as another approach to link statistical and process-based modelling, as it allows the critical assessment of statistical methods (e.g. data sampling or model comparison, Thibaud et al. 2014) by creating and sampling virtual data with process-based models.

Table 1.3. Summary of hybrid model approaches (see also Table 1 in Lurgi et al. 2015).

Type of model linkage	Examples
dispersal	
dispersal kernel is additional term in GLM model equation	Meentemeyer et al. (2008)
SDM-derived habitat suitability is multiplied with probability of dispersal from dispersal kernel	Williams et al. (2008)
SDM-derived habitat suitability of grid cells of a cellular automaton which spatially explicitly simulates dispersal determines colonization probability	DISPERSE (Carey 1996), SHIFT (Iverson et al. 2004), MigClim (Engler and Guisan 2009), Morin and Thuiller (2009)
dispersal direction in simulations by a cellular automaton depends on SDM-derived habitat suitability	Söndgerath and Schröder (2002)
SDM-derived habitat suitability defines focal nodes in a connectivity analysis	Cianfrani et al. (2013)
population dynamics (and dispersal)	
Leslie matrix parameters depend on SDM-derived habitat suitability	Söndgerath and Schröder (2002)
spatial structure of habitat patches (size, quality, location) in a metapopulation model determined by SDM-derived habitat suitability map	Akçakaya (1995), Akçakaya (2000), Lindenmayer and Possingham (1996)
demographic rates depend on habitat suitability	PATCH model (Carroll 2007), Dullinger et al. (2012)
carrying capacity depends on SDM-derived habitat suitability	Zurell, Grimm et al. (2012b), Anderson et al. (2009), Keith et al. (2008), Fordham et al. (2013), Swab et al. (2012), Cheung et al. (2009)
biotic interactions (and dispersal, population dynamics etc.)	
competitive ability of different trait-based plant functional types depends on SDM-derived habitat suitability	BioMove (Midgley et al. 2010)
simple overlay of SDM and DGVM output maps	Case and Lawler (2016)
SDM-derived habitat suitability defines habitat patches for dynamic vegetation model ('hybrid-DVMs')	Albert et al. (2008) Boulangeat et al. (2012)

More relevant to this thesis are 'hybrid' models which feed the output of one model approach into the other. One way is to use abiotic or biotic variables predicted by process-based models as predictors in statistical models (Pellissier et al. (2013), Rickebusch et al. (2008), Schröder et al.

(2008) and **chapter 4** of this thesis). The other way is to use the output of SDMs, static habitat suitability (maps), as input for process-based models (**Table 1.3**, see also Lurgi et al. (2015) for an extensive review of hybrid modelling platforms). In the various efforts to link SDMs with dispersal models, SDM-derived habitat suitability maps are often used to define the establishment probability of grid cells of cellular automata which spatially explicitly simulate the dispersal of individuals. Similarly, SDM-derived habitat suitability may be used to define the spatial structure and carrying capacity of patches in metapopulation models (e.g. RAMAS-GIS, Akçakaya 2001) or to determine demographic rates in matrix population models in order to link SDMs with a process-based approach to population dynamics. More recently, however, the simple relationship between habitat suitability and demographic parameters has been questioned (Thuiller et al. 2014). Finally, Midgley et al. (2010) used SDM-derived habitat suitability to scale the competitive ability of different plant functional types in BioMove, thus affecting community dynamics under climate change. Although many studies incorporate dispersal and (meta)population dynamics into SDMs (**Table 1.3**), biotic interactions require more attention (Thuiller et al. 2013, Wisz et al. 2013, Kissling et al. 2012). In **chapter 4** of this thesis, we will add a novel hybrid approach to **Table 1.3** in order to link SDM predictions with community dynamics including biotic interactions, dispersal and the response to disturbances. Whereas almost all hybrid models listed in **Table 1.3** use SDM-derived habitat suitability as input for various process-based approaches, we use the aggregated results of simulation experiments with a PBM to modify temporal SDM predictions.

1.3. Thesis outline

As a cumulative dissertation, the body of this thesis consists of three manuscripts either published (**chapter 2**) or under review for publication (**chapter 3** and **4**) in scientific, peer-reviewed journals. They are preceded by an introductory chapter (this **chapter 1**) and followed by a synthesis (**chapter 5**), completing the thesis. Although I am the first author of all chapters, I duly acknowledge contributions by co-authors to **chapters 2** to **4** (see separate declaration of contribution). I added selected appendix material for core **chapters 2** to **4** at the end of the respective chapters. Further supplementary material as well as a digital version of this thesis can be found on CD (back cover).

In **chapter 2**, we used sophisticated statistical species distribution models to both understand and predict the treeline of three major boreal tree species in Northern Finland. By investigating the response curves of the resulting models and the relative importance of climatic as well as non-climatic predictors (proxies for edaphic characteristics and biotic interactions), we assessed the sensitivity of this important biome boundary to climate change. Furthermore, we examined the spatial and temporal transferability of the estimated SDMs to assess their suitability in climate change studies.

In **chapter 3**, we used the findings from **chapter 2** to analyze the limited success of a ‘fitted’ process-based model applied to the same problem as in **chapter 2**. Now knowing the importance of non-climatic predictors pointing to dispersal limitation and interspecific competition as important processes of tree distribution in Finnish Lapland, we systematically examined the respective process representation and parameterization in the process-based model. Based on changing climatic correlations over time (**chapter 2**), we stressed the important drawback of bioclimatic limits in ‘fitted’ process-based models.

Having applied statistical (**chapter 2**) and ‘fitted’ process-based approaches (**chapter 3**) to model species ranges in changing environments with limited success, we proposed a novel framework to link both approaches in a ‘hybrid’ model in **chapter 4**. In a different environment now, we assessed the resilience of coastal vegetation to abrupt hydrological changes by simulation experiments with an individual-based model. We then modified temporal SDM predictions according to the results of the resilience analysis, thereby transferring the relevant process detail from PBM to SDM. Whereas previous ‘hybrid’ models focused on *spatial* SDM predictions (habitat suitability maps), we modified SDM-predicted time series using PBM-simulated *temporal* patterns of species response to disturbances.

By critically assessing the performance of a statistical (**chapter 2**) and a process-based model (**chapter 3**) predicting species distributions in changing environments, we stress the importance of understanding the limits of the applied methods. We offer a novel framework to combine the strengths of both approaches for climate change applications in **chapter 4**. Finally, I evaluate the different approaches and discuss ways forward in species distribution modelling (**chapter 5**).

2. Climate change shifts environmental space and limits transferability of treeline models [1]

Abstract

Our study aims at gaining insights into the processes determining the current treeline dynamics in Finnish Lapland. Using forest surveys conducted in 1978 and 2003 we modelled the occurrence and abundance of three dominant tree species in Finnish Lapland, i.e. *Pinus sylvestris*, *Picea abies* and *Betula pubescens*, with boosted regression trees. We assessed the importance of climatic, biotic and topographic variables in predicting tree occurrence and abundance based on their relative importance and response curves. We compared temporal and spatial transferability by using an extended transferability index.

Site fertility, the abundance of co-occurring species and growing degree days were generally the most important predictors for both occurrence and abundance across all species and datasets. Climatic predictors were more important for modelling occurrences than for modelling abundances. Occurrence models were able to reproduce the observed treeline pattern within one time period or region. Abundance models underestimated basal area but captured the general pattern of low and high values. Model performance as well as transferability differed considerably between species and datasets. *P. sylvestris* was modelled more successfully than *P. abies* and *B. pubescens*. Generally, spatial transferability was greater than temporal transferability. Comparing the environmental space between datasets revealed that transferring models means extrapolating to novel environments, providing a plausible explanation for limited transferability.

Our study illustrates how climate change can shift the environmental space and lead to limited model transferability. We identified non-climatic factors to be important in predicting the distribution of dominant tree species, contesting the widespread assumption of climatically induced range expansion.

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[1] An article with equivalent content has been published as:
Schibalski, A, Lehtonen, A, Schröder, B. 2014. Climate change shifts environmental space and limits transferability of treeline models. Ecography 37: 321–335. DOI: 10.1111/j.1600-0587.2013.00368.x.

2.1. Introduction

A treeline is the transition zone between dense forest and tundra (arctic treeline) which can span over many kilometres and is not literally a line but rather a gradient of local presences and absences of trees (Sveinbjörnsson 2000). In Finnish Lapland this zone is relatively broad (400 km, Juntunen et al. 2002) and modified by the glacial topography. Thus, on separate fells in southern Lapland the treeline is an elevational rather than latitudinal transition zone (Veijola 1998).

Numerous studies have applied dendrochronology, fossils and pollen analysis to reconstruct the treeline dynamics during the Holocene climate changes in Northern Finland (Kultti et al. 2006, Helama et al. 2004). They show that the shifting of the species in the past reflects the sequence of their current treeline positions (Appendix A1, **Fig. A1.1**): *Betula pubescens* Ehrh. arrived at 9000 BP, *Pinus sylvestris* L. at 6000 BP and *Picea abies* (L.) Karst. as late as 3000 BP (Eronen et al. 1999). In contrast, *P. abies* forms the northernmost treeline in eastern Fennoscandia and northern Russia (Oksanen 1995). The restriction of *P. abies* to the south in Finnish Lapland might thus not constitute an equilibrium state. The treeline for this species may not be dictated by climatic factors alone, but rather by edaphic factors such as soil type. Sutinen et al. (2005) suggest that the Lapland Granulite Belt in north-eastern Lapland, forming dry, nutrient-poor tills dominated by *P. sylvestris* and *B. pubescens*, is a barrier for *P. abies* treeline advance. Planting experiments and isolated occurrences show that *P. abies* is indeed able to survive on sites far north of its current treeline (Oksanen 1995).

The arctic treeline ecotone is one of the biome boundaries expected to react very sensitively to the ongoing climatic change and thus serves as an indicator for current climate warming (Holtmeier and Broll 2005). A northwards treeline shift has several effects: First, it reduces the treeless arctic biome and thus endangers the species diversity around the pole (Holtmeier and Broll 2007). Second, in a positive feedback, it changes climatic characteristics such as albedo and evaporation and thus alters the climate itself leading to a further warm-up as dark forest surfaces reflect less radiation than snow-covered ground (Grace et al. 2002). Third, it remains unclear whether carbon sequestration by tree growth on yet unforested sites will offset carbon losses due to higher decomposition rates in the warming soil (Hyvönen et al. 2007, Wilmking et al. 2006). Juntunen et al. (2002) report a potential for treeline advance of *P. sylvestris* and *P. abies* in Northern Finland due to an increase in basal area and tree density between 1983 and 1999 as well as an increase in regeneration peaks for Northern Fennoscandia. Intensive regeneration since the 1970s has already been reported for Pallastunturi in Finnish Lapland (Tasanen et al. 1998). However, advance is not the globally uniform response of treelines to climate warming indicating that other restraining factors exist (Harsch et al. 2009).

The anomalous case of *P. abies* in Finnish Lapland as well as past and ongoing treeline dynamics motivate the following questions: (i) What are the processes determining the current treeline position in Finnish Lapland and, thus, (ii) how sensitive is it to future climatic change? (iii) Can we successfully model the abundance of the three dominant species? (iv) Are our models transferable between different time periods or regions; can we successfully predict future treeline patterns using models trained on data from the past (forecasting), and can we reproduce historic patterns (hindcasting) as a prerequisite for model application to climate change scenarios?

2.2. Methods

2.2.1. Data

2.2.1.1. National Forest Inventory datasets

Our datasets are part of the 7th (NFI 7, Kuusela and Salminen 1991) and 9th National Forest Inventory (NFI 9, Tomppo et al. 2011) completed by the Finnish Forest Research Institute (METLA) in 1984 and 2003 respectively. We used only inventory plots in the two Forestry Centre 13 areas "North Lapland" (assessed in both 1978 and 2003) and "Lapland" (assessed only in 2002/03) with differing sampling designs (**Fig. 2.1**). From these initial datasets all plots with a heterogeneous structure (e.g. non-forest vegetation or different stand age) were excluded, and we used only plots on which either no cutting occurred or cutting took place more than 30 years ago. As the NFI 9 samples cover a wider extent than the NFI 7 data, we split the NFI 9 dataset into a northern (NFI 9_N; congruent with NFI 7) and a southern (NFI 9_S) part (Appendix A1, **Table A1.1**). The altitudes, which range from 0 to more than 500 meters a.s.l., are highest in the north-western part which extends into the Swedish Scandes.

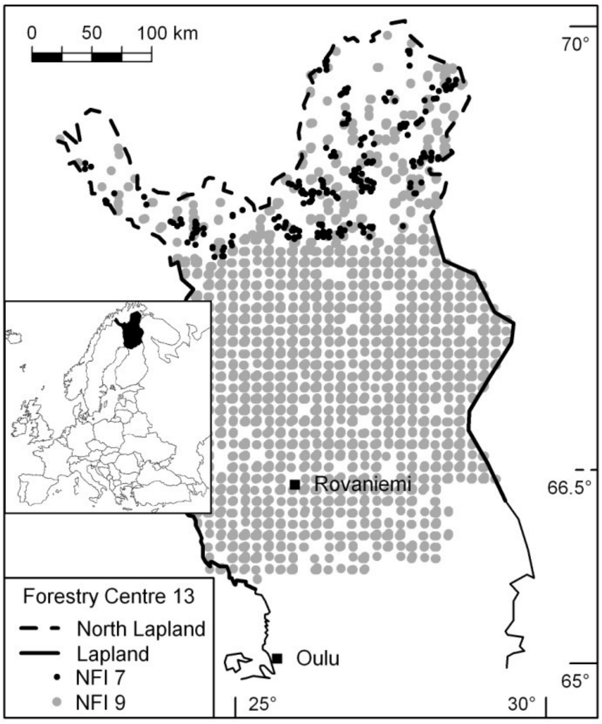

Figure 2.1. Spatial dataset characteristics: different contours distinguish the two areas (with differing sampling design); 'North Lapland' was sampled in both 1978 (black, NFI 7) and 2003 (grey, NFI 9_N) whereas data for 'Lapland' was only available for 2002/2003 (NFI 9_S).

2.2.1.2. Climate data

Climate data made available by the Finnish Meteorological Institute contained daily mean, minimum and maximum temperature and precipitation values in an interpolated 10 × 10 km^2 grid from 1961 to 2007 (Venäläinen et al. 2005). From the daily temperature values we calculated two frost indices according to Jönsson et al. (2004). We chose the accumulated degree days between the onset of dehardening, defined here as a period of four consecutive days with a mean temperature above 5°C, and a minimum temperature below -2°C (spring backlash index, SBI) as well as the number of days with a temperature below the hardiness level during autumn (autumn frost index, AFI). Both indices were calculated over a period of 15 years preceding the inventory year.

Comparing climatic predictors between the two time periods (**Fig. 2.2**) shows that, while the aggregated temperature information contained in growing degree days (GDD, 5°C threshold) seems stable (only slight increase), the short-term temperature development over the year captured by the frost indices differs considerably. Late frosts in spring (SBI) as well as early frosts in autumn (AFI) occurred more often during the years preceding 1978 than 2003 (winter warming). Precipitation in May and August both increased by 10-20 mm over the 25 years.

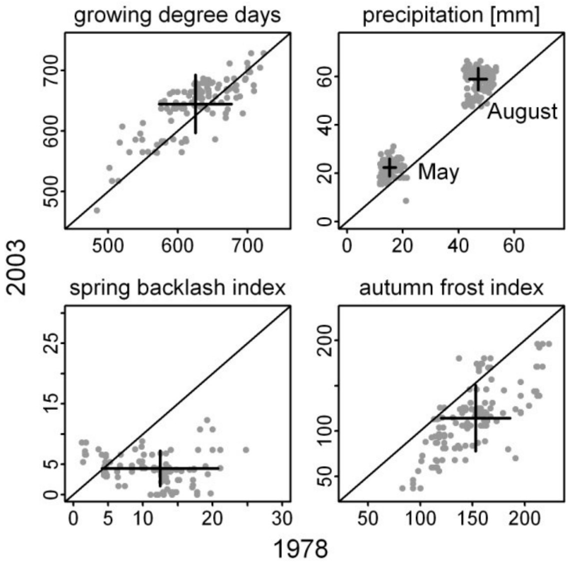

Figure 2.2. Comparison of climatic predictors between 1978 (NFI 7) and 2003 (NFI 9_N). Plus sign indicates mean (intersection) and standard deviation (length of the arms); extreme cases for spring backlash index were omitted for clarity.

2.2.2. Models

2.2.2.1. Response and predictor variables

We weighted the general stand basal area assessed in the field (angle count sampling, METLA 2002) with the proportion of each species on a plot to obtain species-specific stand basal areas (response variable). The datasets cover the northern range boundary of the three species, leading to a skewed distribution (Appendix A1, **Fig. A1.2**) with zero-inflation (Martin et al. 2005) for all three species. The inflated zero values can be classified as *true zeros* according to Martin et al. (2005) as some plots lie beyond the species' treeline and no observer failure is to be expected with trees. **Fig. A1.2** also shows an increase in basal area from 1978 (NFI 7) to 2003 (NFI 9_N).

Table 2.1 summarizes all response and predictor variables. Stand basal area (or presence/ absence) of one species is the response variable, while the stand basal area of the other two species respectively are used as predictors (basal area of co-occurring species). Many predictors are indices integrating a set of environmental conditions or several processes. The frost indices contain information of daily mean and minimum temperatures over the course of the year while growing degree days are cumulative; thus both contain temporal characteristics on differing scales. The topographic indices also contain information about the spatial context: The position index (TPI) is based on the elevation of adjacent sites (Guisan et al. 1999), and the wetness index (TWI) integrates the slope of a site with the upslope contributing area (Quinn et al. 1995), while the radiation index (TRASP) is merely a transformation of aspect (Roberts and Cooper 1989). Site fertility had been assessed in the field during inventory. It distinguishes (in order of decreasing site quality) fresh, sub-dry and poor mineral soils as well as peatland based on a historic tax classification in Finland.

2.2.2.2. Boosted regression trees

In order to assess the question of model transferability, we fitted boosted regression trees (BRT) for each species following the design of model estimation and application summarized in **Fig. 2.3**. Boosted regression trees combine the statistical method of classification and regression trees with boosting, i.e. the aggregation of many simple models to one ensemble of models (see Elith et al. (2008) for an excellent introduction to BRT and Leathwick et al. (2006) for an illustrative example). We chose BRT for their ability to model nonlinear relationships, automatically fit interactions as well as their predictive performance. BRT outperformed generalized additive models (GAM) and variants of classification and regression trees (CART) in a study modelling tree occurrence and basal area in Utah (Moisen et al. 2006), and have been shown to perform very well at species distribution modelling compared to other techniques in numerous studies (e.g. Valle et al. 2013, Revermann et al. 2012, Zurell et al. 2009, Guisan et al. 2007a, Araújo and New 2007, Elith et al. 2006). All BRT models were fitted in `R` version 2.13-0, using `gbm` package version 1.6-3.1 (Ridgeway 2010) and `dismo` package version 0.7-17 (Hijmans et al. 2012). Tuning parameters (e.g. learning rate and tree complexity) are given in **Table A2.1** (Appendix A2), and R-code is provided in Appendix A8 (CD). All model residuals were checked for spatial autocorrelation by computing spline correlograms (Dormann et al. 2007, Bjørnstad and Falck 2001).

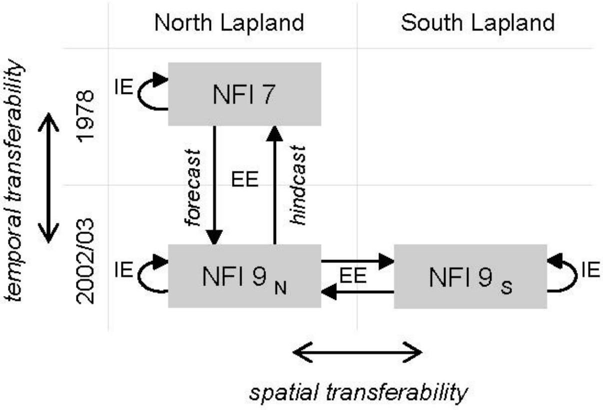

Figure 2.3. Study design. Internal evaluation (IE): models trained on and applied to the same dataset. External evaluation (EE): 1) temporal transfer, i.e. forecasting (NFI 7 → NFI 9_N) and hindcasting (NFI 9_N → NFI 7); 2) spatial transfer between regions (NFI 9_N ↔ NFI 9_S).

Due to the zero-inflation described above, we applied the conditional model concept described by Welsh et al. (1996). Here, the occurrence model first estimates whether a species is present or not, and then the abundance model estimates the basal area of that species based on presence-only data (Fletcher et al. 2005) (see Appendix A7 (CD) for a comparison of the abundance models trained with or without absences). The final expected value for basal area is obtained by multiplying occurrence probability and predicted basal area. This technique has been found to perform very well compared to other methods dealing with zero-inflation (Potts and Elith 2006). In summary, we estimated one conditional model − resulting in occurrence, abundance as well as final predictions for which results are reported − with eleven predictors (**Table 2.1**) per dataset (NFI 7, NFI 9_N and NFI 9_S) for each of the three species. However, the prevalence of *P. abies* − being restricted to the south of Lapland − in the NFI 7 dataset was too low for abundance model building. Thus, neither abundance nor final model results are shown for this species.

Table 2.1. Response (R) and predictor (P) variables with their ranges or classes in the NFI 7, NFI 9_N and NFI 9_S datasets.

variable	unit		NFI 7	NFI 9_N	NFI 9_S	R / P
P. sylvestris stand basal area	[m^2 ha^{-1}]	min	0.0	0.0	0.0	R / P
		median	4.0	6.0	4.0	
		max	20.0	32.0	35.7	
P. abies stand basal area	[m^2 ha^{-1}]	min	0.0	0.0	0.0	R / P
		median	0.0	0.0	1.1	
		max	10.5	18.0	29.8	
B. pubescens stand basal area	[m^2 ha^{-1}]	min	0.0	0.0	0.0	R / P
		median	1.0	0.0	0.0	
		max	11.6	16.1	28.2	
growing degree days GDD [1]	[−]	min	416.0	421.7	631.0	P
		median	629.6	660.3	800.6	
		max	723.1	736.2	1062.4	
spring backlash index SBI [2]	[GDD]	min	1.2	0.0	0.0	P
		median	12.6	4.5	8.7	
		max	79.8	12.3	30.1	
autumn frost index AFI [3]	[d]	min	83	28	12	P
		median	154	111	140	
		max	223	213	235	
May precipitation sum [1]	[mm]	min	11.6	8.7	16.4	P
		median	15.1	24.4	29.4	
		max	21.5	34.7	46.6	
August precipitation sum [1]	[mm]	min	41.9	47.1	36.6	P
		median	47.3	58.9	50.2	
		max	53.4	67.1	70.3	
topographic radiation index TRASP	[−]	min	0	0	0	P
		median	0.6	0.5	0.6	
		max	1	1	1	
topographic position index TPI	[−]	min	-24	-24	-19	P
		median	0	0	0	
		max	42	25	38	
topographic wetness index TWI	[−]	min	10.6	10. 6	10.8	P
		median	13.2	13.4	14.1	
		max	25.4	27.6	29.1	
site fertility [relative frequency]	1	mineral soil, fresh	.14	.04	.16	P
	2	mineral soil, sub-dry	.41	.29	.37	
	3	mineral soil, poor	.39	.45	.33	
	4	peatland	.06	.22	.14	

[1] mean calculated from 10 years preceding the inventory year (1968-1977, 1993-2002)

[2] accumulated GDD between four consecutive days with T_{mean}> 5°C and a day with T_{min}< -2°C

[3] number of days with a temperature below the hardiness level during autumn

[2] mean/ [3] sum calculated from 15 years preceding the inventory year (1963-1977, 1988-2002)

2.2.2.3. Model performance

To assess the performance of each model before (internal evaluation) and after (external evaluation) transferring it to either another time or another region, we calculated the percentage of deviance explained (% dev $_{\text{expl}}$) from a tenfold cross-validation (CV). This value ranges from 0 % (null model) to 100 % (perfect model), while less than 0 % marks a model weaker than the null model. For deviance calculation we used the binomial loss function for the occurrence model and the absolute loss function for the abundance model. As the final predictions are a combination of occurrence and abundance model results, we combined the two loss functions to calculate the deviance of the final model. Thus, for each observation (*obs*) – prediction (*pred*) pair the individual deviance (to be summed) is

$$dev_{ind} = \begin{cases} -2 \cdot \ln(1 - pred_{OCC}) & \\ -2 \cdot \ln(pred_{OCC}) + \left| obs - pred_{ABUND} \right| & \end{cases} \quad if \quad \begin{matrix} (obs = 0) \\ (obs > 0) \end{matrix}$$

However, we only report a single value of explained deviance for the final model based on all observations. To account for the optimism of that single value, we subtracted the difference between the CV-derived value and the more optimistic performance on the full dataset. For the occurrence models, we additionally computed the area-under-the-curve (AUC) statistic ranging between 0.5 for the null model and 1.0 for a perfect model (Swets 1988). Apart from model performance statistics that summarize the goodness-of-fit in one figure, we visually compared maps of observed and predicted basal area values.

2.2.2.4. Model transferability

In order to evaluate model transferability between the two time periods (NFI 7 ↔ NFI 9_N) and two spatial extents (NFI 9_N ↔ NFI 9_S), we adopted the transferability index developed by Randin et al. (2006) for spatial and extended by Dobrowski et al. (2011) for temporal transferability (see **Fig. A3.1**, Appendix A3). The index ranges from 0 (no transferability) to 1 (full transferability). As this one value summarizes both transfer directions in one figure, we also examined the actual goodness-of-fit values reported for the model performance.

Additionally, we compared the relative importance as well as the response curves of each predictor between the three model sets (NFI 7, NFI 9_N, and NFI 9_S). Statistical modelling assumes stationarity of the relationship between response and predictors over time as well as in space (Hothorn et al. 2011, Schröder and Richter 1999). If this does not hold and nonstationarity is not accounted for, the models can hardly be expected to result in successful predictions for new datasets (with differing relative importance or response curves).

Finally, we used tools and code described by Zurell et al. (2012a) to visualize in which cases transferring models between time periods and regions represents extrapolating to novel environments. Environmental overlap masks (function `eo.mask`) highlight cases where predictions are made to novel as opposed to sampled environmental space. When applying these tools to our datasets, first the difficulty of many predictors arises. Only two predictors were used to describe the method (Zurell et al. 2012a) but with 11 predictors almost all cases are novel (because to be classified as analogue the sample needs to fit into one of five bins of all 11 predictors simultaneously). Thus, we only picked subsets of predictors to explore the issue and only report two example cases.

2.2.3. Identifying important processes

In order to analyze the processes determining the current treeline position we compared the relative importance and response curve of each predictor between occurrence and abundance models and between species. The relative importance of a predictor is based on the reduction of model performance when this variable is randomly permuted (cf. Ridgeway 2010). Partial dependence plots visualize the response curve for a single predictor while all other predictors are kept at their mean value. Whereas the relative importance indicates *how much*, partial dependence plots show *how* model predictions respond to a specific predictor. They display whether the species' ecological demands are correctly modelled and thus can function as a plausibility test. In addition, we analyzed the automatically fitted interactions between predictors as described in Elith et al. (2008) and implemented in the `dismo` package. We ranked the interactions according to their magnitude and plotted the four most important interactions in each model as joint partial dependence plots.

2.3. Results

2.3.1. Model performance and transferability

AUC values were (very) high for the internal evaluation and still predominantly high for the external validation (**Table 2.2**). Explained deviances, too, were high for the internal evaluation, but external validation only partly succeeded (positive explained deviances, **Table 2.3**). Generally, model performance was highest for *P. sylvestris* and lowest for *B. pubescens*, and higher for occurrence than abundance models. We found no residual spatial autocorrelation in any of our models. Transferability index (TI) values were again highest for *P. sylvestris*, and generally higher for spatial than temporal transferability. Cases where model transfer failed according to the criterion used by Randin et al. (2006) were correctly mirrored in low TI values (**Table 2.2**).

Table 2.2. AUC for the internal (IE) and external (EE) evaluation of the occurrence model and transferability index based on AUC (TI_{AUC}) for temporal and spatial transferability. Grey figures mark cases where model transfer fails according to Randin et al. (2006), i.e. $AUC_{IE} > 0.7$ but $AUC_{EE} < 0.7$.

	trained on	applied to	*P. sylvestris*	*P. abies*	*B. pubescens*
IE (10-fold CV)	NFI 7	NFI 7	0.91	0.88	0.71
	NFI 9_N	NFI 9_N	0.98	0.97	0.88
	NFI 9_S	NFI 9_S	0.92	0.87	0.83
EE (temporal)	NFI 7	NFI 9_N	0.83	0.80	0.68
	NFI 9_N	NFI 7	0.84	0.82	0.69
EE (spatial)	NFI 9_N	NFI 9_S	0.87	0.69	0.74
	NFI 9_S	NFI 9_N	0.96	0.83	0.86
TI_{AUC}	temporal: NFI 7	↔ NFI 9_N	0.70	0.68	0.59
	spatial: NFI 9_N	↔ NFI 9_S	0.75	0.46	0.68

Table 2.3. Explained deviance values for the internal and external evaluation of the occurrence (occ), abundance (abu) as well as final (fin) models, and transferability index based on explained deviance for temporal and spatial transferability. Grey figures mark cases where the model is weaker than the null model (negative dev$_{expl}$). Mark that high TI values for *P. abies* and *B. pubescens* in comparison to *P. sylvestris* merely reflect the differences between IE and EE model application not the actual model performance which is generally highest for *P. sylvestris*.

		P. sylvestris			*P. abies*			*B. pubescens*		
train	test	occ	abu	fin	occ	abu	fin	occ	abu	fin
internal evaluation (10-fold CV)										
NFI 7	NFI 7	42.1	36.0	33.7	30.6	–	–	8.4	10.0	6.5
NFI 9$_N$	NFI 9$_N$	69.6	38.1	44.1	62.5	12.7	43.6	37.9	16.8	25.3
NFI 9$_S$	NFI 9$_S$	45.7	33.2	32.8	35.0	27.5	22.9	27.1	22.0	24.0
external evaluation: temporal transfer										
NFI 7	NFI 9$_N$	23.3	-2.8	3.6	-8.1	–	–	-10.8	-24.7	-16.8
NFI 9$_N$	NFI 7	-5.5	34.7	24.0	12.9	-34.1	2.1	-8.8	-14.0	-11.6
external evaluation: spatial transfer										
NFI 9$_N$	NFI 9$_S$	25.6	18.7	20.7	-83.9	-7.0	-38.9	10.6	9.5	10.1
NFI 9$_S$	NFI 9$_N$	58.3	4.9	18.4	-71.6	19.8	-41.4	32.1	6.3	20.4
transferability index based on % dev$_{expl}$										
NFI 7 ↔ NFI 9$_N$		0.57	0.67	0.77	0.72	–	–	0.71	0.73	0.72
NFI 9$_N$ ↔ NFI 9$_S$		0.72	0.77	0.82	0.26	0.82	0.43	0.81	0.86	0.86

Scatterplots of observed and predicted basal areas (Appendix A4, **Fig. A4.1**) showed a systematic miscalibration (see also Appendix A4, **Table A4.1** for calibration measures): high basal area values were under- and low values were overestimated. However, the observed spatial pattern of lower and higher basal areas was certainly captured in all three species' cases (**Fig. 2.4**). This is not only true for the internal evaluation but, to a lesser extent, also for the external evaluation. The observed treeline pattern for *P. sylvestris* and *P. abies* in the north was reproduced by the occurrence model as well as the abundance model (see Appendix A4, **Fig. A4.2** for an extension of **Fig. 2.4**). The results were very similar for the temporal model transfer (Appendix A4, **Fig. A4.3**).

In our predictor set we found examples for congruent as well as merely overlapping environmental space for both temporal and spatial model transfer. In **Fig. 2.5**, the left hand side plots are examples of nearly congruent environmental space, i.e. combinations of TPI and TWI ranged within the same limits in both time periods and both regions (analogue). The plots on the right hand side of **Fig. 2.5** illustrate cases of overlapping environmental space, i.e. some combinations of May and August precipitation are sampled in both datasets (intersecting set) but most are only part of one of the two datasets (symmetric difference; novel). The combination of high precipitation values in both months was only sampled in 2003 (precipitation increase, **Fig. 2.2**). Thus, forecasting constitutes predicting to novel environments where these high precipitation values occur. The same applies to combinations of low precipitation values measured only in 1978. Whereas the few novel combinations of TPI and TWI are scattered (**Fig. 2.6**, l.h.s.), the novel combinations of precipitation show a distinct spatial pattern for both datasets (**Fig. 2.6**, r.h.s.). The northernmost tip of Lapland exhibits the combination of low May and high August precipitation that is only sampled in NFI 9_N, while the east of Southern Lapland features combinations of high May and low August precipitation that do not occur in the north.

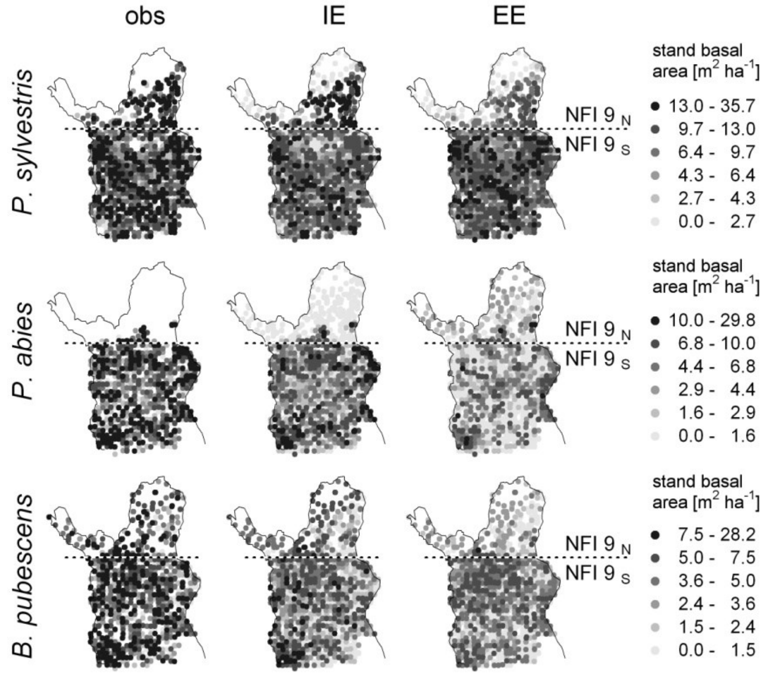

Figure 2.4. Maps of final model predictions for the spatial model transfer. Left: observations (obs). Centre: results of the internal evaluation (IE), i.e. northern predictions by NFI 9_N, southern predictions by NFI 9_S model. Right: results of the external evaluation (EE), i.e. northern part predicted by NFI 9_S model and southern part predicted by NFI 9_N model.

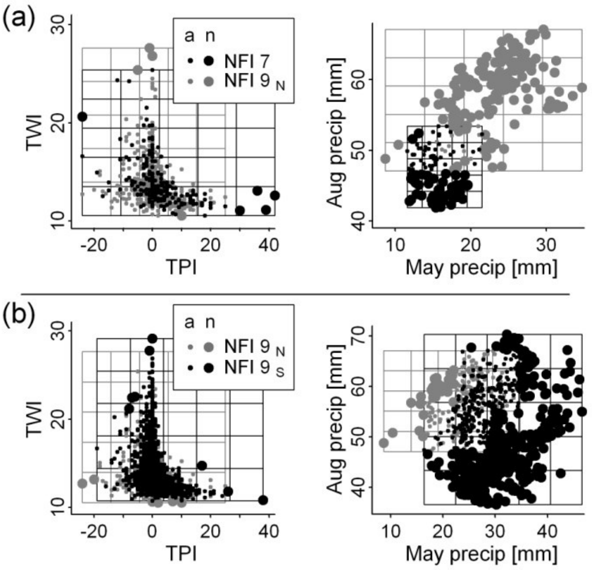

Figure 2.5. Environmental space for two variable combinations showing analogue ('a') and novel ('n') predictor combinations in (a) NFI 7 and NFI 9_N (temporal transfer) and (b) NFI 9_N and NFI 9_S data (spatial transfer). Grid lines depict the bins each gradient is divided into (`eo.mask`, here: 5); cases are marked as novel where one grid exceeds the other. Left: the environmental space covered by both datasets is nearly congruent. Right: there is an overlap between the two datasets but most of NFI 9_N (top) and NFI 9_S (bottom) constitutes novel environment. Note: grey NFI 9_N dots are identical in the upper and the lower panel.

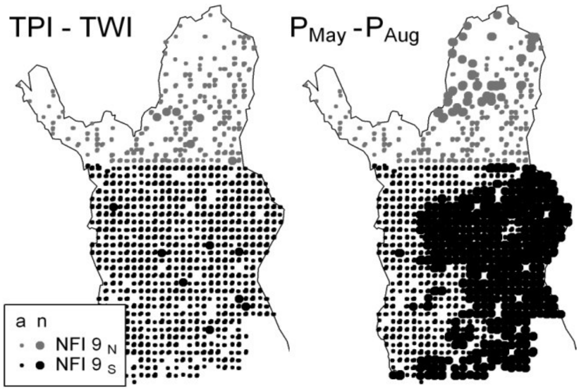

Figure 2.6. Map showing analogue ('a') and novel ('n') predictor combinations (left: topographic position (TPI) and wetness index (TWI), right: May and August precipitation) for NFI 9_N and NFI 9_S, as in **Fig. 2.5b**.

2.3.2. Important processes

The most important predictors for occurrence and abundance across all species and datasets were site fertility, the abundance of co-occurring species and growing degree days (**Table 2.4**). These were also the predictors for which interactions generally ranked among the ten most important (see Appendix A5, **Table A5.1** (and CD) for details on the fitted interactions). Site fertility- as single predictor as well as in interaction with other predictors- was more important in the abundance than in the occurrence models, especially for *P. sylvestris* and *P. abies*. The relative importance of growing degree days (GDD) in the *P. sylvestris* occurrence model was five times higher in 1978 than in 2003, and less important in the south than in the north. For *P. abies* occurrence, the autumn frost index was more important in the north (NFI 7 and NFI 9_N) than in the south (NFI 9_S), and the topographic wetness index contributed considerably more to the model in 1978 than in 2003 (**Table 2.4**). Climatic predictors were generally more important for the

Table 2.4. Relative importance [%] of the predictors in the a) occurrence and b) abundance model trained on NFI 7, NFI 9_N and NFI 9_S datasets. **Bold** figures mark the most important.

	P. sylvestris			*P. abies*			*B. pubescens*		
	NFI 7	NFI 9_N	NFI 9_S	NFI 7	NFI 9_N	NFI 9_S	NFI 7	NFI 9_N	NFI 9_S
(a) occurrence model									
GDD	**50**	9	6	4	4	5	9	3	3
SBI	1	0	2	2	5	5	4	1	5
AFI	3	1	1	**37**	18	3	6	4	2
May prec	4	1	2	1	11	3	10	1	2
Aug prec	2	1	2	2	1	4	3	2	2
TRASP	4	1	1	11	3	5	14	3	3
TPI	2	2	1	2	2	3	2	1	2
TWI	6	1	2	12	2	4	5	2	5
species$_1$ [1]	1	17	**41**	15	**36**	**48**	**27**	**62**	**46**
species$_2$ [2]	5	**46**	28	2	6	6	0	6	9
fertility	22	21	14	12	12	14	20	15	21
(b) abundance model									
GDD	5	4	3	–	3	4	6	3	5
SBI	3	3	2	–	12	2	5	4	5
AFI	3	7	2	–	4	2	7	3	2
May prec	5	5	1	–	1	2	8	3	5
Aug prec	3	4	2	–	2	2	14	6	4
TRASP	3	7	4	–	7	3	6	5	4
TPI	2	3	1	–	1	1	10	2	1
TWI	2	4	4	–	5	4	16	4	8
species$_1$ [1]	0	5	18	–	23	**39**	**26**	**53**	26
species$_2$ [2]	17	18	14	–	**27**	11	0	4	12
fertility	**57**	**40**	**49**	–	15	30	2	13	**28**

[1] i.e. *P. abies* in *P. sylvestris*' case and *P. sylvestris* for *P. abies* and *B. pubescens* models

[2] i.e. *P. abies* in *B. pubescens*' case and *B. pubescens* for *P. sylvestris* and *P. abies* models

occurrence models than the abundance models for which in turn topographic/edaphic predictors were (almost) always more important. Up to 90 % of the model explanation was due to non-climatic predictors making our models relatively insensitive to climate. The relative importance of predictors as well as interaction rankings in the NFI 9_N models often resembled those in the NFI 9_S models more than in the NFI 7 models when averaged across species.

The response curves of the four most important predictors differed between occurrence and abundance models as well as between species (**Fig. 2.7**). Roughly, site fertility and both occurrence and particularly abundance of any species was positively correlated. The correlation of *P. sylvestris* occurrence and site fertility classes, however, varied notably among datasets, especially for less fertile sites. There were clear GDD thresholds for *P. sylvestris* (600) and *P. abies* occurrence (700), while GDD had a steadily positive effect on abundance (best seen for the wider range of GDD in NFI 9_S). In addition, **Fig. A5.2–A5.4** in Appendix A5 (CD) show that this effect is strongest where the abundance of co-occurring species is low. While *P. sylvestris* occurrence correlated negatively with both *P. abies* and *B. pubescens* abundance, the latter two were positively correlat-

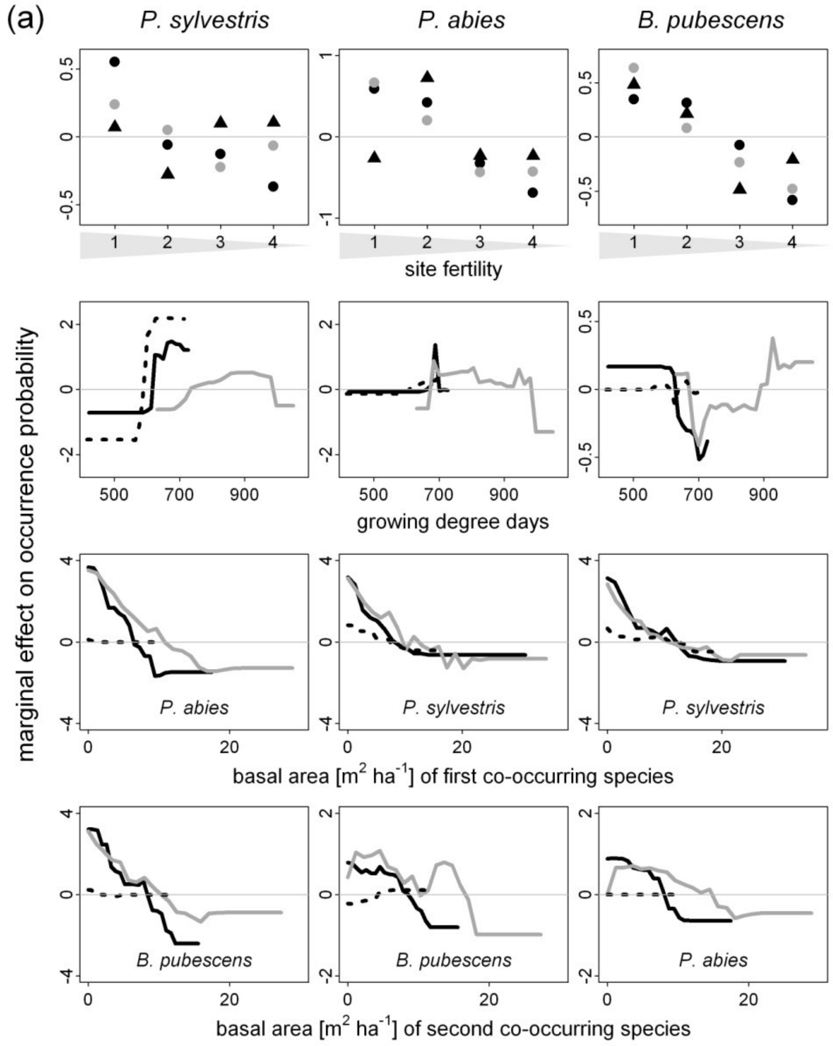

Figure 2.7. Partial dependence plots for the four most important predictors in the occurrence (a) and the abundance models (b) of each species (three columns) for NFI 7 (▲, broken line), NFI 9_N (●, solid black line) and NFI 9_S (●, solid grey line). Partial dependence plots visualize the response curve for a single predictor while all other predictors are kept at their mean value. Site fertility decreases from class 1 to 4.

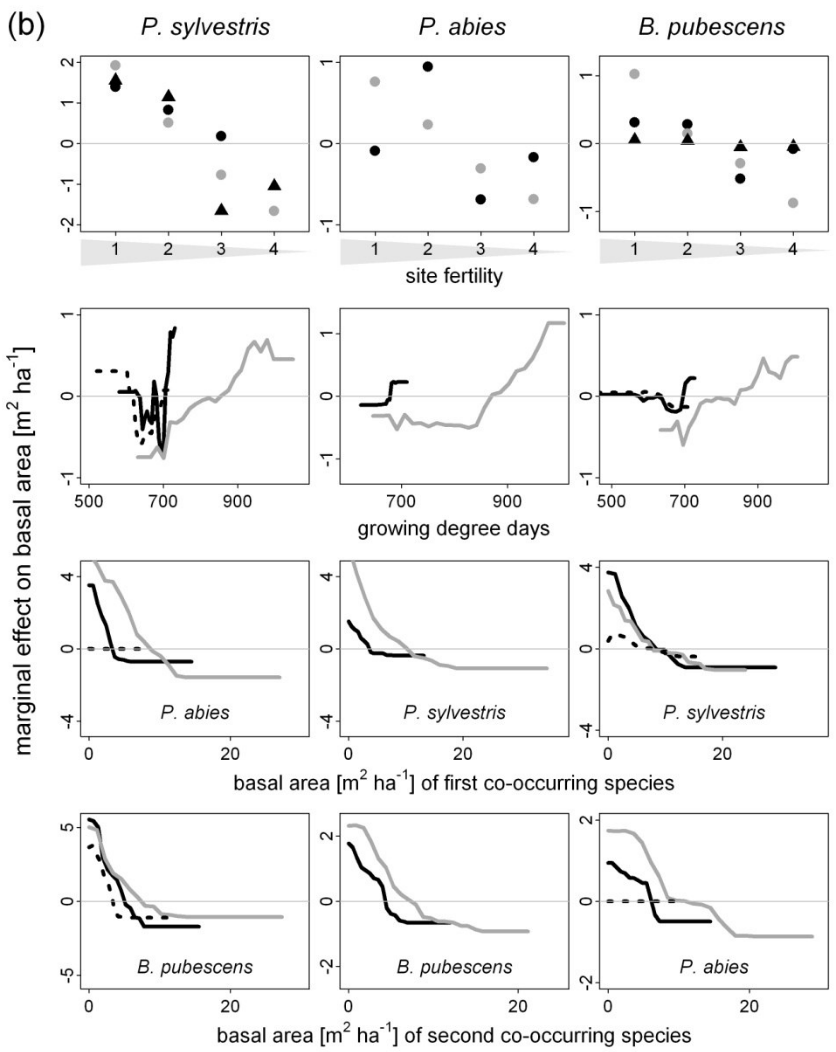

Figure 2.7. Continued.

ed for low abundances. For the abundance however, the curves decreased monotonically for all species combinations. Indeed joint partial dependence plots (**Fig. A5.1**, CD) show that abundance of one species is highest where the abundance of the other two species is lowest. Overall, partial dependence was similar for all three datasets although response curves for NFI 9_N and NFI 9_S were often closer than for NFI 7 and NFI 9_N.

2.4. Discussion

2.4.1. Model performance

Our models performed well at reproducing the treeline in northern Lapland. The overestimation of low and underestimation of high values in our study was also reported by Aertsen et al. (2010) who found that BRT predictions had a narrower range than the observations compared to other statistical modelling techniques.

The difference of model performance between species can have various reasons: On the one hand, the prevalence differs for each species and dataset and thus determines the sample size of the abundance model (Appendix A2, **Table A2.1**). Additionally the current predictor set apparently includes the important processes to model *P. sylvestris* satisfactorily, whereas predictors are obviously missing for *P. abies* and *B. pubescens*. Finally, *B. pubescens* does not form as distinct a treeline as *P. sylvestris* and *P. abies* in the study area and does not follow a strong north-south gradient which reduces the correlation with predictors with a clear spatial trend. Others, too, found that tolerant generalist species (Brotons et al. 2004) and fast-growing pioneer species (Guisan et al. 2007b) like *B. pubescens* were the hardest to predict.

The occurrence models were generally more successful than the abundance models which is in contrast to Meier et al. (2010) who reported the reverse. Moisen et al. (2006) however also reported only mediocre predictions of basal area compared to occurrence probability. Their average correlation between observed and predicted values for three *Pinus* species in North America was 0.45, while our *P. sylvestris* models reach 0.72 averaging all independent model applications (**Table A4.2** in Appendix A4). Similarly, our *P. abies* (0.43 in contrast to their 0.35 for *Picea engelmannii*) and *B. pubescens* (0.51) models do well in comparison. The occurrence of a species is easier to predict as it distinguishes only two states as opposed to a range of possible abundance values. This is especially true if the dataset exceeds the range of a species.

2.4.2. Model transferability

Transferability followed the pattern of model performance and was highest for *P. sylvestris* and lowest for *B. pubescens*. Highly species-specific differences in transferability were also reported by Randin et al. (2006). Transferability was higher between regions than between times when regarding transferability index values. This was also evident in the response curves, relative importance and interaction magnitude of predictors of NFI 9_N often resembling those of NFI 9_S more than those of NFI 7. There are different possible explanations for the limited transferability in our application: As discussed above, the changes of a predictor’s importance over time might be due to the weakening restriction by other factors, like the temperature limitation lessened by climate change. Furthermore, the complex interactions and relationships of different processes summarized within proxies might change over time and in space (Dormann et al. 2013) as indicated by the differing structure of collinearity (Appendix A6, **Fig. A6.1**). Thus, distal predictors lead to models with limited transferability, while proximal predictors yield more robust and wider applicable models (Austin 2002). Additionally, overfitting which is a known issue of BRT (Elith et al. 2008) reduces the generality of our models.

The most convincing explanation for limited transferability, however, is extrapolation to novel environments. As an example illustrating how changes in the environmental space lead to extrapolation and non-transferability, we investigate the temporal transfer of the *P. sylvestris* occurrence model which succeeds for forecasting but fails for hindcasting (**Table 2.3** and Appendix A4, **Fig. A4.3a**). GDD is the most important predictor for the occurrence of *P. sylvestris* in 1978 (50 %, **Table 2.4**), the response curves for this predictor in 1978 and 2003 are very similar (**Fig. 2.7a**) and there is only a slight increase of GDD values over the 25 years (**Fig. 2.2**) and thus no extrapolation− model transfer succeeds. On the other hand the most important predictor in 2003 is *B. pubescens* basal area (46 %) which increased over the 25 years (Appendix A1, **Fig. A1.2**) and whose negative relationship with *P. sylvestris* occurrence is less pronounced in the NFI 7 data. Indeed, all false presences of *P. sylvestris* (i.e. overestimated occurrence probabilities for 1978 by the NFI 9_N model) concur with (very) low basal areas of *B. pubescens* (not shown).

The case of the two precipitation variables in **Fig. 2.5a** shows how climate change (increase of both May and August precipitation from 1978 to 2003) has shifted the sampled environmental space to higher values, leading to a small overlap of analogue samples and two distinct areas of novel environmental space (**Fig. 2.5a**, r.h.s.). Comparing the environmental space of NFI 7, NFI 9_N and NFI 9_S for May and August precipitation shows however, that much of the NFI 7 data might not be sampled in the NFI 9_N dataset but fits well into the NFI 9_S dataset. Here is an example where a transfer between two regions *and* two times might work better than a temporal transfer within one region because climate change has shifted the environmental space.

2.4.3. Processes controlling distribution patterns

2.4.3.1. Site fertility

We found site fertility- as single predictor as well as in interaction with other predictors- to be more important in explaining the abundance of *P. sylvestris* than its occurrence on a site implying resource-limited growth which was indeed found by Susiluoto et al. (2010) for Eastern Lapland. Although *P. sylvestris* thrives best on more fertile soils (positive correlation between abundance and site fertility, **Fig. 2.7b**), its occurrence probability on poor mineral soils or peatland is higher than for *P. abies* and *B. pubescens*. Indeed Sutinen et al. (2002) found on the basis of soil electrical characteristics that *P. sylvestris* is dominant on acidic, nutrient-poor soils while *P. abies* dominates nutrient-rich tills. This indicates competitive exclusion of *P. sylvestris* by *P. abies* and *B. pubescens* on fertile sites and a shift of *P. sylvestris* to a realised niche with less competition, i.e. less fertile sites.

2.4.3.2. Growing degree days

Growing degree days (GDD) contribute more to the occurrence model of *P. sylvestris* than of the other two species, indicating a temperature limitation of *P. sylvestris* in Lapland. Low temperatures have indeed been found to limit *P. sylvestris'* growth in Northern Lapland (Mathisen and Hofgaard 2011, Salminen and Jalkanen 2007). Thus, the slight increase of GDD from 1978 to 2003 might suffice to make temperature less critical in 2003 and so explain the minor importance of GDD in the NFI 9_N model. Similarly, temperature is less limiting in the south which explains the lower relative importance of GDD in the NFI 9_S than the NFI 9_N models. *P. abies* occurrence on the other hand is not only less dependent on GDD, but there are no differences in relative importance between datasets, supporting the hypothesis that *P. abies* is not climatically but edaphically limited in Lapland. For *P. abies* lower GDD requirements for flowering (140 vs. 230) and seed maturation (875 vs. 975 GDD for 95 % mature seeds) have been reported than for *P. sylvestris* (Almqvist et al. 1998, Zasada et al. 1992). Yet, the clear threshold in the response curves for GDD is surprisingly higher for *P. abies* (700) than for *P. sylvestris* (600). For *P. sylvestris*, we suggest this threshold to be an actual physiological minimum, since there were no occurrences below these values. For *P. abies*, however, it might be a mere correlation with the current position of the species' treeline, if the dispersal limitation hypothesis holds true.

2.4.3.3. Autumn frost index

The relative importance of the autumn frost index (AFI) for explaining *P. abies* occurrence is higher in the north than in the south. When temperatures in autumn fall below the hardiness level of *P. abies*, frost damages like bark necrosis and resin flow occur, which in turn can result in pathogen infections (Jönsson et al. 2004). If autumn frost damage was indeed limiting *P. abies* in the north, the relationship between occurrence probability and AFI should be negative. However, the response curves surprisingly reveal a positive relationship in the north, while in the south occurrence probability slightly declines with increasing AFI (Appendix A6, **Fig. A6.2** l.h.s.). Due to cold air drainage (Yoshino 1984), AFI correlates negatively with altitude in Northern Lapland (**Fig. A6.2** r.h.s.). Thus, the relationship between *P. abies* occurrence and AFI is apparently a spurious correlation, while altitude (or rather other site conditions on valley bottoms) is the actual causal variable. When removing AFI from the *P. abies* occurrence model, model performance only decreases for NFI 7 (probably due to the low prevalence of 7 %). The relative importance of AFI is compensated mainly by SBI, *P. sylvestris* abundance as well as August (NFI 7) and May precipitation (NFI 9_N) for which correlation values with AFI are highest (Appendix A6, **Table A6.1**). Relative importance decreased for TWI (NFI 7) and SBI (NFI 9_N) because the loss of the important interaction with AFI reduced the explanatory power of the single predictors (**Table A6.1**).

2.4.3.4. Topographic wetness index

For *P. abies* occurrence, the importance of TWI decreased from 1978 to 2003, while the response curves remained very similar (not shown). *P. abies* is known to occur on wetter sites (Sutinen et al. 2002). Thus, the precipitation increase from 1978 to 2003 might have increased soil moisture and rendered TWI less critical in 2003 leading to the lower relative importance in the model. TWI, however, depends only on topographical features which did not change over the 25 years and thus do not reflect climate change. Furthermore the response curves in the north depict a negative rather than positive relationship (not shown) with highest occurrence probabilities for low TWI (dry sites); the opposite is the case in the south. However, TWI values are higher for peatland (NFI 7 in Appendix A6, **Fig. A6.3**) for which *P. abies* occurrence probability is lower (**Fig. 2.7a**). Thus, the actual relationship here is probably that between *P. abies* and site fertility rather than TWI.

2.4.3.5. Abundances of co-occurring species

We found a negative correlation of *P. sylvestris* and *B. pubescens* abundance suggesting competition, e.g. for light as both species are shade intolerant (in contrast to the shade tolerant *P. abies*). This is in agreement with constrained diameter growth in *P. sylvestris* stands with high proportions of *B. pendula* reported by Hynynen et al. (2011) for Southern Finland. The positive correlation between *P. abies* and *B. pubescens*, while both species are negatively correlated with *P. sylvestris*, is compliant with the findings of Sutinen et al. (2002) confirming *P. abies* and *B. pubescens* to occur on sites of the same soil characteristics. Doležal et al. (2006) and Brandtberg et al. (2000) found evidence for *B. pubescens* improving *P. abies* growing conditions and especially regeneration by soil aeration, efficient nutrient cycling and facilitation of water and nutrient uptake from deep soil, in line with the positive correlation of *P. abies* and *B. pubescens* for low abundances in our models. The positive correlation is absent in the abundance models, however, rather suggesting similar habitat requirements (than facilitation) leading to competition between *B. pubescens* and *P. abies* for high abundances (where the correlation is negative in both models). Size-dependent interspecific interference were identified as cause for *B. pubescens* population decline in a mixed stand with *P. abies* in Lapland (Doležal et al. 2006), and competition-induced loss of *P.*

abies yield due to a shelter of *B. pubescens* was reported for southern and central Sweden (Mård 1996). A further explanation for the decreasing occurrence probability of *B. pubescens* with increasing *P. abies* abundance is forest management, i.e. birch is thinned when mixed stands get too dense to increase *P. abies* yield.

The only climatic predictor we identified as generally most important is GDD. Yet our entire predictors act as proxies for the actual processes we try to cover (distal rather than proximal, Austin 2002). The abundance of co-occurring species, apart from directly influencing the target species as discussed above, can act as a proxy for the environmental conditions tolerated by this species. Thus the two abundance predictors could contain redundant information better represented by more proximal climatic or soil variables. We tested how model performances changed when omitting the two abundances. In contrast to omitting AFI (see above), model performance decreased substantially when removing the abundances, losses ranging from 7.6 to 95.5 % of the original explained deviance. Reduction in explained deviance was slightly lower for *P. sylvestris* than for *P. abies* and highest for *B. pubescens* (being the same ranking as in model performance and transferability). Not surprisingly, model performance loss was highly correlated with the relative importance of the omitted predictors for *P. sylvestris* (Spearman correlation coefficient: 0.83), less so for *P. abies* (0.60), but unexpectedly not at all for *B. pubescens* (-0.03). We conclude that the abundance variables do contain non-redundant information which is in line with what Meier et al. (2010) found for trees in Switzerland.

We found topographic/edaphic predictors to be more important in the abundance models than in the occurrence models. Thus the locally very variable growing conditions (no spatial trends in topographic indices and site fertility) do not help explaining the larger regional trend of decreasing occurrence probabilities towards the north, but they do contribute much to the explanation of the performance on site. On the other hand, the climatic and biotic predictors with a regional trend are more related to the occurrence patterns and are thus more important in these models. The abundance models are trained on presence-only data. Thus, the predictors' ranges are by definition within the ecological niche of the species and do not contain information about range limits - unless decreasing abundance is seen as an indicator. This is the case in the *P. sylvestris* abundance model (Appendix A4, **Figs A4.2b** and **A4.3b**) depicting the treeline by predicting very low abundances where the species is indeed absent. This indicates that *P. sylvestris* is restricted by adverse growing conditions in the north. The situation is different for *P. abies*. The spatial model transfer shows that the NFI 9_S model, lacking the information regarding absences in the north, greatly overestimates *P. abies* occurrence (**Fig. A4.2a**). At the same time, the abundance models (both IE and EE) predict relatively high abundances also for the north where *P. abies* is absent (**Fig. A4.2b**). This suggests that not the growing conditions (at least not those captured by our set of predictors) but another factor still missing from our current models explains *P. abies*' absence in the north, further hinting at a dispersal barrier.

2.4.3.6. Missing processes

Additional processes unaccounted for in the current predictor set due to data unavailability – such as dispersal limitation of *P. abies* - might improve the models. For example, snowfall strongly affects tree survival: heavy snow loads (Finnish: tykky) can cause branch or even stem breakage limiting *P. sylvestris* on hilltops where the more flexible and snow shedding structure of hanging branches favours *B. pubescens* and *P. abies* (Jalkanen and Konôpka 1998). Too low snow cover causes bark abrasion by wind-blown ice crystals, whereas too long snow coverage in spring leads to snow fungi infections (Burdon et al. 1992). Late melting snow accumulations in depressions effectively shorten the growing season (Autio and Colpaert 2005).

P. sylvestris is limited by complex reproduction processes (Juntunen and Neuvonen 2006, Stöcklin 1999): warm, dry summers are required for reproductive bud production (year 1), flowering and pollination (year 2) is impaired by wet weather conditions or late frosts in spring, 890 GDD is the minimum requirement for mature seeds (year 3) and should be followed by suitable air temperature and moisture (affecting cone opening) and wind conditions for primary seed dispersal in the subsequent dormant season; finally, germination (year 4) requires warm and moist soil surface conditions (Hallikainen et al. 2007, Zasada et al. 1992). An index for suitable weather conditions over four years could be useful to mark potential reproduction peaks.

Mass outbreaks of the autumnal moth *Epirrita autumnata* in 1965 and herbivory by reindeer has caused the *B. pubescens* treeline to retreat in Lapland (Lehtonen and Heikkinen 1995). Climate warming is aggravating the influence of *Operophtera brumata* and *Epirrita autumnata* outbreaks on subarctic birch forests (Jepsen et al. 2008). Indirect effects of reindeer overpopulation are the mechanic damage to *P. sylvestris* or *P. abies* seedlings by reindeers digging for lichens below the snow or by reindeers rubbing against the stems when losing the velvet from their antlers (Helle and Moilanen 1993). Lastly, anthropogenic impacts like fires or loggings (Mattsson 1995) have a long lasting impact and often modify the natural combination of factors in a dominating way (Wallenius et al. 2002). In conclusion, a complex variety of different factors is affecting the current treeline position which, due to the longevity of trees, is a result of historical conditions rather than current effects, and important predictors might be missing from our models for especially *P. abies* and *B. pubescens*.

2.5. Conclusion

(i) We identified the abundance of co-occurring species, site fertility and growing degree days as important predictors, suggesting (ii) that the reaction of the treeline to climate change will be constrained by other, non-climatic factors. However, we found growing degree days to decrease in importance from 1978 to 2003 in the occurrence model for *P. sylvestris*, indicating a possible easing of the climatic constraints. Nonetheless, the abundance model predicted decreasing basal areas towards the north signifying true limitation of *P. sylvestris* by adverse growing conditions. This did not hold for *P. abies*, supporting the dispersal limitation hypothesis. *B. pubescens* was the hardest to predict and certainly calls for other processes to be included as predictors. (iii) Our models successfully reproduce observed patterns of presences and absences as well as general abundance patterns. (iv) The models performed considerably worse when applied to other regions and especially time periods, and we identified extrapolation to novel environmental space as plausible cause. Already within the relatively small time span of 25 years, we found not only the shifting of single predictors' ranges but more importantly a change in the *combinations* of predictor values, leading to a shift of the sampled environmental space. By examining BRT properties such as the relative importance of its predictors as well as response curves, some known features of the species' ecology were indeed reproduced by our models, and surprising results could often be explained when further investigating interactions with additional variables.

Acknowledgements

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Additional supplementary material on CD

Appendix A5. Analysis of the automatically fitted interactions between predictors:

Figures A5.1, A5.2, A5.3, A5.4
Tables A5.2, A5.3, A5.4

Appendix A7. Comparison of abundance models trained with and without absences:

Figure A7.1
Tables A7.1, A7.2

Appendix A8. Data and computer code:

Appendix_8.1-BRT_R-code.R
Appendix_8.2-gbm.perspec_mod.R
Appendix_8.3-south.dat
Appendix_8.4-north.dat

Appendix A1

Study area characteristics and stand basal area distribution

Table A1.1. Study area characteristics for the NFI 7, NFI 9_N and NFI 9_S datasets.

	NFI 7	**NFI 9_N**	**NFI 9_S**
inventory year	1978	2003	2002/ 2003
sample size	217	773	3206
latitude	68.2° – 70.0° N	68.2° – 70.0° N	65.7° – 68.2° N
longitude	23.1° – 29.2° E	22.4° – 29.2° E	22.4° – 29.3° E
altitude [m a.s.l.]	70.0 – 560.0	73.9 – 565.8	0.0 – 490.1
stand basal area [m^2 ha^{-1}]	0.5 – 20.0	0.0 – 32.0	0.0 – 37.0

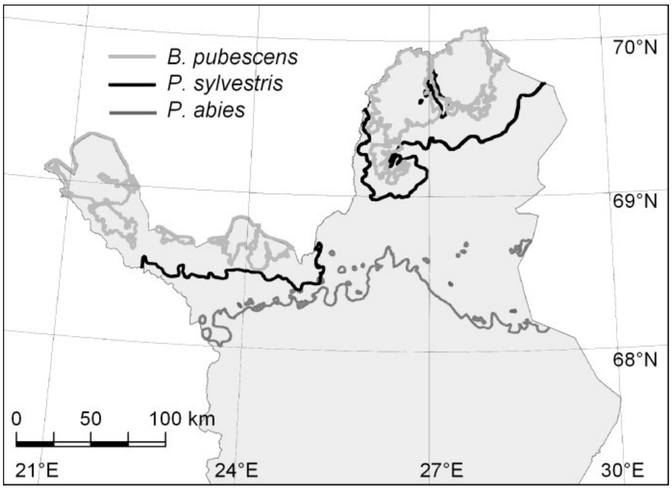

Figure A1.1. Current treeline positions of *Pinus sylvestris*, *Picea abies* and *Betula pubescens* in Finnish Lapland (based on nature survey data by Metsähallitus, 1996–1999).

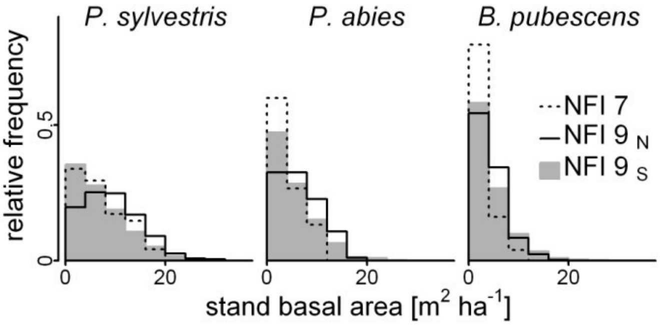

Figure A1.2. Distribution of stand basal area [m^2 ha^{-1}] above zero according to species and dataset.

Appendix A2

Methodological details on boosted regression trees

Table A2.1. Characteristics of the single boosted regression tree (BRT) models for occurrence and abundance.

	occurrence model			abundance model		
distribution (family)	Bernoulli			Laplace		
response variable	0 / 1			truncated [1] basal areas		
fitted values	p (y > 0)			basal area [m^2 ha^{-1}]		
range	[0 , 1]			[MIN , MAX]		
number of observations	NFI 7	NFI 9_N	NFI 9_S	NFI 7	NFI 9_N	NFI 9_S
P. sylvestris	217	773	3206	162	567	2391
P. abies	217	773	3206	15 [2]	92	1709
B. pubescens	217	773	3206	148	377	1458
learning rate [3]	0.001	0.005	0.005	0.001	0.001	0.005
tree complexity [4]	5			5		
bag fraction	0.5			0.5		
number of trees [5]	NFI 7	NFI 9_N	NFI 9_S	NFI 7	NFI 9_N	NFI 9_S
P. sylvestris	2600	1550	2850	5150	4200	2950
P. abies	2950	1950	8250	– [2]	3700	2550
B. pubescens	2000	1150	3350	2200	6550	3250

[1] response vector shortened by the amount of original zeros (i.e. sites without this species)

[2] sample size too small for model building

[3] the learning rate (shrinkage) determines the contribution of each tree to the final ensemble model and, thus, the speed of gradient descent

[4] the tree complexity (i.e. maximum number of splits in a tree) relates to the interaction depth that can be potentially modelled

[5] the number of trees is influenced by the two measures above and was determined by cross-validation (Elith et al. 2008)

Appendix A3

Methodological details on the transferability index

Transferability index (TI) as developed by Randin et al. (2006) and extended by Dobrowski et al. (2011), where GOF can be any goodness-of-fit measure (originally: AUC) and Δ_{MAX} is the maximum difference between internal (IE) and external (EE) evaluation (originally: 0.5 for AUC). The index ranges from 0 (maximum difference between IE and EE, no transferability) to 1 (no difference, full transferability).

$$TI = \frac{0.5\left(\left(1-\frac{|GOF_{A\to A}-GOF_{A\to B}|}{\Delta_{MAX}}\right)+\left(1-\frac{|GOF_{B\to B}-GOF_{B\to A}|}{\Delta_{MAX}}\right)\right)}{1+\left\|\frac{GOF_{A\to A}-GOF_{A\to B}}{\Delta_{MAX}}\right|-\left|\frac{GOF_{B\to B}-GOF_{B\to A}}{\Delta_{MAX}}\right\|} \quad \text{with} \quad \begin{array}{c}\text{A} = \text{region A or} \\ \text{time 1} \\ \text{B} = \text{region B or} \\ \text{time 2}\end{array}$$

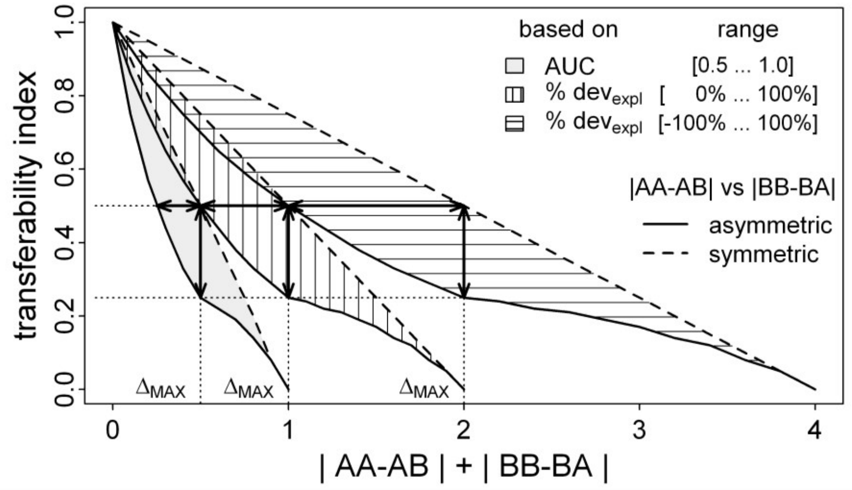

Figure A3.1. Transferability index (TI) values based on AUC or percentage of deviance explained (% dev$_{expl}$) as a function of the sum of absolute differences (|AA−AB|+|BB−BA|) between internal (AA, BB) and external evaluation (AB, BA). The range of possible values (top right corner) corresponds to Δ_{MAX} in the equation above (e.g. 0.5 for AUC). TI = 0 where |AA−AB|+|BB−BA| = 2 Δ_{MAX} (e.g. 1.0 for AUC). For equal *sums* of absolute differences, TI is higher if the two differences (= directions of model transfer) are similar (symmetric, broken line) as opposed to very different (asymmetric, solid line). Although the range of possible TI values (depending on the symmetry) for a given sum of absolute differences stays the same in all three applications (vertical arrows for Δ_{MAX}), the range of sum of absolute differences leading to the same TI value (horizontal arrows for TI = 0.5) increases (lowest for AUC, highest for a range of -100−100 % dev$_{expl}$). That makes TI values based on % dev$_{expl}$ harder to interpret and compare with one another than TI values based on AUC.

Appendix A4

Visualization of model performance, maps of model predictions, and validation results

Table A4.1. Intercept (ideally: 0) and slope (ideally: 1) of the calibration curve (Swets 1988) for the internal (IE) and external (EE) evaluation of the occurrence model.

			P. sylvestris		*P. abies*		*B. pubescens*	
	trained on	applied to	mean	sd [1]	mean	sd	mean	sd
intercept								
IE (10-fold CV)	NFI 7	NFI 7	-5.563	(5.319)	30.018	(19.087)	-0.394	(0.362)
	NFI 9_N	NFI 9_N	0.078	(0.171)	0.906	(0.527)	0.027	(0.040)
	NFI 9_S	NFI 9_S	-0.047	(0.053)	0.009	(0.035)	0.016	(0.032)
EE (temporal)	NFI 7	NFI 9_N	-1.446		2.392		-1.818	
	NFI 9_N	NFI 7	0.380		-0.818		0.528	
EE (spatial)	NFI 9_N	NFI 9_S	0.394		0.943		0.241	
	NFI 9_S	NFI 9_N	-0.342		-2.345		0.373	
slope								
IE (10-fold CV)	NFI 7	NFI 7	7.599	(6.380)	19.408	(11.520)	1.333	(0.352)
	NFI 9_N	NFI 9_N	1.523	(0.320)	1.358	(0.190)	1.098	(0.052)
	NFI 9_S	NFI 9_S	1.028	(0.036)	0.964	(0.036)	1.031	(0.049)
EE (temporal)	NFI 7	NFI 9_N	1.289		1.180		1.661	
	NFI 9_N	NFI 7	0.385		0.636		0.377	
EE (spatial)	NFI 9_N	NFI 9_S	0.635		0.326		0.754	
	NFI 9_S	NFI 9_N	1.549		0.807		1.294	

[1] mean and standard deviation of 10-fold cross-validation

Table A4.2. Pearson and Spearman correlation between observations and predictions

		P. sylvestris		*P. abies*		*B. pubescens*	
trained on	applied to	Pearson	Spearman	Pearson	Spearman	Pearson	Spearman
internal evaluation (10-fold CV)							
NFI 7	NFI 7	0.88	0.89	–[1]	–	0.63	0.64
NFI 9_N	NFI 9_N	0.92	0.94	0.93	0.56	0.82	0.81
NFI 9_S	NFI 9_S	0.79	0.83	0.82	0.82	0.76	0.72
external evaluation: temporal transfer							
NFI 7	NFI 9_N	0.65	0.70	–	–	0.49	0.54
NFI 9_N	NFI 7	0.75	0.74	0.35	0.28	0.41	0.41
external evaluation: spatial transfer							
NFI 9_N	NFI 9_S	0.68	0.70	0.50	0.42	0.48	0.47
NFI 9_S	NFI 9_N	0.79	0.83	0.64	0.40	0.66	0.66

[1] prevalence of *P. abies* in the NFI 7 dataset too small for model building

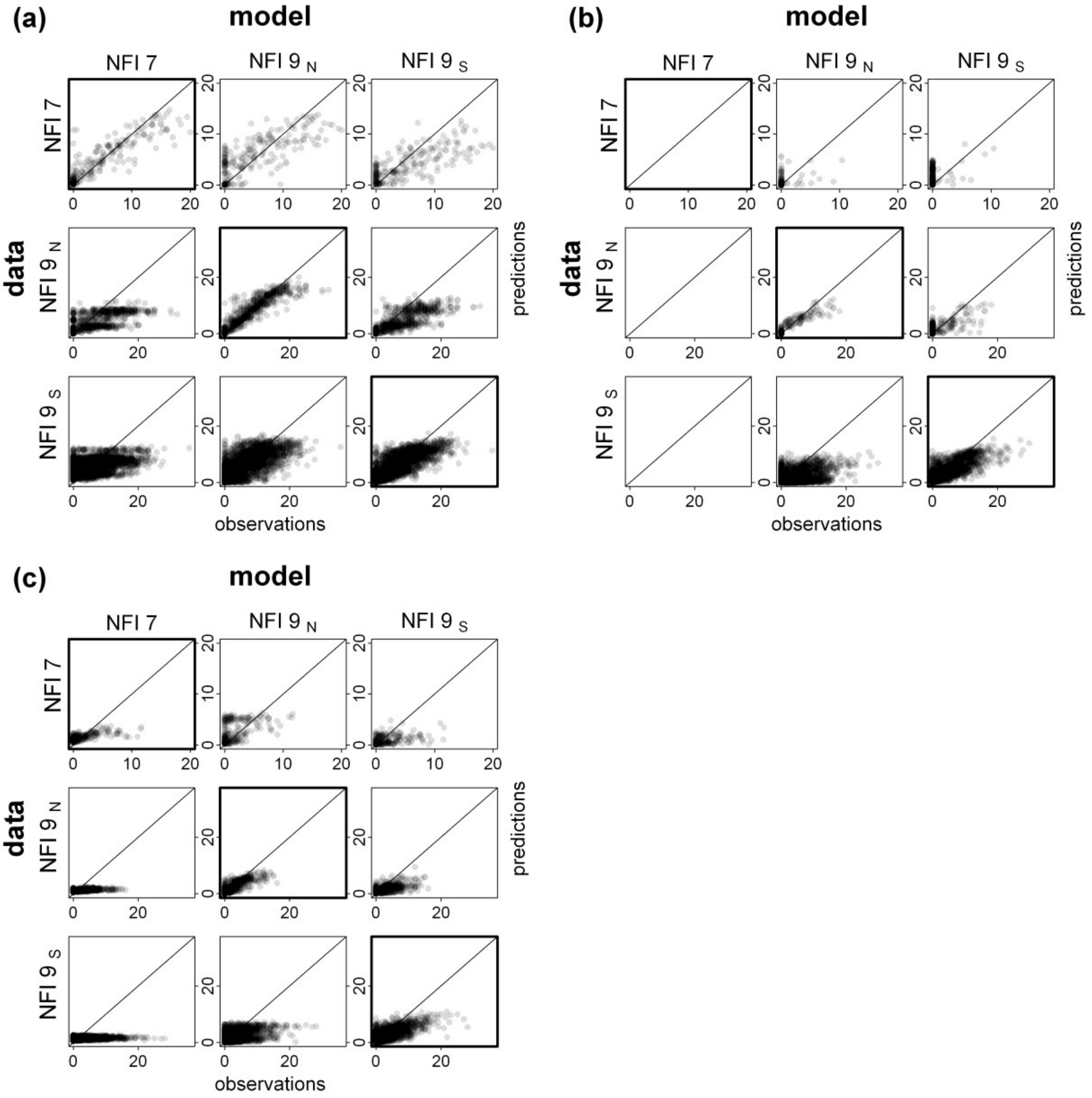

Figure A4.1. Scatterplots of observations and predictions for each model–data combination for *P. sylvestris* (a), *P. abies* (b) and *B. pubescens* (c); e.g. top right figure in each panel shows NFI 9_S model predictions for NFI 7 data. Main diagonal: internal evaluation cases. *Note*: Prevalence of *P. abies* in the NFI 7 dataset was too small for model building (left column in (b)).

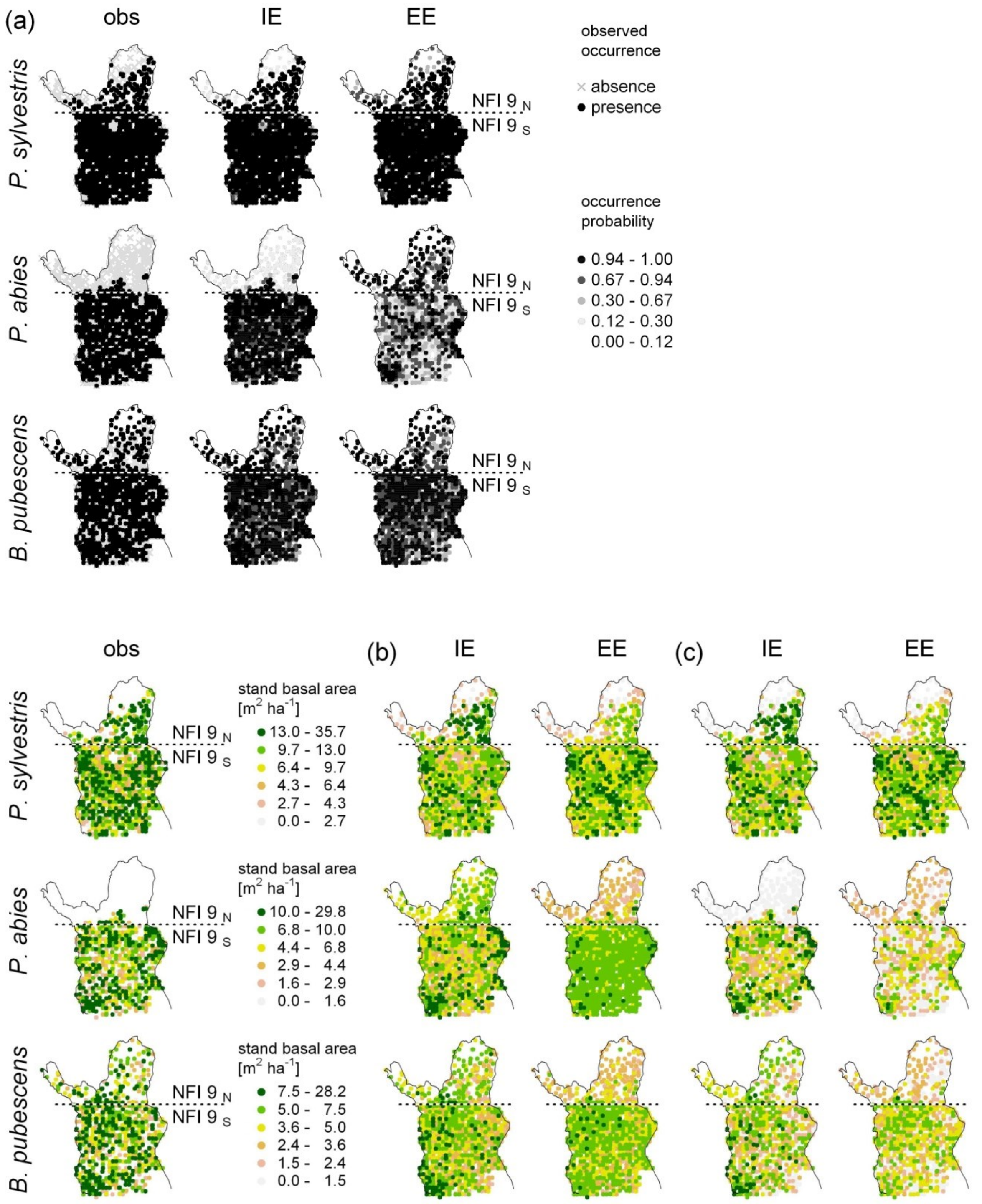

Figure A4.2. Maps of occurrence (a), abundance (b) and final model (c) predictions for the spatial model transfer: observations (obs); results of the internal evaluation (IE), i.e. northern predictions by NFI 9_N, southern predictions by NFI 9_S model; results of the external evaluation (EE), i.e. northern predictions by NFI 9_S model and southern predictions by NFI 9_N model. Note: basal area is already underestimated by the abundance model; it is not an effect of multiplying the two model results to obtain the final model predictions.

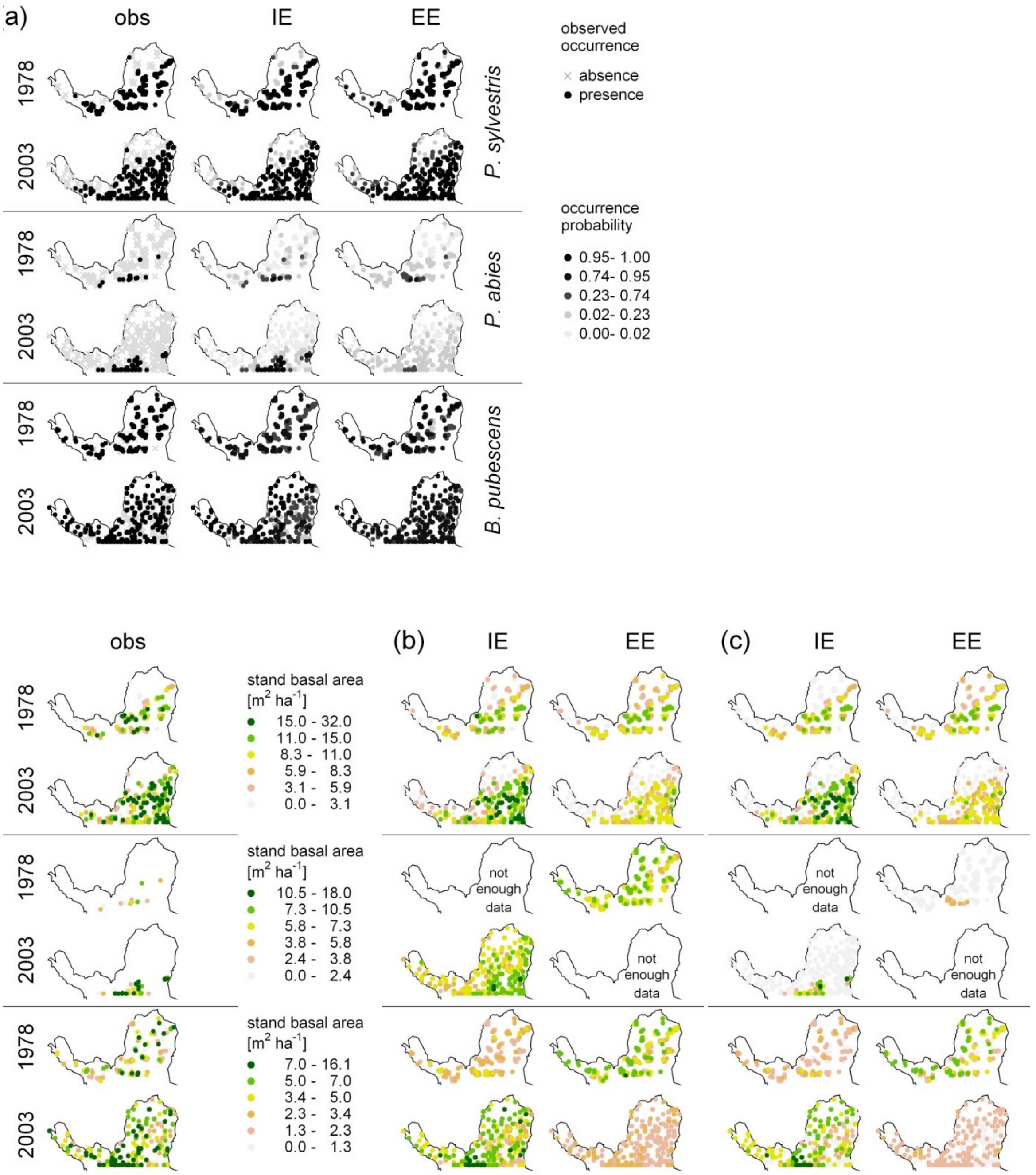

Figure A4.3. Maps of occurrence (a), abundance (b) and final model (c) predictions for the temporal model transfer: observations (obs); results of the internal evaluation (IE), i.e. 1978 predictions by NFI 7, 2003 predictions by NFI 9_N model; results of the external evaluation (EE), i.e. 1978 predicted by NFI 9_N model (hindcasting) and 2003 predicted by NFI 7 model (forecasting).

Appendix A5

Analysis of the automatically fitted interactions between predictors (see also CD)

Table A5.1. Ten most important interactions for each model. The four most important predictors (identified on the basis of relative importance) are marked in bold [1].

NFI7		NFI9$_N$		NFI9$_S$	
occurrence	abundance	occurrence	abundance	occurrence	abundance
P. sylvestris					
GDD – TPI	**B.pub** – **fert**	**P.abi** – **B.pub**	**P.abi** – **fert**	**P.abi** – **B.pub**	**P.abi** – **B.pub**
fert – **GDD**	**fert** – P_Aug	**B.pub** – **GDD**	**B.pub** – **fert**	**P.abi** – **GDD**	**P.abi** – **fert**
B.pub – P_May	**fert** – **GDD**	**P.abi** – **GDD**	**fert** – **GDD**	**GDD** – P_Aug	**B.pub** – **fert**
GDD – TRASP	**fert** – P_May	**B.pub** – **fert**	**fert** – P_May	**B.pub** – **fert**	**fert** – SBI
B.pub – TWI	**B.pub** – P_May	**B.pub** – AFI	**P.abi** – B.pub	**B.pub** – **GDD**	**fert** – TRASP
GDD – TWI	**fert** – TPI	**P.abi** – **fert**	**fert** – AFI	**P.abi** – P_May	P.abi – TRASP
fert – TWI	**fert** – SBI	**GDD** – TPI	**GDD** – TWI	**GDD** – SBI	**fert** – AFI
GDD – P_May	**fert** – AFI	**B.pub** – TPI	**B.pub** – AFI	**P.abi** – **fert**	P_Aug – TWI
B.pub – **GDD**	**B.pub** – **GDD**	**P.abi** – P_May	**GDD** – SBI	P_May – SBI	**B.pub** – TWI
SBI – AFI	**fert** – TRASP	**P.abi** – AFI	AFI – TPI	P_Aug – SBI	TRASP – TWI
P. abies					
AFI – TWI	–	**P.syl** – P_May	**B.pub** – **fert**	**P.syl** – SBI	**P.syl** – **B.pub**
P.syl – **fert**	–	AFI – **SBI**	**P.syl** – **B.pub**	**B.pub** – TPI	**P.syl** – **fert**
P.syl – **GDD**	–	**fert** – **P_May**	**P.syl** – **fert**	**B.pub** – AFI	**P.syl** – **GDD**
AFI – TPI	–	**fert** – **AFI**	**B.pub** – TRASP	**P.syl** – **GDD**	**GDD** – AFI
AFI – P_May	–	**P.syl** – **B.pub**	**fert** – SBI	SBI – TWI	**B.pub** – **fert**
P.syl – AFI	–	**B.pub** – **AFI**	**B.pub** – AFI	P_May – TRASP	**B.pub** – **GDD**
SBI – TRASP	–	**P.syl** – **fert**	**B.pub** – TWI	**fert** – TPI	**fert** – P_Aug
AFI – SBI	–	TPI – **TRASP**	**fert** – AFI	**P.syl** – **B.pub**	**fert** – **GDD**
P.syl – SBI	–	AFI – **P_May**	**fert** – TWI	**GDD** – TPI	**GDD** – SBI
fert – TRASP	–	AFI – **TPI**	**B.pub** – TPI	**B.pub** – TWI	**B.pub** – SBI
B. pubescens					
fert – AFI	TPI – TWI	**P.syl** – **P.abi**	**P.syl** – **P.abi**	**P.abi** – **GDD**	**P.syl** – **P.abi**
P.syl – **fert**	**GDD** – TWI	**P.syl** – **fert**	**P.syl** – **fert**	**P.syl** – **P.abi**	**P.syl** – **fert**
P.syl – P_May	**P.syl** – P_Aug	**P.syl** – AFI	**P.syl** – AFI	SBI – TWI	**P.syl** – P_May
fert – **GDD**	**P.syl** – TWI	**P.syl** – GDD	**P.syl** – TRASP	**P.abi** – TWI	P_Aug – TWI
P_May – TRASP	AFI – TWI	**P.syl** – P_Aug	**P.syl** – P_Aug	**P.syl** – **fert**	**P.abi** – **fert**
P.syl – TRASP	**P.syl** – P_May	**fert** – P_Aug	**P.syl** – SBI	SBI – AFI	**fert** – AFI
TWI – TRASP	P_May – TRASP	**P.abi** – **fert**	**P.syl** – P_May	**fert** – TWI	**fert** – TWI
TWI – P_May	**P.syl** – AFI	**GDD** – AFI	P_Aug – TRASP	P_May – SBI	**P.syl** – TWI
TWI – SBI	TPI – TRASP	**P.syl** – TRASP	**P.syl** – TPI	**P.abi** – AFI	**fert** – TPI
fert – TWI	**P.syl** – SBI	**fert** – SBI	AFI – TWI	SBI – TPI	**P.syl** – SBI

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[1] GDD – growing degree days; fert – site fertility; P.syl – *P. sylvestris* basal area [m^2 ha^{-1}]; P.abi – *P. abies*; basal area [m^2 ha^{-1}]; B.pub – *B. pubescens* basal area [m^2 ha^{-1}]

Appendix A6

Detailed insights into specific predictors, their relationships and relative importance

Table A6.1. Spearman correlation of autumn frost index (AFI) and each predictor (corr), changes in relative importance [%] when AFI is omitted (without – with AFI, Δ_{contr}) as well as interaction size [1] (inter) of AFI and each predictor for the *P. abies* occurrence model.

	NFI 7			NFI 9$_N$			NFI 9$_S$		
	corr	Δ_{contr}	inter	corr	Δ_{contr}	inter	corr	Δ_{contr}	inter
growing degree days	0.16	2	0.02	0.16	6	5.18	0.03	0	0.89
spring backlash index	**0.40**	7	1.52	**-0.48**	-3	83.52	-0.03	0	11.04
May precipitation	0.09	1	4.16	**-0.30**	9	10.25	**-0.58**	0	1.41
August precipitation	**-0.49**	9	0.03	0.02	0	1.26	**-0.30**	0	4.06
topogr. radiation index	-0.05	4	0.36	0.01	2	2.64	0.03	0	3.11
topogr. position index	-0.04	4	5.13	0.09	-1	10.06	0.01	0	9.95
topogr. wetness index	0.23	-4	199.53	**0.30**	-1	1.12	0.23	1	4.23
P. sylvestris [2]	**0.24**	9	3.73	-0.10	6	5.79	-0.05	-1	2.03
B. pubescens [2]	-0.04	1	0.01	0.09	-2	12.91	0.08	0	22.78
site fertility	–	4	0.71	–	1	15.66	–	0	1.09

[1] interaction size assessed with function `gbm.interactions` from `dismo` package version 0.7-17 (Hijmans et al. 2012)

[2] basal area [m^2 ha^{-1}] of co-occurring species

Bold marks higher correlation and thus higher changes in relative importance when AFI is omitted; underlined marks strong interactions leading to a loss of relative importance (negative Δ_{contr}) when AFI is omitted.

Figure A6.1. See next page.

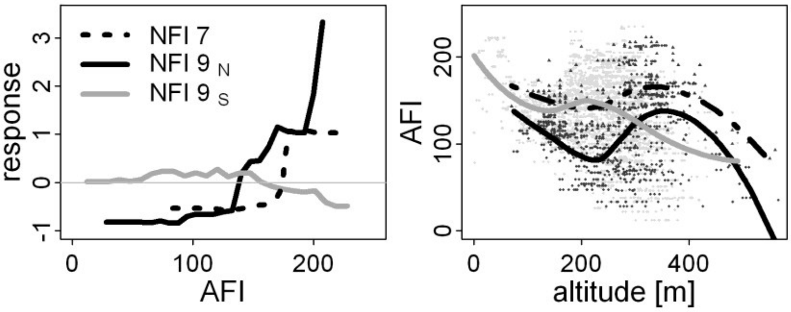

Figure A6.2. Response curves for the autumn frost index (AFI) in the *P. abies* occurrence model (left) and scatterplot of AFI and altitude with loess curves for the NFI 7, NFI 9$_N$ and NFI 9$_S$ datasets (right).

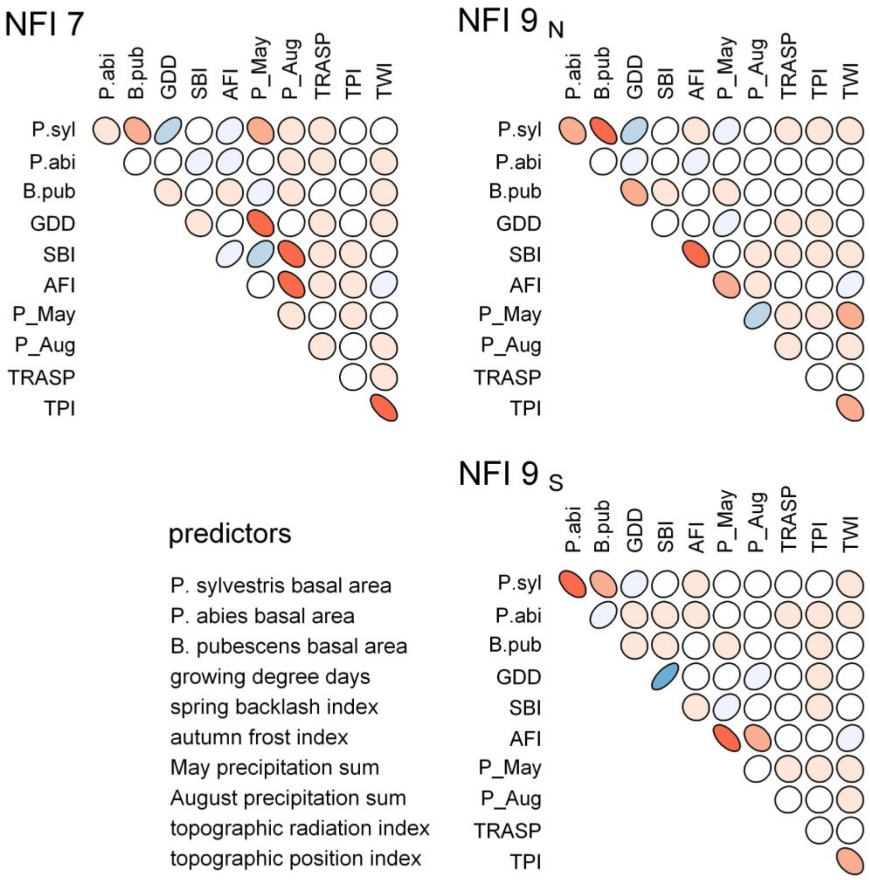

Figure A6.1. Spearman correlation between predictors of the NFI 7, NFI 9_N and NFI 9_S datasets. Form of the ellipse and shade of colour (red: negative, blue: positive) increase with increasing correlation index values. White circle denotes no correlation (Spearman index = 0). TWI = topographic wetness index.

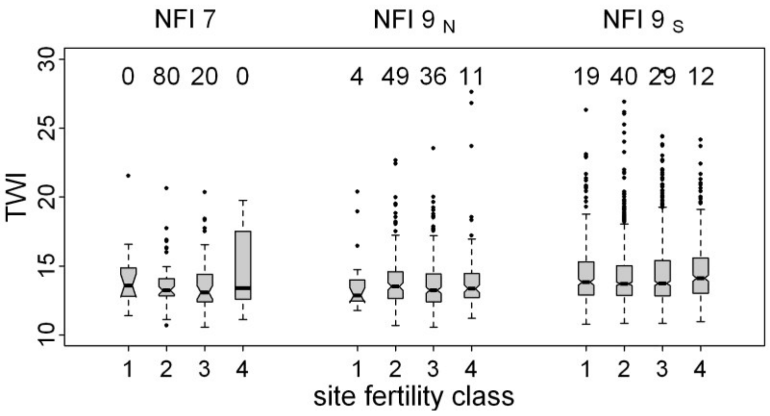

Figure A6.3. Distribution of the topographic wetness index (TWI) in each site fertility class in the NFI 7, NFI 9_N and NFI 9_S dataset. Numbers above the boxplots give the percentage of *P. abies* presences in that class.

3. Comparing correlative and process-based modelling approaches in a boreal forest identifies important areas for model development [2]

Abstract

Models attempting to predict treeline shifts in changing climates must include the relevant ecological processes and be temporally transferable. A previous correlative model study has pointed to nutrients, competition, and temperature as the most important factors for *Pinus sylvestris* L., *Picea abies* (L.) Karst. and *Betula pubescens* Ehrh. treelines in Finnish Lapland. In addition, the observed relationship between conifer occurrence and temperature changed between 1978 and 2003 because of delayed species response to climate warming. Here, we applied a widely used process-based dynamic vegetation model (LPJ-GUESS) to test its capability to simulate observed spatial and temporal patterns of the main tree species in Finnish Lapland and to explore the model representation of important processes to guide further model development. A European parameterization of LPJ-GUESS overestimated especially *P. abies* biomass and the species' northern range limit. But the model successfully captured the temporal pattern of shifting relationships between biomass and temperature. We further demonstrated the restricted temporal transferability of bioclimatic limits used in LPJ-GUESS and similar process-based models. We identified implemented processes to adjust (competition between species, disturbance) and missing processes that are crucial in boreal forests (nutrient limitation, forest management). Key mechanisms of competition are shade and drought tolerance, nutrient limitation, fire resistance, and susceptibility to disturbances (storm, herbivory) which we discussed with respect to boreal ecology. Finally, we reviewed promising model developments regarding missing processes. Insights from a correlative model study guided our analysis of this process-based model application which revealed important areas for further development.

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[2] An article with equivalent content has been submitted as:
Schibalski, A, Lehtonen, A, Hickler, T, Schröder, B. Comparing correlative and process-based modelling approaches in a boreal forest identifies important areas for model development. Silva Fennica (in review).

3.1. Introduction

Arctic treelines are the (more or less) well-defined biome boundaries between dense forest and tundra which have shifted in the past and will continue to shift in the future. Today's spatial pattern of treelines is the combined result of historic developments and current processes: in northern Europe, tree species retreated south during the past glaciations and then advanced northwards again when the climate became more favourable (Payette et al. 2002, Seppä et al. 2002). Recent climate change has led to a rise in annual mean temperatures in Finland by 0.7 °C between 1901 and 2000. Mean winter temperatures in the 1990s were 1.7 °C higher than the preceding 30-year average (Jylhä et al. 2004). The effect of these climatic changes on tree growth is not straightforward. Rising temperature sums, for example, can improve growing conditions of established trees during the growing season *if* accompanied by sufficient soil moisture (Moen et al. 2008, Holtmeier et al. 2003, Sveinbjörnsson et al. 2002). Warmer winters, on the one hand, reduce seedling mortality in particular due to consistently milder temperatures (Kullman 1997). On the other hand, loss of snow insulation during single or multiple events of winter warming has led to reduced reproduction and higher mortality in sub-Arctic shrubs (Bokhorst et al. 2011).

In addition to the uncertain response of the treeline to ongoing climatic changes, other factors can limit a possible treeline advance, e.g. competition by shrubs. The crowberry shrub *Empetrum hermaphroditum* allelopathically reduces germination of *Pinus sylvestris* L. seeds (Zackrisson and Nilsson 1992) as well as nitrogen uptake of both *P. sylvestris* (Nilsson et al. 1993) and *Betula pubescens* Ehrh. (Weih and Karlsson 1999), leading to nitrogen limitation in *B. pubescens* in northern Sweden (Sveinbjörnsson et al. 1992). In the south of Finnish Lapland, the Tanaelv and Lapland Greenstone Belt form moist nutrient-rich soils dominated by *Picea abies* (L.) Karst. stands (Sutinen et al. 2005). They are bordered to the north (> 68 °N) by the Lapland Granulite Belt (Cagnard et al. 2011) which is at most 80 km wide. Its dry nutrient-poor soils dominated by *P. sylvestris* stands act as a dispersal barrier for *P. abies* (Sutinen et al. 2005). This could explain why *P. abies* is restricted to the south of Lapland while surviving in isolated outposts (natural and planted) far north of its current treeline (Oksanen 1995). Aakala et al. (2014) provide another example of tree limitation by non-climatic factors. They found an observed event of increased *P. sylvestris* establishment in the late 1970s and early 1980s on a fell in Eastern Fennoscandia to be unrelated to any temperature variable they included in their study. Instead, the recruitment event coincided with a decrease in reindeer density and thus herbivore pressure. Thus, more than climatic limitation is needed to explain the current treeline location in Finnish Lapland.

Models trying to reproduce spatial patterns like the current position of a treeline, and predict temporal developments like range shifts under climate change, need to include the relevant ecological processes. Models, in general, can be classified according to their method of process representation. On the one hand, correlative (or empirical, phenomenological) models statistically relate species occurrence (presence/absence) or abundance (e.g. basal area or biomass sum of tree stands) to various environmental predictors (Elith and Leathwick 2009). They include processes and ecological knowledge implicitly through the choice of their predictor variables. Process-based models, on the other hand, explicitly simulate processes and causal relationships via mathematical equations (Dormann et al. 2012). One of the differences between correlative and process-based models relevant to climate change studies is their transferability (Gustafson 2013). Correlative models often incorrectly assume stationary relationships between response and predictors when applied to different regions or time periods (but see Hothorn et al. (2011)

who propose a framework that explicitly addresses nonstationary effects). This leads to low generality, which was specifically explored by Schibalski et al. (2014) in their study of *P. sylvestris*, *P. abies* and *B. pubescens* treelines in Finnish Lapland. The climate had changed over the relatively short time period of 25 years (1978-2003), consequently shifting the predictor space covered by the data sets used to estimate correlative models, thus limiting their temporal transferability. Limited transferability is an issue concerning hindcasting (where it can be assessed if validation data is available), and even more so for forecasting, which is repeatedly carried out with climate scenario data (e.g. Bálint et al. 2011, Kearney et al. 2010, Yates et al. 2010). Process-based models, on the other hand, do not rely as heavily on empirical calibration, which should increase their applicability across space and time (Cuddington et al. 2013). However, Dormann et al. (2012) have deliberately distinguished between 'forward' and 'fitted' process-based models. 'Forward' models require no calibration at all and are thus independent of data (which is used for external validation). In the more common 'fitted' models, at least some parameters are calibrated on datasets and thus share, to a lesser extent, the transferability issues of correlative models.

Here, we followed up on results from a correlative model study that investigated processes determining the current treeline position of *P. sylvestris*, *P. abies* and *B. pubescens* in Finnish Lapland (Schibalski et al. 2014). Schibalski et al. (2014) analyzed the relative importance and response shape of climatic, edaphic and biotic predictors in their occurrence (presence-absence) and abundance (basal area) models for 1978 and 2003. They identified site fertility, abundance of co-occurring species and growing degree days (GDD) as the most important predictors explaining the three tree species' occurrence and abundance in Finnish Lapland.

Despite the warming over the study period of 25 years, the underlying forest inventory data of 1978 and 2003 showed no clear latitudinal treeline advance (however, see Aakala et al. (2014) for an example of altitudinal *P. sylvestris* treeline advance in Eastern Fennoscandia). This is in line with a decrease of *P. sylvestris* treeline advance from 97 m year^{-1} (1914-1980) to 13.8 m year^{-1} (1980-2009) in northernmost Norway (Hofgaard et al. 2013). The time lag between warming climate and species response was visible in the model response curves, i.e. the statistical relationship between the occurrence of *P. sylvestris* or *P. abies* and GDD. In this curve, the threshold between low (absence) and high (presence) probabilities of occurrence corresponded to a lower GDD in 1978 than 2003.

The interesting questions of climatic vs. edaphic limitation, the role of competition, and the observed delay in the species response to recent climate change make Finnish Lapland a suitable case study for a second modeling approach. Thus, we applied an established and widely used 'fitted' process-based dynamic vegetation model (LPJ-GUESS, http://iis4.nateko.lu.se/lpj-guess/, Smith et al. 2001) to predict the ranges and biomass of *P. sylvestris*, *P. abies* and *B. pubescens* in the same region and over the same time period as the correlative model study.

Our aims were to test the general capability of the model (i) to simulate the spatial biomass pattern and ranges (treelines) of the three main tree species in Finnish Lapland, and (ii) to simulate the time lag between climate change and species response as revealed by the correlative model study (Schibalski et al. 2014); as well as (iii) to explore the representation of competition, climate and edaphic factors in LPJ-GUESS, revealing potential shortcomings and thus guiding further model development.

To assess model performance, we (i) compared the spatial biomass pattern and range limit simulated by LPJ-GUESS with observed biomass (forest inventory data, 2011), and (ii) compared the response curves relating simulated biomass to GDD between 1978 and 2003. To explore process representation in LPJ-GUESS (iii), we analyzed the parameterization of currently implemented processes with respect to the ecology of boreal forests, especially in Fennoscandia, and reviewed additional process implementation in other existing LPJ-GUESS versions.

3.2. Material and methods

3.2.1. LPJ-GUESS

3.2.1.1. General model description

LPJ-GUESS is a flexible biome-scale model for simulating vegetation biogeography and dynamics, as well as biogeochemical cycles at regional to global scales. It shares many ecophysiological process-representations with the widely used Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM, Sitch et al. 2003, Smith et al. 2001). But vegetation dynamics and vegetation structure are simulated at a higher level of detail, allowing the parameterization of individual species as opposed to broader plant functional types. Vegetation dynamics are simulated as the emergent outcome of growth and competition for light, space and soil resources among woody plant individuals and a herbaceous understorey based on their functional traits. Plant-physiological processes like photosynthesis and respiration, as well as the exchange of carbon and water between vegetation, soil, and atmosphere, are simulated on a daily basis. Vegetation growth, biomass allocation, establishment, and mortality are simulated once at the end of a simulation year. Tree mortality occurs as a function of growth efficiency, as trees reach their maximum age and as a result of fire and a stochastic patch-destroying disturbance which recurs within an expected mean interval of, here, 200 years. This patch-destroying disturbance kills all trees in a patch and represents rare events such as pest calamities or windstorms (see Hickler et al. (2012) for more details). Wildfires are modelled based on temperature, fuel (litter) load and moisture (Thonicke et al. 2001) and affect trees according to their species-specific fire resistance.

Vegetation dynamics are simulated in each of a number (50 in this study) of replicate patches (0.1 ha) representing ‘random samples’ of each simulated locality or grid cell. Each model grid cell is homogeneous in terms of soil texture, atmospheric CO_2 concentration and a set of climatic variables (daily temperature, precipitation, and radiation). Its size is determined by the spatial resolution of this input data (10×10 km^2 in this study). Multiple patches are simulated to account for the distribution within a landscape representative of the grid cell, as vegetation stands differ in their histories of disturbance and stand development (succession). The output from individual patches is averaged to characterize the average vegetation per grid cell.

In this study, we used the version parameterized for major European tree species and plant functional types by Hickler et al. (2012), with an additional species-specific water supply function (Schurgers et al. 2011). Bioclimatic limits determine which species can establish and survive in a model grid cell, and were fitted by visually comparing the continental-scale distribution of species with the geographic variation in the bioclimatic limits (Hickler et al. 2012). This makes LPJ-GUESS a ‘fitted’ process-based model according to Dormann et al. (2012).

3.2.1.2. Species characterization in LPJ-GUESS

In LPJ-GUESS, the simulated (tree) species are discriminated by leaf or needle functional traits, leaf area to sapwood cross-sectional area ratio, phenology, fire resistance, root distribution, bioclimatic limits for establishment (minimum GDD (5°C); maximum monthly winter temperature, representing the chilling requirement of northern species; minimum plant-available water content of the upper soil layer during the growing season, also influencing the species-specific water supply function, with more water available for a given soil water content for species with a lower limit, Schurgers et al. 2011) and survival (minimum monthly winter temperature), as well as life history strategy (related to shade tolerance, see below). All parameters are listed in Appendix B1, **Table B1** (see also Hickler et al. 2012). The simulations of this study were carried out in 'cohort mode' in which cohorts of individuals recruited in the same patch in a given year are represented by a single average individual and are thus assumed to retain the same size and form as they grow.

In LPJ-GUESS, shade tolerance defines an important trade-off during succession: Shade-intolerant species like *B. pubescens* require more light for establishment (par_{min}, **Table B1**) than shade-tolerant species. Shade-intolerant species also have higher maximum establishment rates (est_{max}, **Table B1**) under high-light conditions, but establishment rates rapidly decline as the canopy closes and less radiation reaches the forest (α, **Table B1**). They also suffer more from growth-efficiency mortality (greff, **Table B1**) as the canopy closes and growth is diminished due to increasing competition for light. However, as a result of higher sapwood to heartwood conversion ($turn_{sapwood}$, **Table B1**), shade-intolerant species grow faster under high-light conditions. For a full description of the associated equations see Hickler et al. (2012) and Smith et al. (2001). The associated parameters were fitted to yield realistic succession patterns in selected European forests, but not including sites from northern Scandinavia (Hickler et al. 2012).

3.2.1.3. Environmental input data and setup of model runs

As environmental input data, LPJ-GUESS requires daily mean air temperature, precipitation sum, radiation, atmospheric CO_2 and soil texture. We used soil data from two National Forest Inventories (described in *section 3.2.3*) to assign each plot one of the nine soil classes in LPJ-GUESS which differ in terms of water holding capacity and thermal diffusivity (Sitch et al. 2003, Table 4). In our study region, medium textures dominate (70 %), but there are organic soils in the southern part of Finnish Lapland (21 %, Appendix B, **Fig. B1**).

For regional climate input, we used monthly mean and minimum temperature, precipitation and radiation in an interpolated 10×10 km^2 grid from 1961 to 2003 (Venäläinen et al. 2005), and linear interpolation between monthly values to construct the daily inputs. In contrast, atmospheric CO_2 was given as annual averages, not further regionalized (Appendix B, **Fig. B2**). From 1978 to 2003, mean monthly temperatures have increased significantly ($p < 0.001$, Wilcoxon rank sum test) in all months except June and December (**Fig. 3.1** and Appendix B, **Fig. B3**). Similarly, growing degree days have increased, but we found spatial differences across Finnish Lapland with decreases in some areas (Appendix B, **Fig. B4**). Monthly precipitation sums have increased for all months but September over the 25 years (**Fig. 3.1** and Appendix B, **Fig. B3**).

LPJ-GUESS grows vegetation from bare soil. To reach approximate equilibrium conditions, we let the model run for 1000 years before the actual simulation period (1961-2003). As input data for this spin-up, we recycled the oldest 30 years of historical climate data (with detrended temperatures).

To assess the model's capability to simulate the spatial biomass pattern and ranges (treelines) of the three main tree species in Finnish Lapland (aim (i)), we ran the model with all three species together (called 'multi-species' hereafter), thus including biotic interaction. We compared above-and belowground biomass [kg m^{-2}] per species and grid cell with observed biomass data (described in *section 3.2.2*). In addition, we ran the model separately for each species alone, i.e. without the competition of the other two species (called 'single-species'). We were thus able to assess the influence of interspecific competition in LPJ-GUESS (aim (iii)) and gain insight into the species' performance independent of competing species.

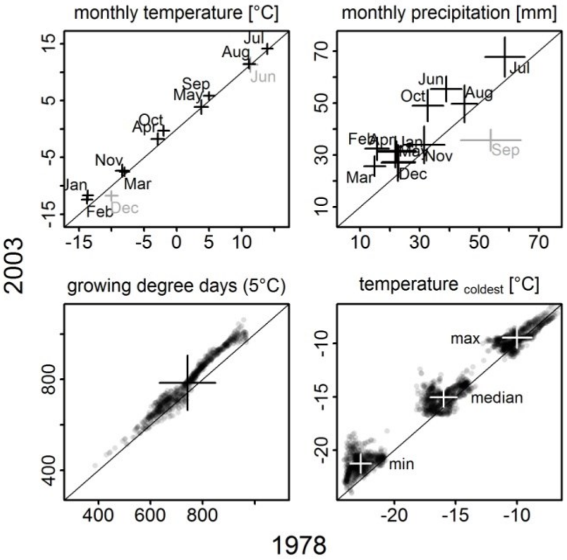

Figure 3.1. Comparison of climate variables between 1978 and 2003. Monthly mean temperatures and precipitation sums, as well as GDD, were averaged over 10 years preceding the simulation year (1968-1977, 1993-2002); the mean temperature of the coldest month was averaged over 17 years preceding the simulation year (1961-1977, 1986-2002). Plus signs indicate median (intersection) and standard deviation (length of the arms). Black (or white in the last panel) signs mean that values were significantly higher in 2003 than 1978, grey means the opposite ($p < 0.001$, Wilcoxon rank sum test). For GDD and coldest month mean temperatures, individual grid cell values are shown in addition to their median and standard deviation. See Appendix B, **Fig. B3** for more detailed information on monthly mean temperature and precipitation sums.

3.2.2. Multi-Source National Forest Inventory data

We compared LPJ-GUESS biomass estimates from the multi-species run with biomass estimates from the Multi-Source National Forest Inventory (MS-NFI, Tomppo et al. 2008) for Finnish Lapland. These biomass estimates are a combination of field observations and satellite imagery from 2011, publicly available online (http://kartta.metla.fi/index-en.html). MS-NFI biomass estimates are provided as single biomass components [10 kg ha^{-1}]: living and dead branches, roots, stump, stem with bark and stem residual, as well as foliage or needles. To directly compare LPJ-GUESS results with the MS-NFI data, we added up the single biomass components for *P. sylvestris*, *P. abies* and broad-leaved trees (including *B. pubescens*).

3.2.3. National Forest Inventory data

We used National Forest Inventory (NFI) data on the basal area of *P. sylvestris*, *P. abies* and *B. pubescens* in 1978 (NFI 7, Kuusela and Salminen 1991) and 2003 (NFI 9, Tomppo et al. 2011), also used in Schibalski et al. (2014), to investigate the temporal pattern of delayed species response to climate warming over the 25 years (aim (ii)). To this end, we compared response curves between 1978 and 2003 for both correlative and ‘fitted’ process-based model results. Response curves graphically describe the relationship between e.g. a species’ occurrence (presence-absence) and a predictor variable like GDD (Schibalski et al. 2014, cf. Fig. 7a). Using boosted regression trees (Elith et al. 2008) as in the correlative model study (Schibalski et al. 2014), we estimated the same relationship between biomass simulated by LPJ-GUESS and GDD. We compared the shape of the curves, the location of thresholds on the GDD gradient and the shifting of that threshold between 1978 and 2003 for both observed (NFI, correlative model) and simulated data (LPJ-GUESS, ‘fitted’ process-based model).

3.3. Results

3.3.1. Spatial patterns

The total biomass, i.e. the biomass sum of all three species, was overestimated by LPJ-GUESS (**Fig. 3.2a**, observed and simulated biomass) in Finnish Lapland. However, the spatial trend of northwards decreasing biomass observed in the MS-NFI data was reproduced by LPJ-GUESS.

For *P. sylvestris*, the biomass range matched between the LPJ-GUESS output (multi-species run) and MS-NFI data (**Fig. 3.2a**), except for the far north (> 69 °N) where the LPJ-GUESS biomass predictions were too high. The spatial pattern of high and low biomass was not reproduced correctly as the simulated biomass increased towards the north, while the observed biomass actually decreases towards the treeline (**Fig. 3.3**; see Appendix B, **Fig. B5** for a colour version). Without the competition of the other two species (single-species run), the simulated biomass was much higher, obviously exceeding the observed values, but the spatial pattern of northwards decreasing biomasses was correctly captured (**Fig. 3.2b**).

For *B. pubescens*, we found a similar pattern: the range of biomass was similar between the LPJ-GUESS output (multi-species) and MS-NFI data (**Fig. 3.2a**), especially when taking into account that MS-NFI data comprised *all* deciduous species. In the far north, where no other deciduous species prevail, the MS-NFI estimate equalled *B. pubescens* biomass, and the match between LPJ-GUESS simulations and MS-NFI observations was good. In the south, LPJ-GUESS underestimated the MS-NFI data which includes other deciduous species coexisting with *B. pubescens*. Again, the correct spatial trend of northwards decreasing biomass in the single-species model run was effectively reversed when including competition (**Fig. 3.3**). In Finnish Lapland, *B. pubescens’* range limit is much less distinct than the two conifers’ clear treelines, which was reflected by both observed and simulated biomass (**Fig. 3.3**).

Finally, *P. abies* was greatly overestimated in both biomass range (**Fig. 3.2a**) and species range (LPJ-GUESS did not capture the distinct treeline at ~ 68.5 °N). Although LPJ-GUESS simulated a decrease in biomass towards the north, the range limit of *P. abies* in the model was not reached and is obviously far north of the observed treeline (**Fig. 3.3**). In contrast to the other two species, the multi-species and single-species model runs yielded virtually the same results for *P. abies*.

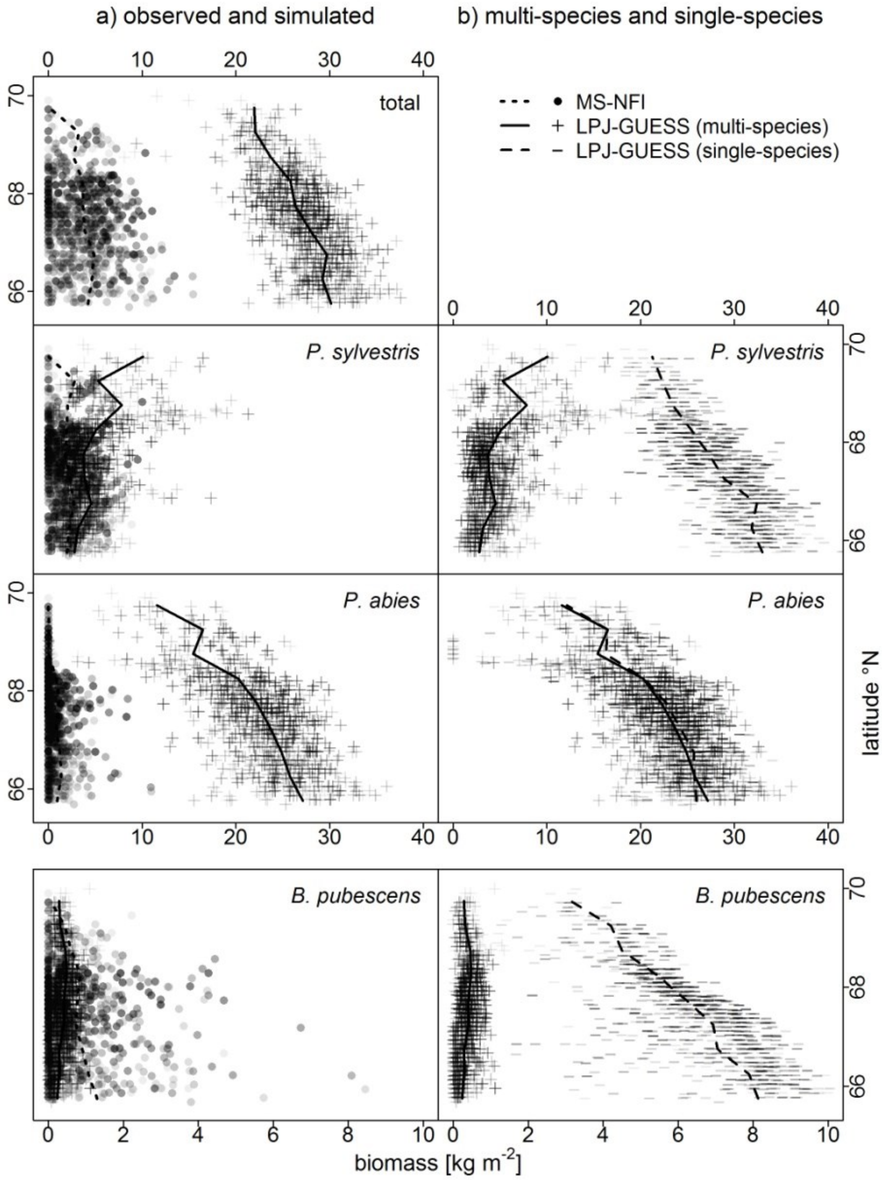

Figure 3.2. Comparison of a) observed (MS-NFI data) and simulated biomass [kg m^{-2}] (LPJ-GUESS, multi-species run), and, b) multi-species (i.e. with competition) and single-species (without competition) LPJ-GUESS runs, by latitude bands (lines are means within 0.5 ° latitude bands). Symbols are transparent to visualize the distribution of values. Note the different range of biomass values for *B. pubescens*.

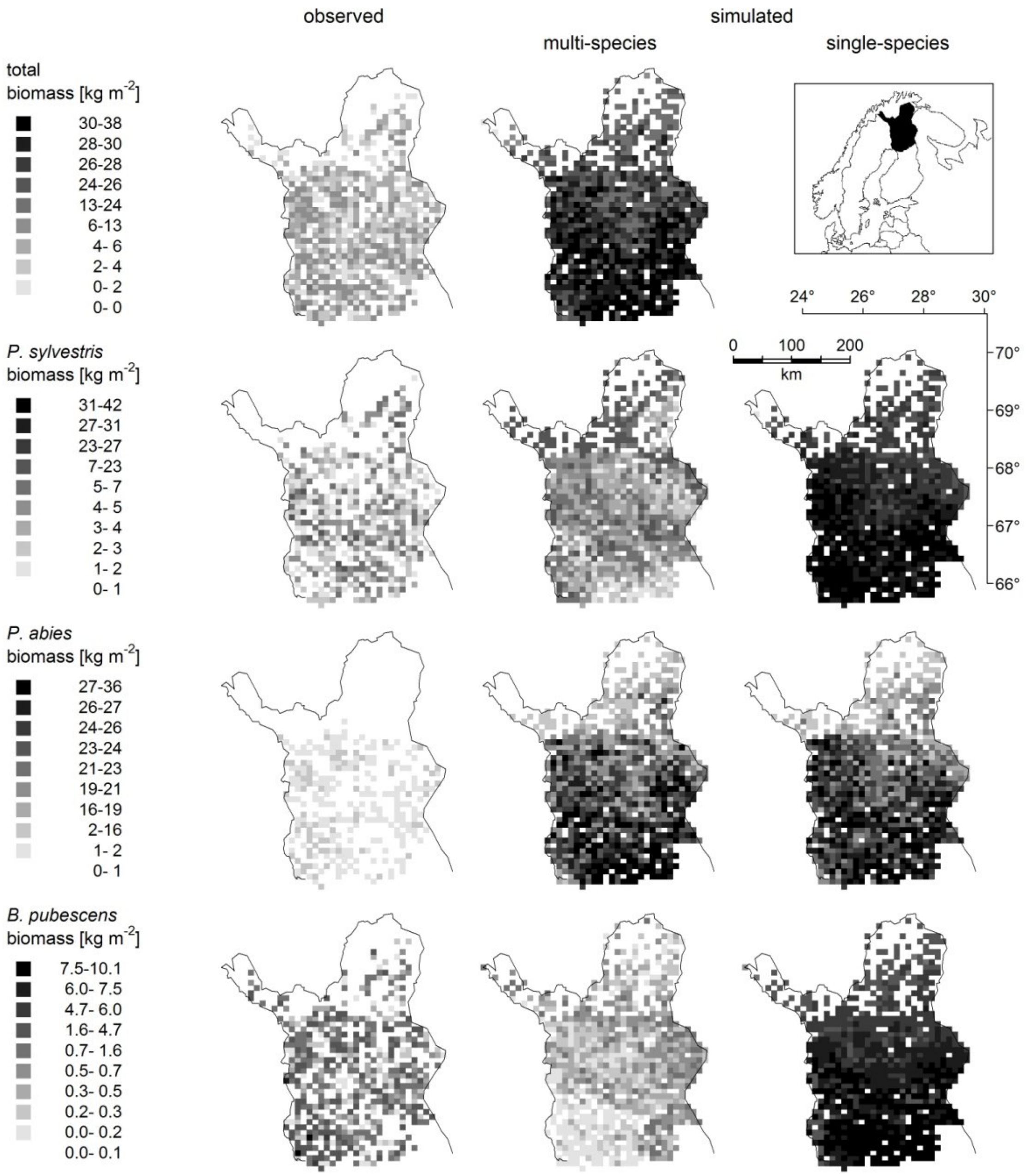

Figure 3.3. Map comparison of total and species-specific biomass [kg m^{-2}]: observed data (MS-NFI, 2011) and results from multi-species and single-species LPJ-GUESS simulations (averaged over 1994-2003). To maximize visibility of spatial differences but retain comparability between observations and simulations, we used quantiles to define classes for each species and the total. This results in the irregular class spacing and reflects the different biomass distributions (cf. **Fig. 3.2**). See Appendix B for a colour version of this figure (**Fig. B5**).

3.3.2. Temporal patterns

Simulated biomass increases from 1978 to 2003 were distributed throughout Lapland for *P. abies* and *B. pubescens* (**Fig. 3.4**); they were not associated with a treeline advance. In contrast, simulated biomass increases of *P. sylvestris* were concentrated in the far north of our study region (**Fig. 3.4**) with the greatest biomass increase (2.06 kg m^{-2}) at 69.9°N.

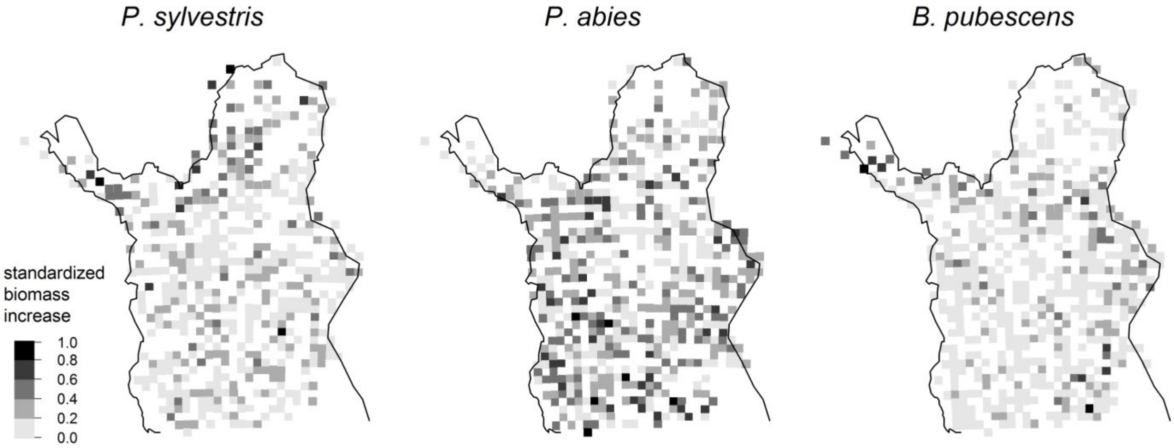

Figure 3.4. Maps of standardized simulated biomass increases [kg m^{-2}] from 1978 to 2003 (LPJ-GUESS, multi-species) for *P. sylvestris*, *P. abies* and *B. pubescens*. Black means highest biomass increase.

In the correlative study (Schibalski et al. 2014), the time lag between climate warming (e.g. GDD increase, **Fig. 3.1**) and the response of slow-growing tree species manifested itself in model response curves, i.e. the relationship between species occurrence probability and growing degree days (**Fig. 3.5**, observed). In 1978, the GDD value for which the probability of *P. sylvestris* occurrence started to increase from zero (absence) was approx. 570 as opposed to 600 in 2003 (**Fig. 3.5**, observed). Similarly, the GDD threshold for *P. abies* presence was 600 (1978) as opposed to 630 (2003).

For *P. abies*, the comparison of response curves derived from biomass simulated by LPJ-GUESS (instead of observed presence-absence data) between 1978 and 2003 showed a similar shape. Although the GDD thresholds were lower than observed (approx. 540 in 1978 and 570 in 2003), they were at a similar distance, i.e. approx. 30 GDD (**Fig. 3.5**, simulated, multi-species). As in all figures previously, the results from multi- and single-species model runs were virtually identical for *P. abies* and nearly reversed for *P. sylvestris* (**Fig. 3.5**). Thus, for *P. sylvestris* there was a mismatch in both curve shape and time lag (**Fig. 3.5**, multi-species). Without competition (**Fig. 3.5**, single-species), however, the shape of *P. sylvestris* response curves matched well between correlative (observed) and process-based model (simulated), and the time lag was approx. 30 GDD, although GDD thresholds were lower than observed (530 in 1978 and 570 in 2003).

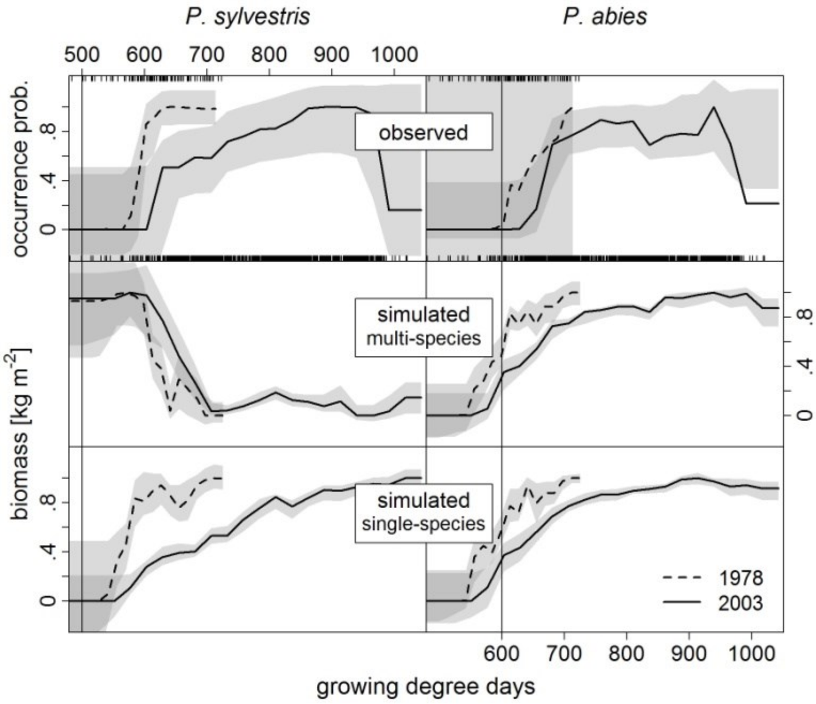

Figure 3.5. Species-specific statistical response curves of observed occurrence (NFI, see Schibalski et al. 2014) and simulated biomass (LPJ-GUESS) to growing degree days (averaged over the ten years preceding the inventory year, i.e. 1968-1977 and 1993-2002; given as rug plot in the upper panels: top 1978, bottom 2003). Vertical lines mark the bioclimatic limit used in LPJ-GUESS for the respective species ($GDD_{5,min}$, **Table B1**). Responses were standardized to enhance comparability. Transparent bootstrapped confidence bands (0.95) were calculated following the procedure detailed in Coutts (2011) and Coutts and Yokomizo (2014), using the boot.ci function in R (Canty and Ripley 2013). Note: The prevalence of *P. abies* was very low in the 1978 NFI dataset (7 %) leading to the excessive bootstrapped confidence band (top right).

3.4. Discussion

3.4.1. Total biomass overestimation

Total biomass was overestimated, which is in accordance with other studies applying LPJ-GUESS to Scandinavia. Smith et al. (2008) found LPJ-GUESS to overestimate conifer forest biomass, leaf area index and tree density in northern Fennoscandia unless the model was constrained by satellite data. As in similar dynamic vegetation models (e.g. Zaehle et al. 2010, Sokolov et al. 2008, Thornton et al. 2007), however, primary production, a key driver of the simulated biomass, in LPJ-GUESS is substantially lower in northern forests when accounting for nitrogen limitation compared to the unlimited model version (Smith et al. 2014). Including nitrogen cycling in LPJ-GUESS reduced the overestimation of gross primary production from 56 % to 18 % in boreal forests (Fleischer et al. 2015). This confirms the general assumption that forest growth in the region is heavily limited by soil nutrients, in particular, nitrogen (Lupi et al. 2013, Vitousek and Howarth 1991). Although nitrogen limitation has been implemented within the global LPJ-GUESS version based on broader plant functional types (Smith et al. 2014), these developments have not yet been combined with regional tree species parameterization (see also discussion of species-specific nutrient limitation in *section 3.4.3.4*).

Another process that could potentially reduce total biomass to the observed level is disturbance. In LPJ-GUESS, patch-destroying disturbances are a stochastic process, determined by the disturbance interval (parameter), which destroys all biomass in a patch. Our return interval for patch-destroying disturbance of 200 years, which was adopted as an average across Europe (Hickler et al. 2012), is probably too long. Increasing the disturbance frequency would effectively restrict biomass accumulation, especially that of the slower growing conifers. However, the susceptibility to disturbances in Finnish Lapland differs between species (see *section 3.4.3.6* below). This should be accounted for to correct not only total biomass levels in the single-species model runs but also spatial patterns influenced by inter-specific competition in the multi-species model run.

The omission of forest management in our version of LPJ-GUESS (but see Jönsson et al. (2015) for a new model version including forest management) surely contributes to the overestimation of the conifer biomass. Forest management in Finnish Lapland is limited mainly to the southern part (south of about 68 °N) and the Lake Inari region. It consists of fellings, including thinning and clearcutting, as well as e.g. preparation of regeneration areas (clearing, prescribed burning and soil preparation, Ylitalo 2013). Rotation times in Lapland range between 60 and 150 years compared to 40 to 100 years in the south (Äijälä et al. 2014). Thus, the inclusion of region-specific management measures in the model could alleviate the biomass overestimation, especially where forests are used more intensively.

3.4.2. Treeline dynamics and GDD

In accordance with the findings of Schibalski et al. (2014), the spatial pattern of simulated biomass increases between 1978 and 2003 did not indicate a treeline advance of *P. abies* (*B. pubescens* lacks a clearly defined treeline in Finnish Lapland). For *P. sylvestris*, however, simulated biomass increases did indeed concentrate in the far north of our study region. This suggests that *P. sylvestris* is more susceptible to climate warming than *P. abies* because it is climatically limited in Finnish Lapland. Schibalski et al. (2014) draw similar conclusions from the fact that in their *P. sylvestris* occurrence model, the importance of GDD was lower in 1978 than in 2003, and lower in southern Lapland than northern Lapland. GDD were higher in 2003 and southern Lapland, respectively, and thus less limiting than in 1978 and northern Lapland.

LPJ-GUESS captured the observed time lag of the response to climate change between 1978 and 2003 (**Fig. 3.5**). The deviating pattern of *P. sylvestris* in the multi-species model run is caused by *P. abies* distorting the spatial distribution of *P. sylvestris* biomass. Different ecological processes could explain this observed pattern. First, recruitment limitation includes seed production limitation (enough seeds need to be produced in established stands), seed dispersal limitation (seeds need to arrive at newly favourable locations from established stands) and establishment limitation (arrived seeds have species-specific requirements concerning temperature, soil moisture and light for germination; seed predation and herbivory of seedlings, as well as competition among seedlings, can lead to establishment failure). Second, even species successfully established on newly favourable sites need time to outcompete already present species established in the past (successional lag).

Recruitment limitation is partly captured in LPJ-GUESS, as the number of established saplings of a species also depends on the net primary production of the species in the simulated grid cell. In the general parameterization (Smith et al. 2001), however, the occurrence-independent background establishment normally dominates. Thus, the process representation of establishment in

LPJ-GUESS is not detailed enough to cover the various aspects of recruitment limitation, and the species-specific parameterization would require detailed ecological knowledge. However, that our model version (i.e. without recruitment limitation) correctly captures the time lag of climate change and vegetation response, allows the hypothesis that successional lags rather than recruitment limitation are indeed the reason. Definitively confirming this hypothesis, however, requires a model version that includes dispersal and possibly a more detailed representation of establishment, parameterized for European boreal forests. Snell et al. (2014) implemented dispersal for three temperate tree species in north-eastern North America whose historic migration rates they could reproduce in simulation experiments in an imaginary landscape. It would be crucial to combine this promising model development with the European species parameterization to assess the effect of dispersal limitation on range shifts.

Apart from the temporal pattern of GDD thresholds for *P. sylvestris* and *P. abies*, GDD are an essential bioclimatic limit in LPJ-GUESS: we can directly compare the species-specific parameter 'minimum growing degree days for establishment' ($GDD_{5,min}$ in **Table B1**) to the response curves in **Fig. 3.5**. For *P. abies*, the parameter value is 600 GDD, which fits the observed data very well - at least for 1978. Nonetheless, LPJ-GUESS overestimated *P. abies* beyond its current treeline, indicating that it is not climatically limited in Finnish Lapland. This concurs with the finding of Schibalski et al. (2014) that the relative importance of GDD in the *P. abies* models was lower than for *P. sylvestris* - evidence that temperature limitation is not what keeps *P. abies* from occupying the far north of Finnish Lapland.

For *P. sylvestris*, the parameter value of $GDD_{5,min}$ is 500 GDD (**Table B1**), which is much lower than any threshold (1978 or 2003) in the observations. Increasing the parameter for *P. sylvestris* from 500 to 625 GDD (suggested by the response curves in **Fig. 3.5**) should efficiently restrict *P. sylvestris* in the north (**Fig. 3.6**). Statistical fine-tuning such as this can improve LPJ-GUESS parameterization for a particular time (or place, e.g. Pappas et al. 2015). However, as we can already see from the climate change over the 25 years, this correlation changes over time and parameters would need to be adjusted again to effectively restrain the species in the model. Here, 'fitted' process-based models like LPJ-GUESS underlie the same equilibrium assumptions as do correlative models. They are also subject to the same problems when these assumptions are violated by applying the models to ongoing climate change. Snell et al. (2014), who advocate using dynamic global vegetation models (DGVM) such as LPJ-GUESS to simulate range shifts, are aware of this issue. They propose Bayesian methods for parameterization (Hartig et al. 2012, van Oijen et al. 2005) and point to 'next-generation DGVMs' (Scheiter et al. 2013) which simulate plant individuals with potentially unique trait combinations.

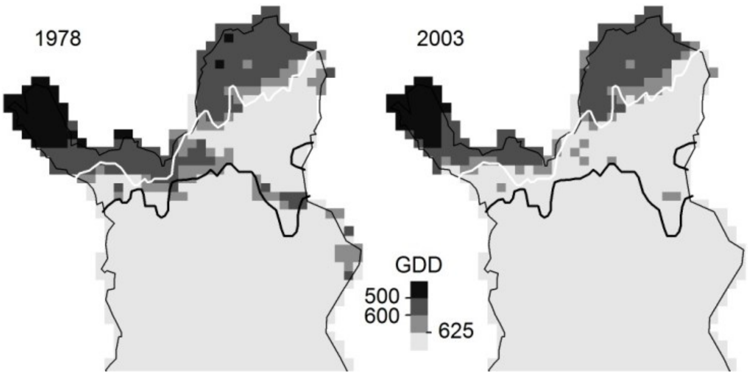

Figure 3.6. Maps of growing degree days for 1978 (1968-1977) and 2003 (1993-2002) with treelines of *P. sylvestris* (white) and *P. abies* (black). Treelines had not changed between 1978 and 2003 and are defined as the marginal sites occupied by the respective species.

3.4.3. Competition between tree species

3.4.3.1. Species imbalance

There was virtually no effect of the presence of the other two species on *P. abies* in the multi-species LPJ-GUESS run. The biomass values and spatial patterns of *P. sylvestris* and *B. pubescens*, however, were largely affected by *P. abies* presence. Especially *P. sylvestris* biomass distribution along the latitudinal gradient was distorted in the multi-species run (**Fig. 3.2**). In the single-species run, *P. sylvestris* biomass decreased gradually towards the north, correctly indicating that the species slowly approached its range limit due to unfavourable growing conditions in the model, albeit further north compared to the observations. In the multi-species run, however, highest *P. sylvestris* biomass was found in the north coinciding with the lowest *P. abies* (and *B. pubescens*) biomass. This suggests that *P. abies* was by far too competitive in the model. It also demonstrates that competition plays a pivotal role in LPJ-GUESS which is in agreement with its importance as a predictor in the correlative models of Schibalski et al. (2014).

The model's inability to correctly reproduce the occurrence pattern of especially *P. abies* in Northern Lapland is in accordance with recent studies applying LPJ-GUESS: in a Holocene vegetation reconstruction study, Miller et al. (2008) were not able to correctly model *P. abies'* occurrence in Finland and Sweden over time. In their simulations of the current treeline in Arctic Europe, Fang et al. (2013) found that LPJ-GUESS did capture the coniferous treeline, but failed to correctly predict species-specific treelines. *P. abies* occurred north of its observed treeline where it suppressed *P. sylvestris* as additional simulation experiments showed. This is in line with our findings, and Fang et al. (2013) attributed the competitive strength of *P. abies* to its shade tolerance.

3.4.3.2. Shade tolerance

Competition for light is crucial in closed-canopy forests as predicted in our simulations (incorrectly in the far north). Shade tolerance-related parameters in LPJ-GUESS include minimum light requirement for establishment, maximum establishment rate and growth-efficiency-related mortality (**Table B1**). Wramneby et al. (2008) demonstrated that LPJ-GUESS is highly sensitive to shade tolerance-related parameters and that unfortunately, the uncertainty of these parameters is very large. *P. abies* is ranked shade-tolerant in LPJ-GUESS giving it considerable advantage under light limitation (which is more probable in our case as total biomass was overestimated and thus shading must be greater than observed). On the other hand, *B. pubescens* is ranked shade-intolerant giving it the advantage of higher establishment rates and growth efficiency under optimum light conditions. Finally, *P. sylvestris* is ranked intermediate shade-tolerant with parameters between those of *P. abies* and *B. pubescens*. It is thus trumped by both competitor species, i.e. *P. abies* which tolerates shaded conditions as well as *B. pubescens* which benefits most efficiently from light abundance after disturbances. *P. abies* effectively distorted *P. sylvestris* and *B. pubescens* biomass distribution in the multi-species run, resulting in LPJ-GUESS's failure to correctly simulate the species balance observed in Finnish Lapland. We thus concur with Wramneby et al. (2008) in that shade tolerance is a very important trait in LPJ-GUESS which can dominate over other physiological differences between species (**Table B1**).

In the following, we discuss competitive advantages that *P. sylvestris* and *B. pubescens* might have over *P. abies* and why the two species apparently fail to play off their strengths in our simulations. These potential advantages include drought tolerance, lower nutrient demand, fire resistance, and susceptibility to other disturbances. Some processes are already implemented in the LPJ-GUESS version used for this study but might need to be re-parameterized for our application, while others require further model development.

3.4.3.3. Drought tolerance

P. sylvestris outcompetes *P. abies* on dry, acidic, nutrient-poor sites as known from field observations (Sutinen et al. 2005) and experiments (Ingestad 1979). Accordingly, dry conditions should favour *P. sylvestris* over *P. abies* and *B. pubescens* in LPJ-GUESS as it has 40 % of its roots distributed in lower soil layers compared to 20 % for the other two species, is thus able to take up more water at low soil moisture contents (see water uptake function, Appendix B, **Fig. B6**) and requires less soil moisture for establishment (awc_{min}, **Table B1**). Soil texture in LPJ-GUESS influences the water holding capacity and thermal diffusivity of a soil, but Wolf et al. (2008a) showed that the vegetation outcome is rather insensitive to different soil moisture and soil temperature representations. LPJ-GUESS is, however, very sensitive to changes in soil depth. As no soil depth data was available for the study region, a uniform soil depth of 1.5 m was assumed. However, shallower soils do exist, at least locally. This simplification thus weakens *P. sylvestris*' advantage due to drought tolerance. Recently, topographic effects on soil hydrology have been included in LPJ-GUESS (LPJ-DH; Tang et al. 2014), which might lead to more realistic simulations of competitive balances along topographic gradients.

3.4.3.4. Nutrient limitation

Apart from drought tolerance, lower nutrient demand is a species trait favouring *P. sylvestris* over *P. abies*. A general proxy for soil fertility was also one of the most important predictors in Schibalski et al. (2014). Above, we discussed that the general implementation of nitrogen limitation in LPJ-GUESS (Smith et al. 2014) could reduce the biomass overestimation we found in our application. In order for nutrient limitation to affect the competitive strength of individual species in LPJ-GUESS, however, it would need to be implemented species-specifically, e.g. comparable to the species-specific water uptake function (Appendix B, **Fig. B6**) by Schurgers et al. (2011). It is questionable, however, whether we have enough process understanding to include species-specific responses to soil nutrients in a process-based framework. Mixed in with issues of soil fertility are also management decisions: on dry and nutrient poor sites, forest managers will favour the superior species *P. sylvestris* by actively thinning *P. abies* and *B. pubescens*, which are less successful on these sites anyway (Äijälä et al. 2014). This positive feedback could potentially increase the competitive advantage of *P. sylvestris* over *P. abies* and *B. pubescens*. Empirical response functions could be included in LPJ-GUESS to account for the effects of nutrient limitation (including the additional effect of active thinning on managed poor sites), but this would be subject to the same criticism we raise concerning bioclimatic limits reducing the generality of 'fitted' process-based models.

3.4.3.5. Fire

Susceptibility to disturbance is another characteristic that differentiates between species and thus influences the competitive strength of a species if disturbances play an important role. Under climate change, disturbance regimes are expected to change regarding timing, frequency, intensity and extent, thus potentially increasing the importance of disturbances for forests in future (Dale et al. 2001). In LPJ-GUESS, two types of disturbances are already implemented: fire and a generic biomass-destroying disturbance that kills all individuals in a patch.

P. sylvestris is well adapted to survive moderate fires by its thick bark (heat insulation), high crown base (preventing crown scorching) and deep root system (Fernandes et al. 2008). This is collectively reflected in LPJ-GUESS by a four times greater probability to survive fires of *P. sylvestris* compared to *P. abies* and *B. pubescens* (r_{fire}, **Table B1**). Thus, frequent fires could favour *P. sylvestris* over *P. abies* in our simulations. However, since the beginning of the 20th century, anthropogenic fire suppression in Fennoscandia has greatly extended the interval of forest fires (Zackrisson 1977). Additionally, the mean fire interval increases from 20 years in the south (58 °N, 1401-1998) to more than 500 years in the north (69 °N, 1400-2001, Larjavaara et al. 2005). Thus, forest fires in Finland today are infrequent, small (the mean burnt area for the whole of Finland was 537 ha in 1994-2003, Ylitalo 2013), and no longer play an important role in forest ecology. In line with this, fires did not play an important role in our simulations, as LPJ-GUESS underestimates natural fire cycles in northern Scandinavia.

3.4.3.6. Other disturbances (wind damage, pest calamities, herbivory)

Other disturbances, however, do play an important role in our study region. In Lapland, a higher proportion of forest land is classified as damaged to some degree (58.5 %) compared to the rest of the country (45.6 %), mainly due to the direct and indirect effect of the harsher climate (Ylitalo 2013). Disturbances in Lapland are mainly due to abiotic factors (wind, snow, frost, drought, nutrient imbalance and fire), fungi and moose or reindeer damage (Ylitalo 2013). Importantly, however, the effect on species differs: *P. sylvestris* is less affected by abiotic disturbances, but more prone to insect damage than *P. abies* and *B. pubescens* (Nevalainen et al. 2010). Consequently, it is difficult to define an average return time for patch-destroying disturbances as currently implemented in LPJ-GUESS because not all species (i.e. the whole patch) are affected equally. Here, the generalized process representation that encompasses a wide variety of potential disturbances fitting for different ecosystems in global applications is not detailed enough for our regional application.

There are, however, attempts to implement more detailed process representations of specific disturbances. In their version of LPJ-GUESS, Lagergren et al. (2012) implemented species-specific storm sensitivity. Wind damage is indeed one of the most common causes of tree mortality in Finland (besides snow and fungi, Nevalainen et al. 2010) and causes huge economic losses (Hanewinkel and Peyron 2013). Lagergren et al. (2012) effectively weakened *P. abies* (storm sensitivity = 1.0) compared to *P. sylvestris* (0.5) and deciduous species (0.1) which is in line with the ranking of these three species in terms of resistance to breakage from experiments (Peltola et al. 2000). It also confirms the role species-specific susceptibility to disturbances could play in promoting species balance in process-based models.

Wind damage increases the probability of pest calamities by providing brood trees for e.g. *Ips typographus* L., the spruce bark beetle (Komonen et al. 2011). Jönsson et al. (2012) coupled LPJ-GUESS with an *I. typographus* population model and thus successfully simulated observed outbreaks patterns across Sweden. In their model version of LPJ-GUESS, an additional type of tree mortality, only affecting *P. abies*, was damage by *I. typographus*. A similar approach is needed for *B. pubescens* and *Epirrita autumnata* L., the autumnal moth. Mass outbreaks of *E. autumnata* in Lapland have caused the *B. pubescens* treeline to retreat (Lehtonen and Heikkinen 1995).

Observations of recent outbreaks of two species of moths (*E. autumnata* and *Operophtera brumata* Bkh.) in northern Fennoscandia suggest that climate warming will aggravate the damaging impact of calamities on *B. pubescens* forests (Jepsen et al. 2008).

In Lapland, the effect of herbivores differs greatly between tree species, seasons and regionally. Apart from insect calamities discussed above, Kozlov (2008) found foliar damage of *B. pubescens* by background insect herbivory to increase from the north (1 - 2 % at 70°N) to the south (5 - 7 % at 60°) of Fennoscandia. During summer, *B. pubescens* forests are intensely browsed by reindeer (Stark et al. 2007), while reindeer dig for lichens in winter, mechanically damaging *P. sylvestris* and *P. abies* seedlings (Helle and Moilanen 1993). High reindeer densities might even limit *P. sylvestris* recruitment to the extent of preventing treeline advance (Aakala et al. 2014). On the other hand, reindeer grazing reduces competition for *P. sylvestris* (which is not normally grazed itself), esp. *Cladina* lichens which negatively affect *P. sylvestris* mycorrhiza development (Brown and Mikola 1974). Thus, direct and indirect effects of herbivores differ among tree species, and net effects are far from unanimously discussed (Weisberg and Bugmann 2003) which complicates the inclusion of herbivory in LPJ-GUESS. Nonetheless, Zöckler et al. (2008) did include the effect of reindeer grazing in LPJ-GUESS simulations via rule-based updates of the resulting vegetation maps (grid cells in which reindeer population was estimated to be high by a separate model were forced from ‘boreal forest’ to ‘open tundra’ during post-processing). This very simplified way of coupling LPJ-GUESS with reindeer predictions was sufficient to analyze the development of open habitat for tundra birds in Zöckler et al. (2008). But for an application in our case, process representation would need to be refined to offset direct and indirect, positive and negative effects on individual tree species.

3.4.4. Scale issues with process-based vegetation models

As similar ‘fitted’ process-based dynamic vegetation models, LPJ-GUESS has been parameterized at certain scales (globally by e.g. Smith et al. (2014), for Europe by Hickler et al. (2012)). Generally, an application on a smaller scale requires accounting for study region-specific processes and the ecology of the main tree species (e.g. Hickler et al. (2004) and Tang et al. (2012) for northeastern U.S.; Hickler et al. (2012) for Europe; Seiler et al. (2014) for Bolivia). Zhang et al. (2013) applied LPJ-GUESS to the whole Arctic at an accordingly coarse resolution and reported a good match between observed and predicted treelines, albeit of plant functional types rather than species. Furthermore, they assessed potential natural vegetation - a common LPJ-GUESS application (e.g. Zhang et al. 2014, Zhang et al. 2013, Hickler et al. 2012, Wolf et al. 2008b) but difficult to validate with observations and recently critically discussed (Loidi and Fernández-González 2012, Chiarucci et al. 2010). In our study region, even the arctic version of LPJ-GUESS (Zhang et al. 2013) incorrectly predicted the whole of Finnish Lapland to be a boreal evergreen forest (while the northernmost part is only occupied by *B. pubescens*, **Fig. 3.3**). The flexible model design of LPJ-GUESS makes regional adjustments possible, but the parameterization is in many cases challenging. One European parameterization, which reproduces European-wide potential natural vegetation types (Hickler et al. 2012), is clearly not applicable to the study area here, and we expect that the same is true for other smaller-scale regional applications.

3.5. Conclusions

We used insights from a correlative model study to guide our analysis of the results of a 'fitted' process-based dynamic vegetation model which helped reveal crucial shortcomings in its general parameterization for our regional application. Our simulations showed that LPJ-GUESS, with its generalized European parameterization (sufficient for the continental scale), overestimated *P. abies* and consequently total forest biomass and simulated the range limit of especially *P. abies* too far north when applied to northern Finland (aim (i)). We discussed possible reasons: the parameterization of processes already implemented in the model, in particular competition between species and disturbance, as well as the lack of processes in the model which apparently are very important in boreal forests (nutrient limitation, forest management). Concerning competition between species, we specifically discussed shade and drought tolerance, nutrient limitation, fire resistance, and susceptibility to other disturbances like storm and herbivory with respect to the ecology of boreal forests and Fennoscandia in particular (aim (iii)). This discussion can equally inform other modelling studies of *P. sylvestris*, *P. abies* and *B. pubescens* in Scandinavia, and of boreal forests in general. We reviewed recent model developments in the LPJ-GUESS community relevant to boreal forests, each of them promising in their particular application but regrettably separate from each other. A new model version for boreal forests that consistently integrates the considerable progress made by the different working groups would immensely improve the applicability of LPJ-GUESS on the regional scale.

On a different note, we used findings from a correlative model study about the limited transferability of statistical relationships to stress the similar limitations of 'fitted' process-based models like LPJ-GUESS which use bioclimatic limits to restrain species in their simulations. Our study, covering merely 25 years, already revealed a shift in statistical thresholds calling for re-parameterization (aim (ii)). We thus advise the same caution appropriate to correlative models when applying 'fitted' process-based models, especially in climate change studies.

Acknowledgements

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Appendix B

Additional information on LPJ-GUESS parameterization, input data and results

Species characterization in LPJ-GUESS (see also Hickler et al. 2012)

Trees establish under suitable temperature ($T_{c,min}$, $T_{c,max}$ and $GDD_{5,min}$), soil moisture (awc_{min}) and light conditions (par_{min}) which differ for each species (**Table B1**). The number of actual saplings is drawn from a Poisson distribution with a species-specific expectation (a function of maximum establishment rate est_{max} and constant α, **Table B1**). Each sapling is then allocated an initial biomass and size for the first year.

Trees grow in biomass, height, and diameter as the net primary production accrued by an average individual per simulation year is allocated to leaves, fine roots, and sapwood, following a set of prescribed allometric relationships (Sitch et al. 2003). Species-specific parameters affecting growth (**Table B1**) describe the growth form ($k_{la:sa}$, k_{allom1}), foliage (SLA, a_{leaf}), phenology (k_{chillb}), tissue turnover ($turn_{leaf}$, $turn_{sapwood}$) as well as soil water uptake and thus drought resistance (z_1, k_{uptake}) of each species.

Tree mortality in LPJ-GUESS is caused by i) background mortality related to species longevity (a_{ind}), ii) low growth efficiency (greff), which is strongly influenced by competition, particularly for light, iii) winter temperatures falling below a species-specific limit ($T_{c,min}$), and iv) fire (r_{fire}, **Table B1**).

The following parameters are determined by higher-level classification and thus do not differ between the three tree species investigated in this study. All three species are *trees* and thus share the C3 photosynthetic pathway where photorespiration reduces the efficiency of photosynthesis. Thus, these species are more sensitive to CO_2 increase, which could enhance their productivity as opposed to e.g. tropical grasses with the C4 pathway. They are also all *boreal* species sharing higher respiration rates and lower optimum temperatures for photosynthesis compared to temperate species.

Table B1. Selected species-specific parameters in LPJ-GUESS for *P. sylvestris*, *P. abies* and *B. pubescens*, affecting the competition between these three species.

parameter	meaning	*P. sylvestris*	*P. abies*	*B. pubescens*
shade_ tolerance	shade tolerance class; determines par_{min}, est_{max}, α, $turn_{sapwood}$, greff	intermediate	tolerant	intolerant
establishment				
$T_{c,min}$	min. coldest month mean temperature [°C] [1]	-29	-29	-
$T_{c,max}$	max. coldest month mean temperature [°C] [1]	-1.0	-1.5	-
$GDD_{5,min}$	min. growing degree days (5°C)	500	600	350
awc_{min}	min. fraction of plant-available water content [2]	0.25	0.43	0.5
par_{min}	min. forest floor PAR [3] [MJ m^{-2} day^{-1}]	2.0	1.25	2.5
est_{max}	max. establishment rate [saplings m^{-2} $year^{-1}$]	0.1	0.05	0.2
α	recruitment shape parameter; negatively affects establishment rate as canopy closes	6	2	10

Table B1. Continued.

growth				
$k_{la:sa}$	leaf area to cross-sectional area ratio	2000	4000	5000
k_{allom1}	allometric constant; affects crown area	150	150	250
SLA	specific leaf area [m^2 kgC^{-1}]	9.3	9.3	24.3
a_{leaf}	leaf longevity [years]	2	4	0.5
k_{chillb}	chilling requirement for budburst (constant)	100	100	400
$turn_{leaf}$	leaf turnover ratio	0.5	0.25	1.0
$turn_{sapwood}$	sapwood to heartwood turnover ratio	0.065	0.05	0.08
z_1	fraction of roots in upper soil layer	0.6	0.8	0.8
k_{uptake}	shape parameter of water uptake function	0.5	0.86	1.0
mortality				
a_{ind}	max. non-stressed longevity [years]	500	500	200
greff	growth efficiency parameter [g C m^{-2} leaf^{-1} year^{-1}]; defines inflection point of sigmoid mortality function	80	40	100
$T_{c,min}$	min. coldest month mean temperature [°C] [1]	-30	-30	-
r_{fire}	probability of surviving fires	0.4	0.1	0.1

[1] over the last 20 yrs; [2] growing-season average in the upper soil layer; [3] photosynthetically active radiation

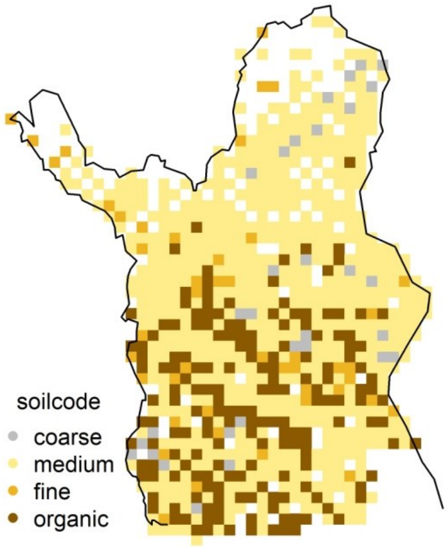

Figure B1. Map of the soil characteristics classified into the nine-class soil code of LPJ-GUESS (Sitch et al. 2003, Table 4).

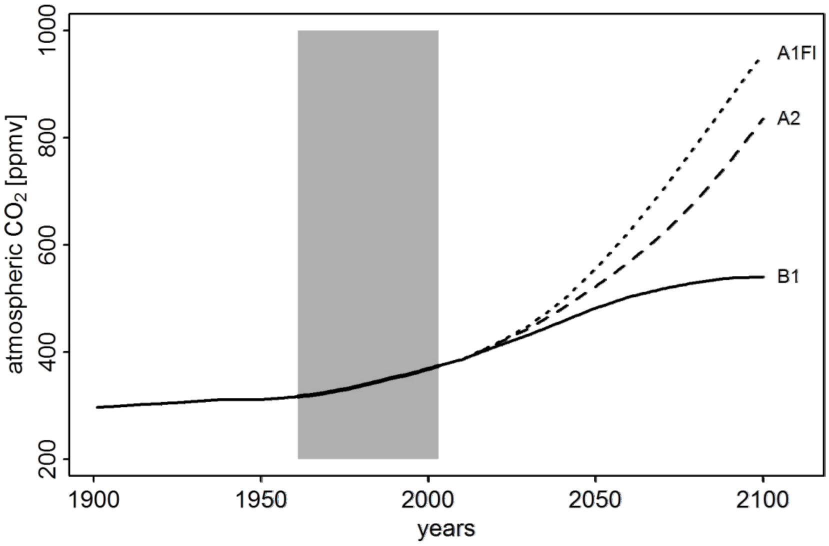

Figure B2. Atmospheric CO2 content [ppmv] used as LPJ-GUESS input (annual values). Our simulation period is highlighted as grey box. For reference, predicted future CO2 concentrations are shown for emission scenarios A1FI, A2 and B1.

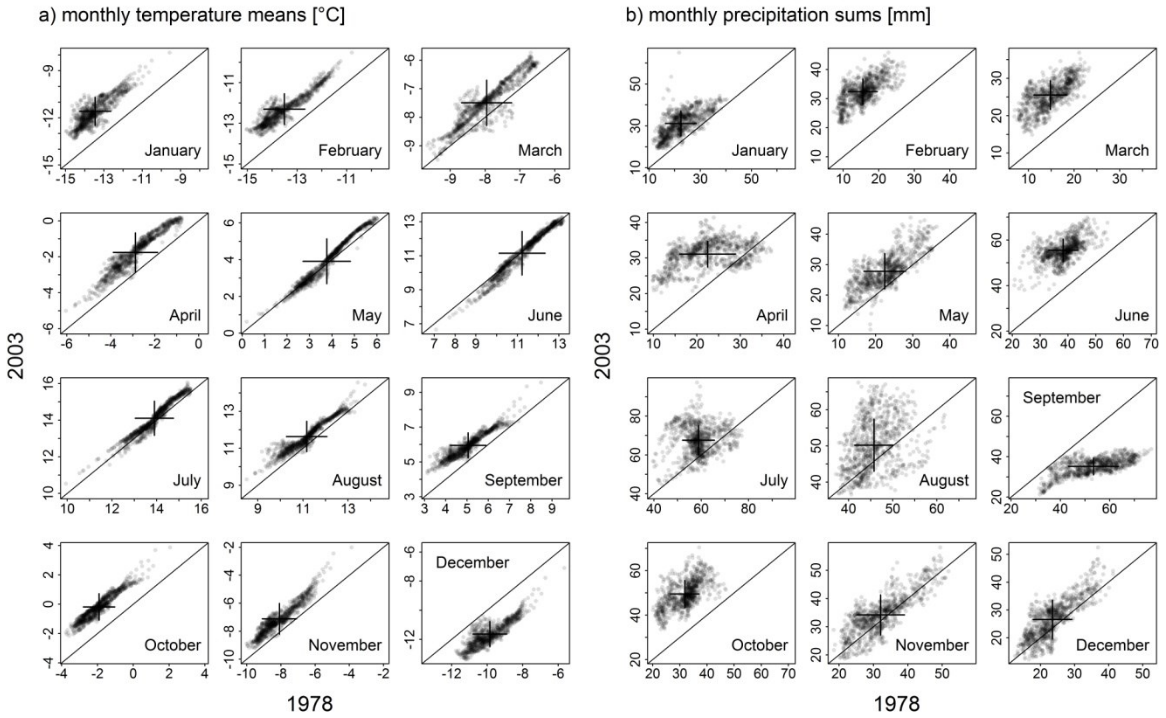

Figure B3. Comparison of a) monthly mean temperatures and b) monthly precipitation sums between 1978 (1968-1977) and 2003 (1993-2002). Plus signs indicate median (intersection) and standard deviation (length of the arms). The difference between 1978 and 2003 is significant in all cases ($p < 0.001$, Wilcoxon rank sum test).

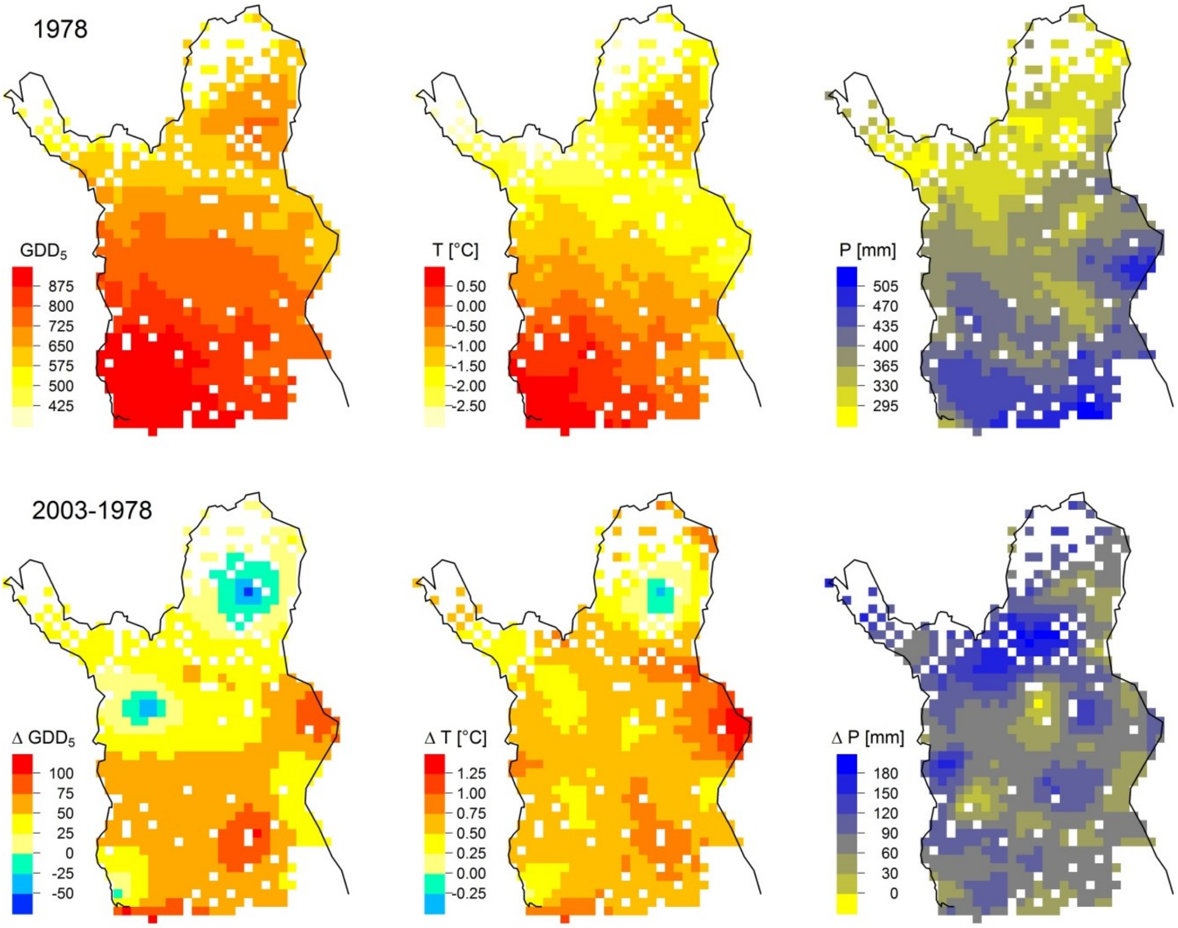

Figure B4. Maps of growing degree days (5°C), annual mean temperature [°C] and annual precipitation sum [mm] in 1978 (upper row) and changes from 1978 to 2003 (lower row).

Figure B5. See next page.

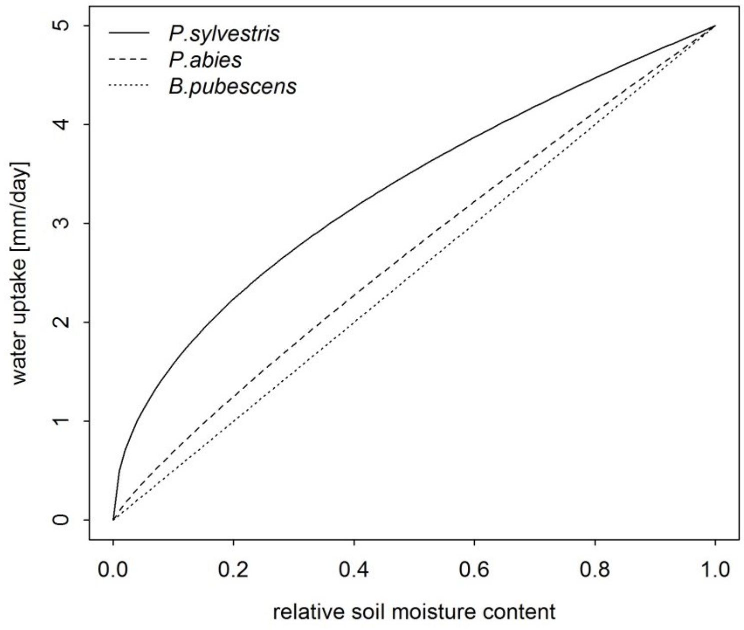

Figure B6. Water uptake as a function of relative soil moisture content (Schurgers et al. 2011), parameterized for *P. sylvestris* (k_{uptake} = 0.5), *P. abies* (k_{uptake} = 0.86), and *B. pubescens* (k_{uptake} = 1.0, **Table B1**).

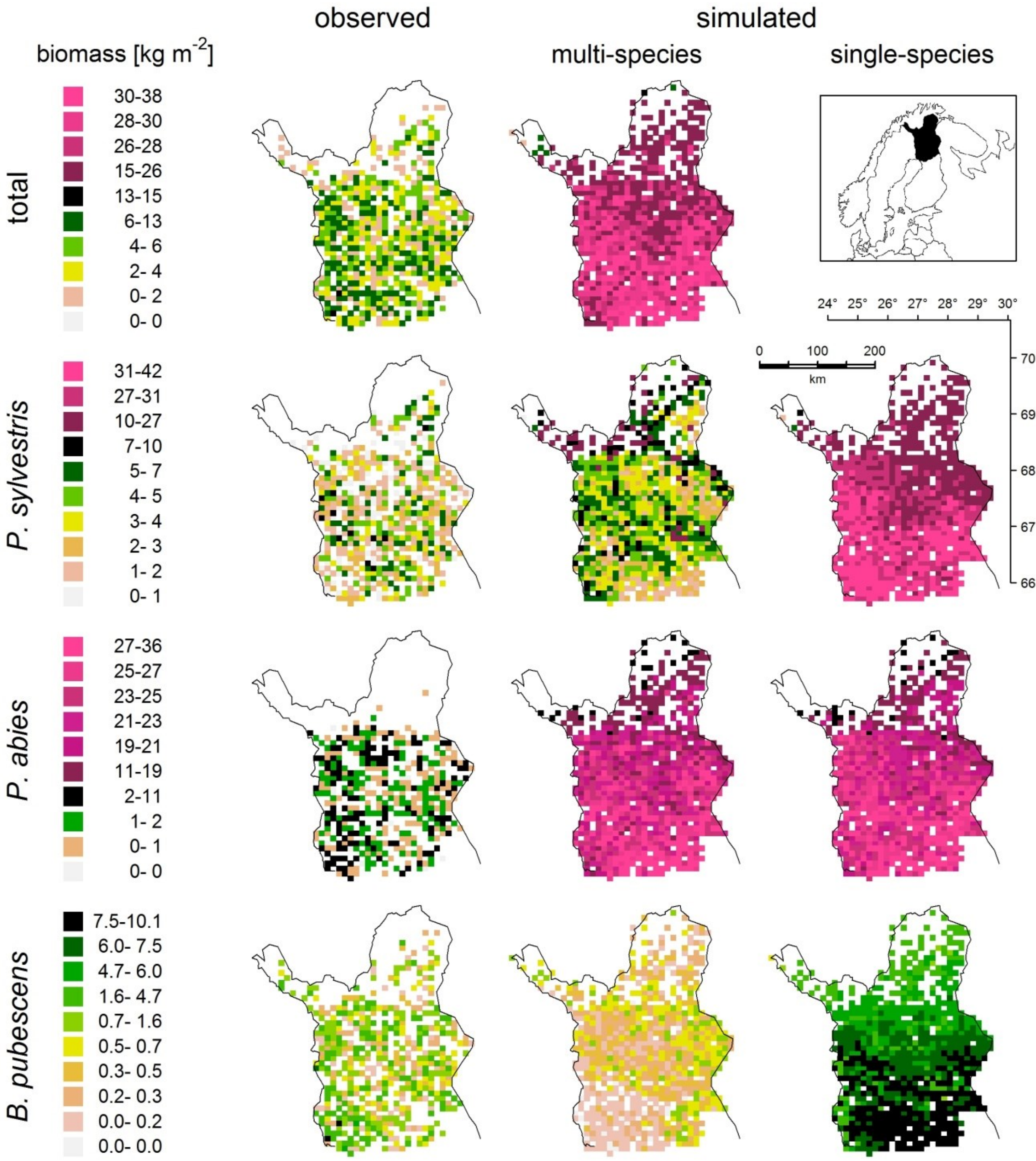

Figure B5. Map comparison of total and species-specific biomass [kg m^{-2}]: MS-NFI data (2011) and results from multi-species and single-species LPJ-GUESS runs (averaged over 1994-2003). ‘Natural’ colours (white to black) cover the range of the observed values (i.e. the upper limit of the black class is always the maximum of the respective MS-NFI data); ‘artificial’ colours (shades of magenta) cover the predictions that exceed the observed value range (model overestimation).

4. Resilience of coastal vegetation under environmental change analyzed by coupling a statistical and a process-based model [3]

Abstract

Resilience analysis of ecological systems is a major research focus covering a wide range of research questions from biodiversity conservation to ecosystem (service) management. Model simulations can assess resilience, measured as the return time to conditions prior to a disturbance. This requires process-based models (PBM) that implement relevant processes like regeneration and reproduction and thus successfully reproduce transient dynamics. Such models are often complex and thus limited to either short-term or small-scale applications, whereas many research questions require species predictions across larger spatial and temporal scales. We suggest a framework to couple a PBM and a statistical species distribution model (SDM) which transfers the results of a resilience analysis by the PBM to SDM predictions. The resulting hybrid model combines the advantages of both approaches: the convenient applicability of SDMs and the relevant process detail of PBMs in abrupt environmental change situations. First, we simulate disturbance events of a certain magnitude and compare *treatment* and *control* communities (resilience analysis by PBM). We then condense simulated species responses into two measures: adjustment times and *control-treatment* differences which we then use to correct SDM predictions.

To demonstrate our framework, we investigate the effect of abrupt groundwater level and salinity changes of one-year duration on coastal vegetation at the German Baltic Sea. We found two example species to be largely resilient. Only salinity increases exceeding 2 g l^{-1} did result in longer adjustment times. Consequently, modifications of SDM predictions consisted mostly of smoothing out peaks in the occurrence probability that were not confirmed by the PBM. We thus found the SDM to underestimate the resilience of vegetation to the disturbances investigated, which we could correct with the proposed model coupling. Although demonstrated with two example models, our flexible framework can easily be applied to other PBM and SDM types.

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[3] An article with equivalent content has been submitted as:
Schibalski, A, Körner, K, Maier, M, Jeltsch, F, Schröder, B. Resilience of coastal vegetation under environmental change analyzed by coupling a statistical and a process-based model. Ecological Applications (in review).

4.1. Introduction

Resilience (Carpenter et al. 2001, Holling 1973) is a major research focus covering a wide range of research questions from biodiversity conservation (Bengtsson et al. 2003, Walker 1995) to ecosystem (service) management (Kohler et al. 2017, Winfree and Kremen 2009, Folke et al. 2004). While ecological resilience is defined as the magnitude of disturbance that can be absorbed before the system changes its structure, engineering resilience is defined by the resistance to disturbance and the speed of return to the equilibrium after a disturbance (Holling 1996). At a lower level, the resilience of vegetation, i.e. plant communities, populations or individual species, is an important aspect of ecosystem resilience. Resilience and resistance of vegetation to various disturbances have been studied by field experiments, remote sensing monitoring and modeling. Field experiments compare vegetation treated with a simulated disturbance of a given magnitude with control samples after certain time periods. By this method, MacGillivray et al. (1995) assessed the resilience of five herbaceous communities to fire, frost and drought, Cole (1995) analyzed the resistance, tolerance and resilience of 18 vegetation types to trampling, and Speed et al. (2010) studied the response to herbivory by geese on the level of community, plant functional type, and species. Another way to observe resilience is comparing remote sensing data (usually, the normalized difference vegetation index, NDVI) before and after naturally occurring disturbances as done by Díaz-Delgado et al. (2002) and Bisson et al. (2008) for wildfires in the Mediterranean as well as De Keersmaecker et al. (2015) for short-term climate anomalies on the global scale. A third way to study resilience is modeling: either by examining the mathematical properties of differential equations (see Meyer (2016) for a mathematical review of resilience in ecology, and Yizhaq et al. (2005) and Ridolfi et al. (2006) for examples of vegetation-hydrology feedbacks) or by dynamic simulations. The latter uses models to ‘observe’ the response to disturbance - comparable to field experiments and remote sensing monitoring - by simulating and comparing time series of e.g. vegetation development with and without disturbances. Models from both vegetation and animal ecology applied in this context include non-spatial coupled differential equations (van de Koppel and Rietkerk 2004, Ortiz and Wolff 2002) and transition matrix models (Done 1987), as well as spatially explicit individual-based (Cordonnier et al. 2008, Foppen et al. 1999) and other simulation models (Mumby et al. 2006). Despite their differences in complexity, temporal (and spatial) resolution and process detail, all these models can be classified as process-based models (PBM). What makes PBMs inherently fit for resilience studies and sets them apart from statistical models, is their potential for continuous simulation over time, i.e. one time step depends on the conditions of the previous time steps. PBMs thus explicitly account for the history of sites, and they can capture temporal patterns like succession and other transient dynamics, which is a prerequisite of resilience analysis. The required detail of process, however, leads to complex models that require very specific data to parameterize and a lot of computational time and effort to run large-scale, long-term simulations. The trade-off between spatial and temporal resolution restricts long-term simulations (often needed to fully assess the response to disturbance) to small spatial extents. While these process-based simulation models allow the analysis of resilience, they are not suitable for large-scale, long-term predictions at the same time.

Statistical species distribution models (SDM) which mathematically describe observed relationships between the environment and the distribution of a species (Schröder 2008) have proven to be a convenient tool for large-scale, long-term application and are extensively used (Elith and

Leathwick 2009). Their advantages over PBMs are (i) less computational effort and (ii) more flexibility concerning required input data. However, SDMs are based on assumptions inconsistent with resilience analysis: they assume the ecosystem to be in equilibrium (Guisan and Theurillat 2000), they do not allow extrapolation beyond the training data range (Zurell et al. 2012a), and they assume stationarity of the estimated relationships across space and time (Schibalski et al. 2014). All of these assumptions are frequently violated when studying abrupt environmental changes (disturbances) by means of resilience analyses. In contrast to PBMs, SDMs for a given species compute the habitat suitability of a certain site for discrete points in time assuming stable conditions, thus ignoring relevant processes like dispersal (or its limitation) in space, succession over time and other transient dynamics. Therefore, SDMs predict instant responses to disturbances that do not affect the predictions for subsequent points in time, thus often overestimating the ability of species to recover from disturbances. At the same time, they underestimate the ability of species to persist for some time under unsuitable habitat conditions to either eventually go extinct if conditions remain unsuitable (extinction debt, Hylander and Ehrlén 2013) or to have survived an intervening period of low suitability (resistance; see distinction between resilience and resistance in Lepš et al. 1982).

Therefore, the aim of this study is to couple both model approaches combining their strengths, i.e. the speed and convenience of statistical modeling and the relevant detail of process-based modeling. We propose a flexible framework for coupling an SDM and a PBM that can be easily extended to other model types than used in our illustrative example. In most existing model coupling approaches (‘hybrid models’, Dormann et al. 2012), statistically derived habitat suitability maps provide input data for spatially explicit PBMs (e.g. Zurell et al. 2012b, Söndgerath and Schröder 2002). In contrast, our approach first assesses the resilience of individual plant species by simulating their response to abrupt, temporary environmental changes (i.e. disturbances) with the PBM. In a second step, we use the results of the resilience analysis to modify predictions of time series by the SDM. The resilience analysis also already indicates the potential error of “unassisted” SDMs, i.e. if resilience is high and thus recovery or adaptation times are short, the deviation of the PBM predictions from the SDM predictions will be small or short-term.

To demonstrate the framework, we use environmental and vegetation data from the collaborative research project COMTESS (Sustainable coastal land management: Trade-offs in ecosystem services). COMTESS investigated the impact of climate change, sea level rise and different land management options on the hydrological conditions, consequently the distribution of coastal vegetation and ultimately ecosystem service provision of coastal areas at the Baltic and North Sea coast. Here, we used plot-level data on species distributions and environmental conditions to estimate SDMs for 61 species. Additionally, we used collected data on plant traits to adapt and parameterize an existing individual-based model (IBC-grass, Weiss et al. 2014). This PBM explicitly models the response of plant individuals to salt and water stress (resistance) as well as regenerative and reproductive processes (resilience) with high temporal and spatial resolution. Modeled time series of hydrological conditions (2010-2100) served as example case of environmental variables undergoing abrupt, temporary changes (disturbance).

In this study, we i) analyze the resilience of coastal plant species to abrupt, temporary changes of groundwater level and salinity by simulating species responses to disturbances of different magnitudes with a PBM. Additionally, we ii) propose a novel, flexible framework to couple a statistical and a process-based model that enables large-scale, long-term predictions of species distributions accounting for the effects of transient dynamics in the face of abrupt environmental changes.

4.2. Materials and methods

4.2.1. Illustrative example: coastal vegetation facing climate change and sea level rise

The following data, collected on 318 sites along the German, Danish and Dutch Baltic and North Sea coast (3.7-13.4°E, 51.3-56.3°N, Appendix C1, **Fig. C1.1**), was used to estimate SDMs (see *section 4.2.2*): presence/absence of coastal plant species (from a total pool of 230 species, 61 species were abundant enough to fit statistical models), groundwater level [cm above soil surface] (biweekly time series, August 2011 – December 2012), groundwater electrical conductivity [mS cm^{-1}] (same temporal resolution; transformed into groundwater salinity [g l^{-1}] following Fofonoff and Millard Jr. 1983) and biomass removal [%] (difference in biomass amount inside/outside grazing exclosures over whole growing period). In addition, the following data on plant traits was used to parameterize an existing PBM (see *section 4.2.3*): seed mass, single dry weights of plant components (leaves, stems, flowers and seeds), maximum individual plant mass, specific leaf area, spacer length and biomass, releasing height and canopy height. See Cebrián-Piqueras et al. (2017) for a detailed description of data collection in the COMTESS project.

Mean annual groundwater levels ranged from -100 cm (maximum depth of measurement pipe) to 51 cm (mean ± standard deviation: -35 ± 27 cm), and mean annual groundwater salinity from .03 to 26.9 g l^{-1} (mean ± standard deviation: 8.2 ± 8.3 g l^{-1}) across all 318 sites. Biomass removal ranged from 0 to 96 % (mean ± standard deviation of sites with agricultural use: 52 ± 28 %), and half of the sites (160) were fallows (i.e. not grazed or mown). Covering a wide range of groundwater level and salinity values in space ensured that possible future conditions occurring in long-term simulations (2010-2100) were included in the training data (space-for-time substitution, Blois et al. 2013, Pickett 1989).

Using WETTREG climate data (Enke et al. 2005; realization 5a) and assuming a linear sea level rise until 2100 of 1.05 m, Kliesch et al. (2016) applied FEFLOW (Diersch 2014) to simulate annual time series (2010-2100) of groundwater level [cm] and salinity [g l^{-1}] for hydrotopes (polygons with homogeneous hydrological and soil characteristics) in space. Land use intensity (biomass removal by grazing or mowing) was derived based on today's land use and assumed constant over time. We applied the SDMs to this spatio-temporally explicit data to create our illustrative example.

For our example case, we selected one of 20 scenario combinations regarding climate change (IPCC emission scenario A2, IPCC 2007), sea level rise (1.05 m, high-end estimate by the BALTEX Assessment of Climate Change for the Baltic Sea Basin, Grinsted 2015) and land management (business-as-usual) investigated by COMTESS. We chose one of the four COMTESS study sites: Michaelsdorf (907 ha; 61 hydrotopes; 12.56°E, 54.36°N) a peninsula in Northeastern Germany reaching into the Saaler Bodden, sheltered from the open Baltic Sea by offshore island Darss (**Fig. 4.1**). The study region is low-lying (50 % of the area < 0.5 m.a.s.l.), heavily drained by ditches and two pumping stations and protected from waves by a low sea wall (**Fig. 4.1**). We excluded two settlements (2 hydrotopes) as well as forested areas (17) and two small fields (2) at higher elevations from vegetation modeling (61 – 21 = 40 hydrotopes for vegetation modeling). The main part of the peninsula is intensively (33 %) and extensively grazed grassland (25 %) with a coastal reed belt without agricultural use (8 %). As hydrological simulations show, elevated areas (> 4 m.a.s.l.) of the study region exhibit low but very variable groundwater levels and no salinization (**Fig. 4.1**). In contrast, low-lying areas exhibit high groundwater levels which are kept relatively constant over time by pumping and drainage (see pumping rates in **Fig. C1.2**, Appendix C). However, water management cannot prevent the salinization of low-lying areas: mean groundwater salinity rises by 75 % from 1.6 g l^{-1} in 2010 to 2.7 g l^{-1} in 2100 (**Fig. 4.1**). In contrast to thick clay layers insulating the hinterland of the North Sea coast from salinization (de Louw et al. 2010), sandy, permeable soils dominate the German Baltic Sea coast (Forster et al. 2003). Thus, sea level rise directly translates into increases of groundwater level (mitigated by increased pumping) and salinity in the low-lying hydrotopes along the coastline (**Fig. 4.1**). We selected three example hydrotopes: (A) a low-lying (0.37 m.a.s.l.), extensively used (35 % biomass removal) coastal reed which is as saline as the adjacent Bodden water (rising from 4.4 g l^{-1} in 2010 to 5.3 g l^{-1} in 2100) and projected to be permanently inundated from 2062 (**Fig. 4.1**); (B) an equally low-lying (0.34 m.a.s.l.) intensively used (80 % biomass removal) grassland with lower groundwater levels (even decreasing towards 2100 as lower precipitation (**Fig. C1.2**, Appendix C1) is not offset by sea level rise) and lower salinity (**Fig. 4.1**); and (C) a high-lying (2.22 m.a.s.l.), thus dry (groundwater level < -2 m) and non-saline (rising from 0 g l^{-1} in 2010 to 0.07 g l^{-1} in 2100), intensively used (81 % biomass removal) grassland close to the settlement, field and forests in the south-west of the study region.

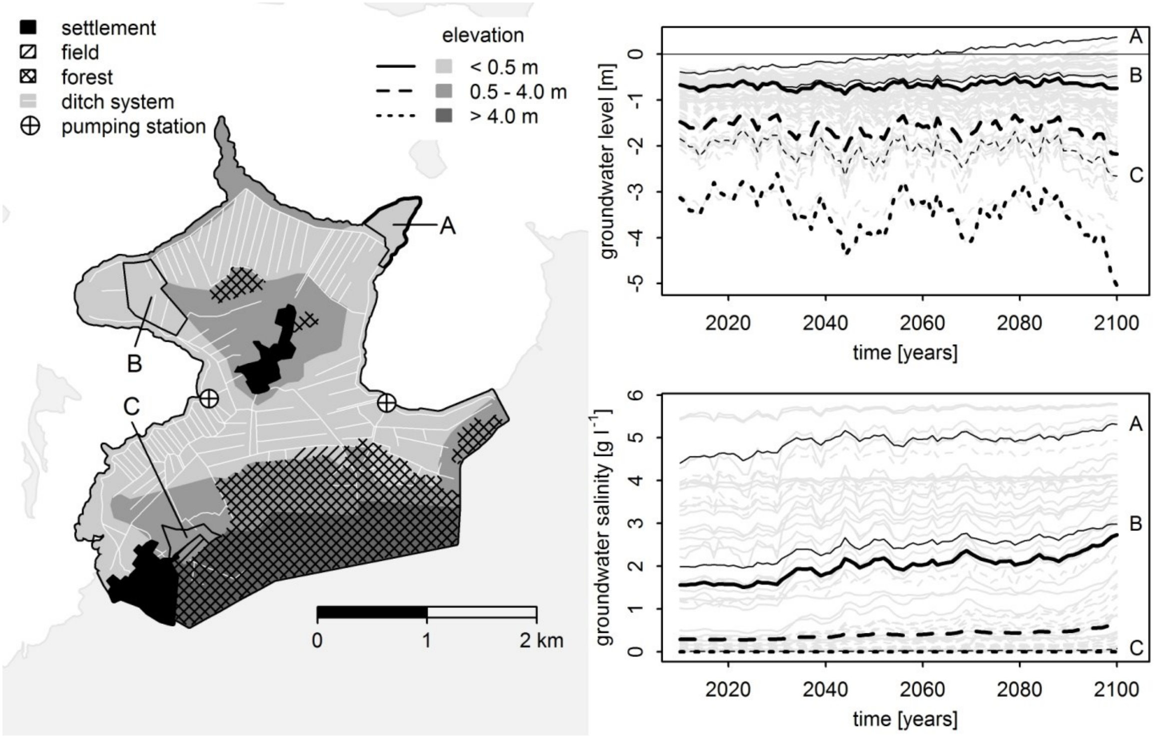


Figure 4.1. Map of study area Michaelsdorf with elevation classes and land use types (left) and time series of groundwater level and salinity (right). Single polygon time series (n=61) in grey with elevation class signified by line type; area-weighted mean of all polygons belonging to one elevation class in bold. Polygons A, B, C are examples revisited in **Fig. 4.11** and described in *section 4.2.1*. See **Fig. C1.1** in Appendix C1 for regional context.

4.2.2. Statistical species distribution models

We used the data described in *section 4.2.1* to fit boosted regression trees (BRT) as an example for statistical species distribution models in our framework. Predictors were mean annual groundwater level [cm], mean annual groundwater salinity [g l^{-1}] (both aggregated from biweekly measurements, see *section 4.2.1*) and annual biomass removal [%], and the response was species presence/ absence. Boosted regression trees are a combination of classic statistical models (classification and regression trees) and advanced machine learning methods (boosting, Elith et al. 2008). They have been routinely and successfully applied to similar ecological data and studies as ours (Valle et al. 2013, Revermann et al. 2012, Zurell et al. 2009, Guisan et al. 2007a, Leathwick et al. 2006, Elith et al. 2006). We fitted all BRT models in `R` (version 3.3.1, R Core Team 2016) with packages `gbm` (version 2.1-1, Ridgeway 2015) and `dismo` (version 1.1-1, Hijmans et al. 2016) and adopted the default settings for BRT tuning parameters learning rate (0.01), tree complexity (1, i.e. stumps) and bag fraction (0.75) in the `dismo` package. The number of trees in the final model, depending on learning rate and tree complexity, was determined by 10-fold cross-validation (Elith et al. 2008) and varied between species (**Table 4.1**). Spline correlograms (Dormann et al. 2007) revealed no spatial autocorrelation in the model residuals.

Table 4.1. Characteristics of boosted regression tree models for *L. perenne* and *S. maritimus* (sample size = 318, learning rate[1] = 0.01, bag fraction[2] = 0.75, tree complexity[3] = 1).

	Lolium perenne	*Scirpus maritimus*
model characteristics		
prevalence (presences:absences)	0.21 (55 : 263)	0.11 (32 : 286)
number of trees	900	1450
explained deviance [%] (mean ± SE)	56.2 ± 6.7 %	30.8 ± 6.5 %
AUC (mean ± SE)	0.95 ± 0.013	0.88 ± 0.022
relative predictor importance[4]		
groundwater level [cm]	21 %	32 %
salinity g l^{-1}	25 %	64 %
biomass removal [%]	53 %	4 %

[1] the learning rate (shrinkage) determines the contribution of each tree to the final ensemble model and, thus, the speed of gradient descent

[2] the bag fraction is the proportion of training data used for tree fitting in each iteration

[3] the tree complexity (maximum number of splits in a tree) relates to the interaction depth potentially modeled; stumps (tree complexity=1) mean there are no interactions included

[4] the relative importance was determined by random permutation (cf. Ridgeway 2015)

To demonstrate our framework, we selected two examples from the pool of 61 model species which, on the one hand, are both common, dominant and important ecosystem service providing species in the region, and on the other, occur in very different habitats: *Lolium perenne* (L.), the most important pasture grass, and *Scirpus maritimus* (L.), forming reed stands in brackish conditions. Model performance, as described by explained deviance [0…100 %] and area-under-the-ROC-curve AUC [0.5…1.0] (Swets 1988) from 10-fold cross-validation, was good for both species and better for *L. perenne* than *S. maritimus* which could be explained by the higher prevalence in the data set (**Table 4.1**). Response curves graphically represent the model relationship between response (occurrence probability) and one predictor variable at a time while holding the other predictors constant at their respective mean. In our models, they plausibly describe the known ecology of the two example species. *L. perenne* occurs on dry (groundwater level < -50 cm), non-saline (presence < 6 g l^{-1}) sites, and its occurrence probability increases along the land use intensity gradient (**Fig. 4.2**, grey). In stark contrast, *S. maritimus* occurs on wet (groundwater > -50 cm), fallow sites of intermediate salinity (5-15 g l^{-1}; **Fig. 4.2**, black). The amplitude of the curves in **Fig. 4.2** relate to the relative importance of the predictors in the model (**Table 4.1**) which differs between species. For *L. perenne*, biomass removal [%] is the most important predictor (53 %), while salinity explains most of *S. maritimus* occurrence (64 %). The importance of predictors in a model affects how sensitive the modeled species is to changes in these variables. As we do not analyze the species response to changes in land use intensity in this study, the low impact of this variable in the *S. maritimus* model (4 %) is of no consequence here.

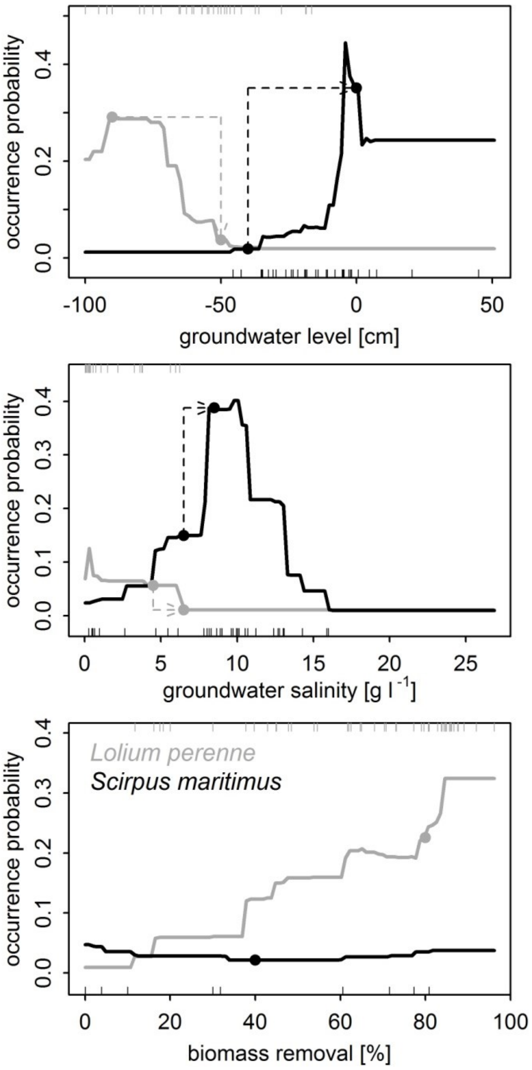


Figure 4.2. Response curves of the statistical occurrence models for *L. perenne* (grey) and *S. maritimus* (black). The range covered by the response curves equals the range of observed data the models are based on. Rug plots indicate values of sites on which *L. perenne* (grey, top) and *S. maritimus* (black, bottom) were present. Arrows show increases of groundwater level (40 cm) and salinity (2 g l^{-1}) during example change event in **Fig. 4.7**; biomass removal was held constant at 80 % (*L. perenne*) and 40 % (*S. maritimus*) in that example (**Fig. 4.7**).

4.2.3. Process-based model

As an example for a process-based model we used a well-established individual- and trait-based model (IBC-grass; Weiss et al. 2014, May et al. 2009) which was further developed to include the limiting effects of high groundwater levels and salinity at the coast (IBC-grass_coast, see complete model description following the ODD protocol (Overview, Design concepts, Detail; Grimm et al. 2006) in Appendix C2, CD). IBC-grass_coast is an individual-based, spatially explicit model adopting a zone-of-influence approach (Weiner et al. 2001) which was originally designed to reproduce effects of disturbances like grazing on small-scale community patterns in grasslands (May et al. 2009). The spatial resolution of the model is 130×130 cm^2 with weekly time steps (30 weeks making up one vegetation period). Competition for space, light and soil resources among individuals, plant and spacer growth as well as grazing and trampling mortality are calculated every time step (i.e. weekly). Seed production and dispersal, establishment, winter mortality and cutting are limited to certain weeks in the vegetation period. Processes in IBC-grass being modelled at the level of individuals belonging to plant functional types (PFT) or even species (applied here) allows the analysis of model results on the level of individuals (mean individual yield, Pfestorf et al. 2016), populations (population size, Reeg et al. 2017), species (abundance, Pfestorf et al. 2016) as well as the community (PFT diversity or community biomass, Weiss and Jeltsch 2015). Here, we aggregated model results into a measure of species-specific occurrence comparable to SDM-predicted occurrence probability: proportion of replicate model runs (n=50) in which the given species was present, ranging from 0 to 1.

In IBC-grass, 14 trait-related parameters determine species responses to environmental conditions and thus their competitive strength. Two parameters were added in IBC-grass_coast to account for resistance to inundation (at higher respiratory costs) and tolerance to salinity in our application. Apart from plant trait data collected within the COMTESS project (see *section 4.2.1*), additional species-specific trait values for model parameterization were taken from trait data bases BiolFlor (Kühn et al. 2004), CloPla (Klimešová and de Bello 2009) and LEDA (Kleyer et al. 2008), see also **Table C3.2** in Appendix C3 (CD). As we had no measurements for the new trait parameters (respiratory cost under inundated conditions and salinity tolerance) we calibrated the model in two steps (full description in Appendix C3, CD), i.e. single-species and multi-species model runs in five distinct habitat types typical for the study area (intensive and extensive grassland, wet meadow, salt marsh and reed). Environmental conditions between the habitat types varied concerning groundwater level and salinity, nutrient supply as well as land use intensity described by grazing intensity and cutting frequency (**Fig. C3.6**, Appendix C3). Comparison with sampled COMTESS plots (each assigned one of the five habitat types by expert knowledge) yielded different numbers of successful parameter combinations per habitat type, ranging from 197 (intensive grassland) to only 11 (wet meadow; see number of settings in **Fig. C3.6**, Appendix C3). Out of these, parameterizations were drawn randomly (with replacement) for 50 replicate model runs per simulation experiment (see *section 4.2.4.1*) which were aggregated into the occurrence measure defined above. Each habitat type occupied a certain range on the groundwater level and salinity gradient, e.g. intensive/ extensive grassland showed groundwater levels ≤ -50 cm and salinities ≤ 1 g l^{-1} as opposed to salt marshes with groundwater levels around -20 cm and ≥ 4 g l^{-1} (**Fig. C3.6**, Appendix C3). Because the initial conditions differed between habitat types, the same disturbance event simulated per habitat type (see *section 4.2.4.1*), e.g. groundwater level increase of 20 cm combined with a salinity increase of 2 g l^{-1}, resulted in different final conditions (i.e. during the change event, **Fig. C1.3**, Appendix C1).

IBC-grass successfully reproduces community dynamics like competitive exclusion or co-existence (Pfestorf et al. 2016, Körner et al. 2014), succession (Weiss and Jeltsch 2015) and species-specific responses to resource and seed limitation (Weiss et al. 2014). Weiss and Jeltsch (2015) specifically used simulation experiments with a similar version of IBC-grass to investigate the resistance of grassland communities to succession after the abandonment of grazing. We thus assume that the PBM is superior to the SDM in the event of abrupt environmental changes, as it dynamically models the development of species communities over time. For the purpose of demonstrating our model coupling framework, we therefore assume the PBM predictions to be ‘true’, and we correct deviating SDM predictions accordingly. Our example PBM can be replaced by any other process-based model which includes the relevant process detail (e.g. species-specific competition) and can perform the simulation experiments described in *section 4.2.4.1*.

4.2.4. Coupling two model approaches – the framework

The framework we are suggesting focuses on the applicability of the resulting coupled model, as large quantities of data needed to be processed in our example study. Therefore, we propose a two-step procedure. The first part involves conducting simulation experiments with the PBM (resilience analysis), while in the second part the SDM application is modified according to the results of step 1 (**Fig. 4.3**).

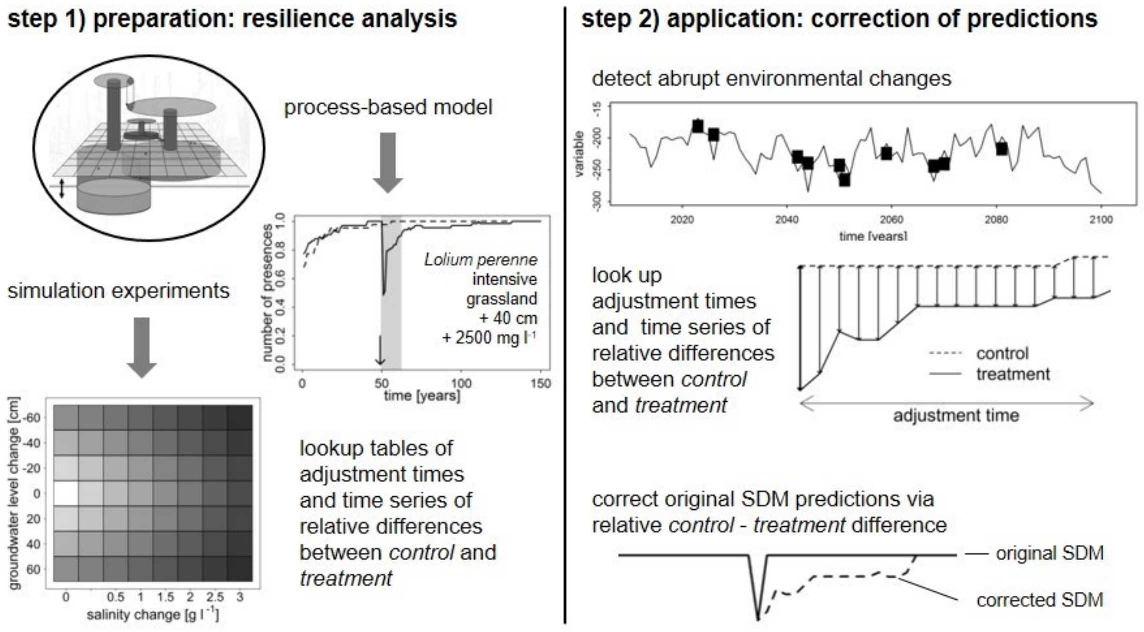


Figure 4.3. Concept of two-step procedure: simulation experiments with the process-based model (resilience analysis) in step 1 result in species-specific lookup tables which are used in step 2 to correct statistical model predictions.

4.2.4.1. Step 1) Preparation: resilience analysis

Disturbances are characterized by their duration, frequency, area and magnitude (intensity and severity, White and Pickett 1985). For the resilience analysis in step 1, we considered abrupt changes of groundwater level and/or salinity which occurred once in the simulated time series (frequency), which lasted for one year (duration) and affected the entire model patch (130 × 130 cm², size). An abrupt change (disturbance) was detected (i) if either groundwater level or salinity (or both) exceeded their respective threshold from one year to the next (i.e. $|\text{variable}_{\text{year1}} - \text{variable}_{\text{year2}}| > \text{threshold}$), and (ii) if groundwater level or salinity (or both) in the following year was again within the value ± threshold of the year prior to the change event (i.e. $|\text{variable}_{\text{year1}} - \text{variable}_{\text{year3}}| \leq \text{threshold}$). The thresholds were variable-specific and ranged between -60 to 60 cm (at least |20 cm|) for groundwater level (thus, encompassing both drier and wetter conditions) and between 0.25 and 3 g l^{-1} for groundwater salinity (thus, only considering salinity increases).

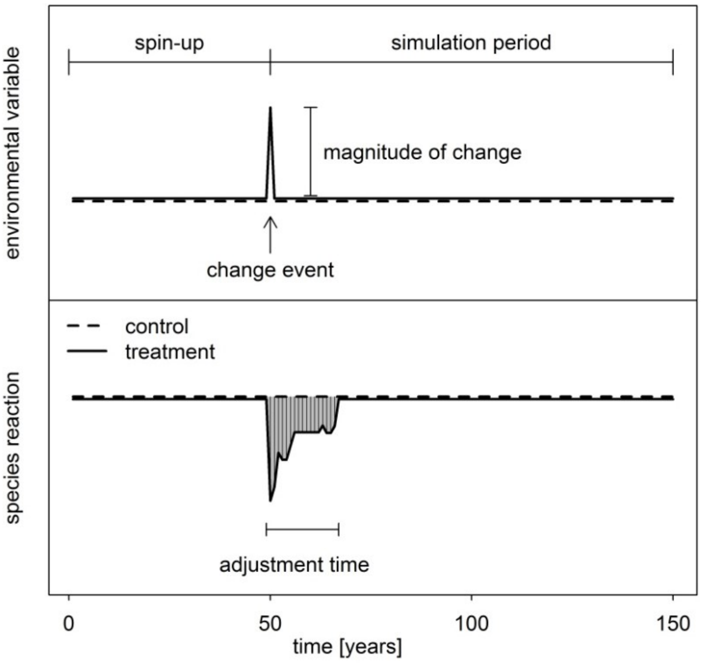
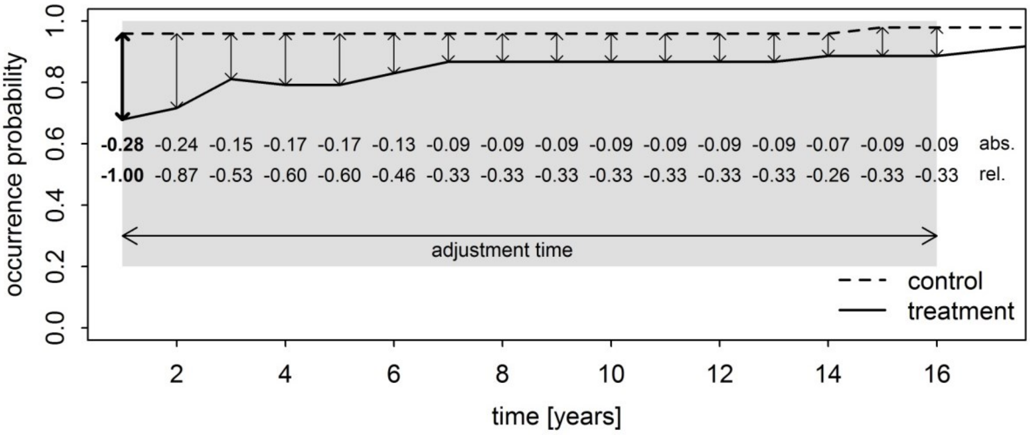


Figure 4.4. Concept of the simulation experiments performed by the process-based model for temporary one-year change. After a spin-up phase of 50 years, environmental conditions are changed by a certain magnitude for one year and then returned to the previous level (upper panel). The species reaction is compared between *treatment* (with change event) and *control* (without change event). The adjustment time is the number of years with significant differences between *control* and *treatment*. For each year within the recovery time, the difference between *control* and *treatment* is recorded for later correction of the statistical model (see also **Fig. 4.5**).

We recorded two aspects of a species' response to the change event of a certain magnitude. First, we determined the adjustment time as a direct measure of resilience by comparing two settings (**Fig. 4.4**): In the *treatment* setting, we let the model spin up for 50 years with constant environmental conditions, then changed the conditions for one year, after which they returned to the previous level for 100 simulation years. In the *control* setting, the change event was missing. Thus, starting in the first year after the change event, the *control* setting is what the SDM (unaware of the previous year's conditions) predicts. Both, *control* and *treatment* settings were repeated 50 times, each time drawing randomly from the pool of successful parameterizations per habitat type (see *section 4.2.3*). The adjustment time was then determined as the number of years for which *control* and *treatment* settings differed significantly after the change event (see Appendix C3, CD). We recorded the adjustment time between *control* and *treatment* for each magnitude of change in lookup tables for each species and each of the five habitat types (see *section 4.2.3*).

Second, for cases with adjustment times > 0 years, we recorded the relative annual difference between *control* and *treatment* settings (**Fig. 4.5**). The maximum difference between *control* and *treatment* was set to +1 (if the species responded positively to the change, i.e. *treatment* > *control*) and -1 (if the species responded negatively to the change, i.e. *treatment* < *control*), respecttively. There were cases for which the response peaked immediately, i.e. in the year of the change itself (**Fig. 4.5a**), whereas in other cases the response was delayed (time lag after the change event, **Fig. 4.5b**).

a) *Lolium perenne*



b) *Scirpus maritimus*

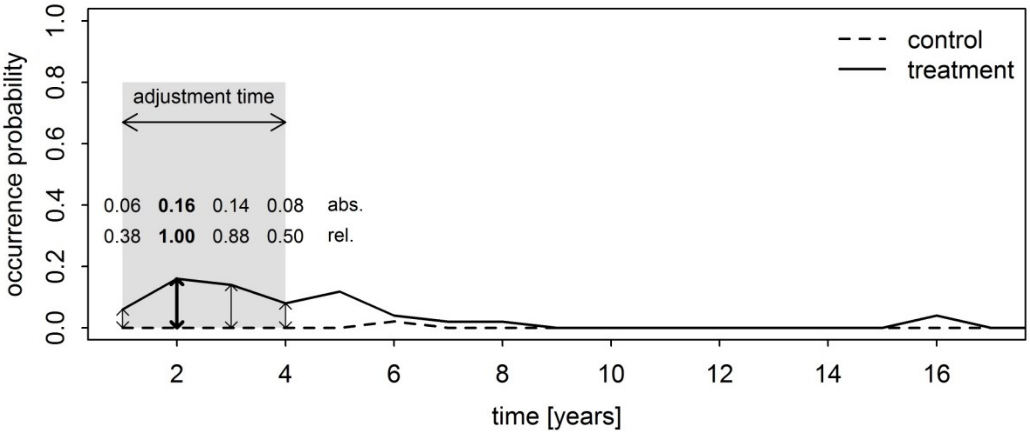


Figure 4.5. Examples of the simulation experiment with 40 cm groundwater level and 2 g l^{-1} salinity increase for a) *L. perenne* and b) *S. maritimus*. Grey shading marks the adjustment time, i.e. significant difference between *control* (broken line) and *treatment* (solid line). Table figures give significant absolute (abs.) and relative (rel.) differences between *control* and *treatment* per year which are used for correction.

4.2.4.2. Step 2) Application: correction of predictions

First, we created the original SDM predictions by applying our species-specific SDMs (see *section 4.2.2*) to the predicted groundwater level, salinity and biomass removal time series (COMTESS data, see *section 4.2.1*), resulting in time series of occurrence probability for each species. Next, we used the same definition of abrupt temporary changes as in the simulation experiments in step 1 for the application of the framework in step 2, and thus identified abrupt one-year change events in groundwater level and salinity time series.

We then had to determine in which of the five lookup tables (= habitat types) for each species to find the adjustment time (and relative *control-treatment* differences) corresponding to a specific combination of groundwater level and salinity change. We used the predictions of 33 species to automatically classify the habitat type as described in Appendix C4. Based on the presence of typical species for each habitat type (e.g. *Phragmites australis* and *S. maritimus* for reed), we assigned each hydrotope one of the five habitat types per simulation year. We could then retrieve PBM simulation results for a specific change event (combination of groundwater level and salinity change) in a specific habitat type and compare them to the predicted SDM response.

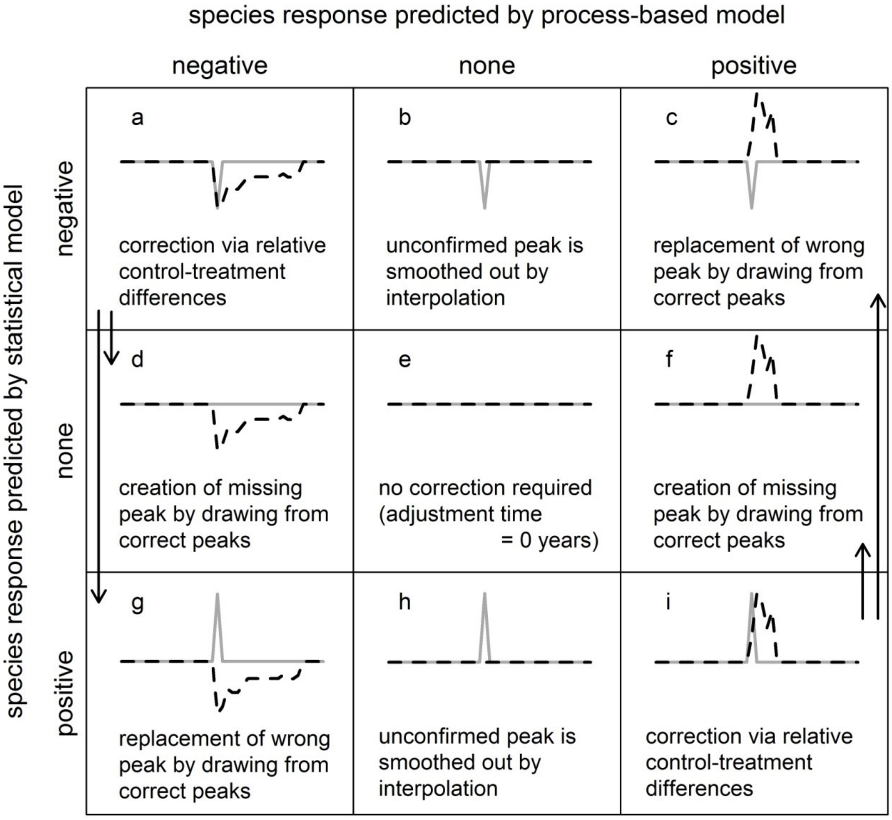


Figure 4.6. Summary of possible combinations of responses predicted by process-based vs. statistical models and their handling in our proposed framework. Arrows indicate that cases of agreement between SDM and PBM (a, i) are used to create missing SDM peaks (d, f) and replace wrong peaks (g, c).

Figure 4.6 shows a summary of potential combinations of modeled species response to change by process-based vs. statistical model and how we propose to handle them. On the main diagonal both models agree concerning type (peak vs. no response) and direction (positive vs. negative), whereas in the remainder of the table their predictions differ. If both models, PBM and SDM, predict no species response to a change (**Fig. 4.6e**), there is no correction required.

If both models agree on the direction of peaks (negative, **Fig. 4.6a**, or positive, **Fig. 4.6i**), we use the recorded adjustment time and annual relative difference between *control* and *treatment* from step 1 to modify the SDM prediction as follows: First, the SDM-predicted peak is assigned 100 %. Second, for the adjustment time (i.e. the years following the change event, including the year the change event takes place, with a significant difference between *control* and *treatment* in the simulation experiment), we replace the original SDM predictions with the percentage of the SDM-predicted peak (= 1) as simulated by the PBM in step 1 (**Fig. 4.5**). By modifying the SDM predictions in a *relative* way, we accounted for the absolute difference between what the PBM predicted in the *control* setting and the SDM prediction (as the 50 PBM runs cover a range of different initial conditions from the pool of successful parameterizations (**Fig. C3.6**, Appendix C3), they cannot be directly compared to the SDM prediction of one specific case).

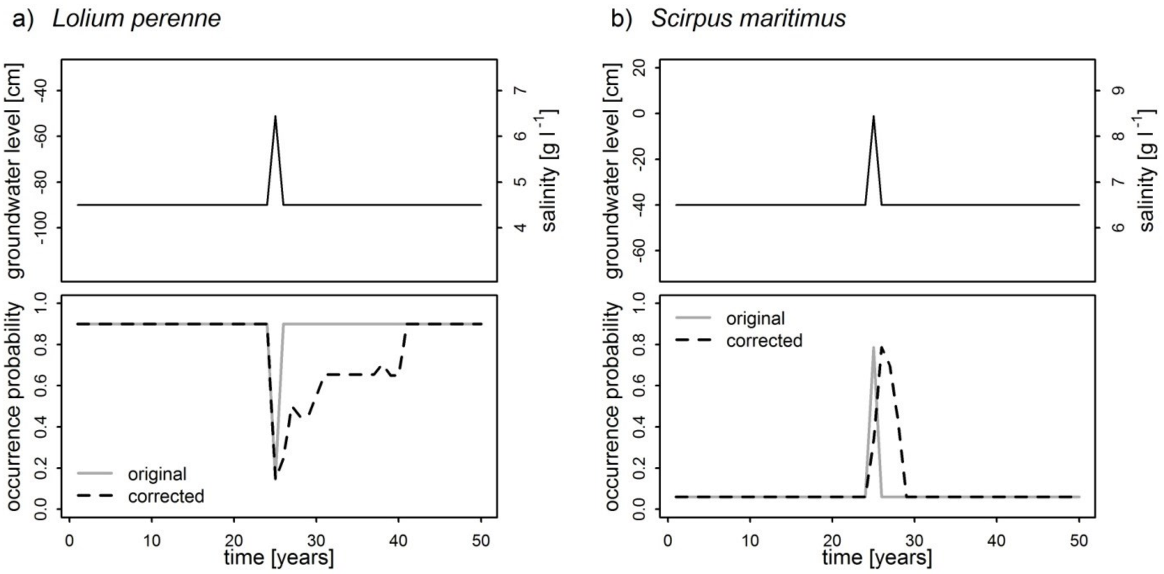


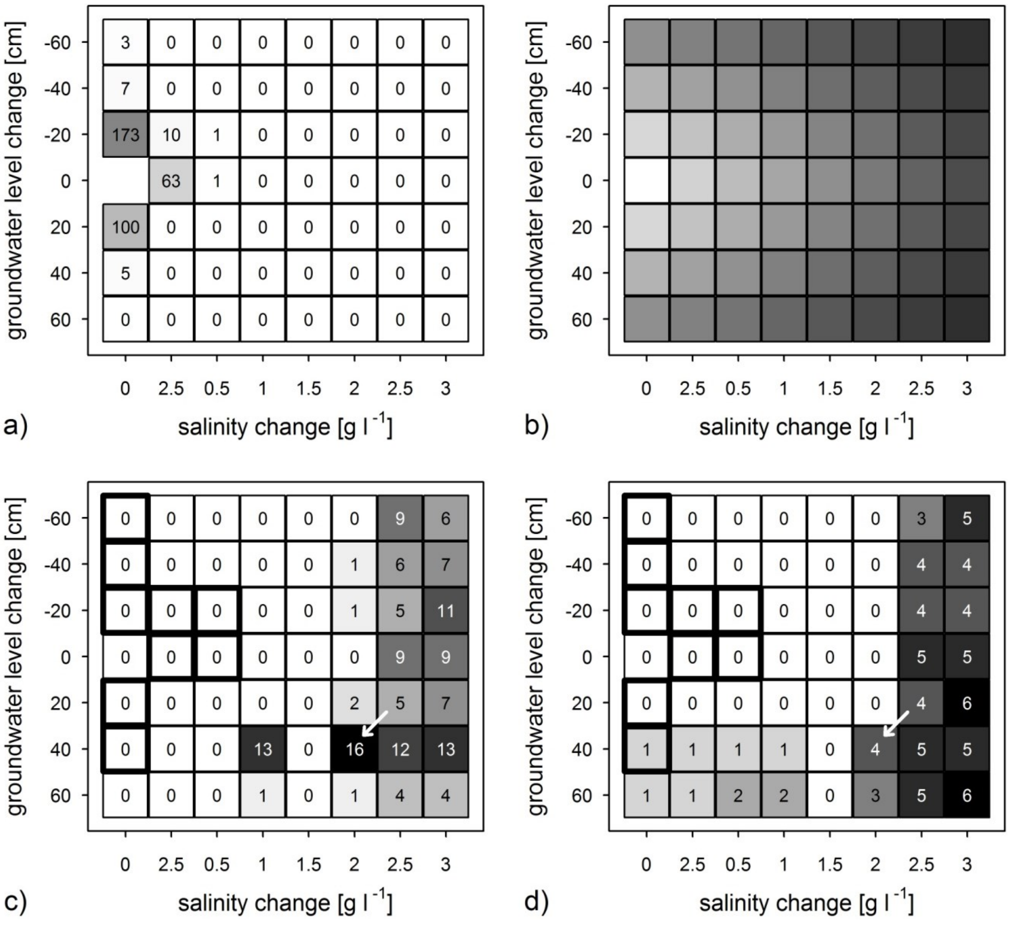
Figure 4.7. Example of an abrupt one-year change of groundwater level (+ 40 cm) and salinity (+ 2 g l^{-1}) to which two species respond differently (habitat type = intensive grassland): while a) *L. perenne* responds negatively, b) *S. maritimus* responds positively to wetter and more saline conditions (note different initial groundwater level and salinity conditions). Solid, grey lines are original predictions of the statistical models; broken, black lines are corrected via relative *control-treatment* differences.

To demonstrate this procedure, we constructed an example with a groundwater level increase of 40 cm and a salinity increase of 2 g l^{-1} (**Fig. 4.7**). From the simulation experiment for this combination of groundwater level and salinity change (**Fig. 4.5**), we know that *L. perenne* needs 16 years to recover from the temporally unsuitable conditions (negative response; see also decrease in occurrence probability in response curves, **Fig. 4.2**), while *S. maritimus* benefits for four years from the temporally beneficial conditions (positive response, **Fig. 4.2**). In contrast, the SDM only predicted a positive response for *L. perenne* and a negative response for *S. maritimus* in the year of change and a return to the initial occurrence probability in the following year (**Fig. 4.7**, original prediction). The corrected prediction then mirrored the development of the *treatment* setting in relation to the *control* setting from step 1 (compare **Fig. 4.5** and **Fig. 4.7**, corrected prediction). Consequently, for *S. maritimus*, the SDM-predicted peak was moved to the year after the change event as simulated by the PBM. Should the effect of one change event still continue when the next change event occurs, we suggest using the absolute maximum of all corrections (**Fig. C1.4**, Appendix C1).

If the SDM predicts a response unconfirmed by the PBM (negative, **Fig. 4.6b**, or positive, **Fig. 4.6h**), we smooth out the incorrect peak by interpolating between the years before and after the change event. In cases where the opposite is true (**Fig. 4.6d** or **f**) or where SDM and PBM predict peaks in opposite directions (**Fig. 4.6c** or **g**), we create missing peaks and replace wrong-direction peaks by drawing from the pool of correct SDM peaks (**Fig. 4.6a** or **i**). We choose the SDM peak from previous SDM applications (in other years or hydrotopes) that falls into the same class of groundwater level and salinity change (e.g. +40 cm and +2 g l^{-1}) and is closest to the current case in terms of groundwater level, salinity and biomass removal (10 year-average prior to change event, **Fig. C1.5**, Appendix C1). These three environmental variables are the main predictors of the statistical models (see *section 4.2.2*). The newly assigned peak is then modified following the procedure described above for cases in which PBM and SDM agree on the direction of response (**Fig. 4.6a** or **i**).

4.3. Results

4.3.1. Occurring cases of abrupt environmental change



a)

groundwater level change [cm]	0	2.5	0.5	1	1.5	2	2.5	3
-60	3	0	0	0	0	0	0	0
-40	7	0	0	0	0	0	0	0
-20	173	10	1	0	0	0	0	0
0		63	1	0	0	0	0	0
20	100	0	0	0	0	0	0	0
40	5	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0

c)

groundwater level change [cm]	0	2.5	0.5	1	1.5	2	2.5	3
-60	0	0	0	0	0	0	9	6
-40	0	0	0	0	0	1	6	7
-20	0	0	0	0	0	1	5	11
0	0	0	0	0	0	0	9	9
20	0	0	0	0	0	2	5	7
40	0	0	0	13	0	16	12	13
60	0	0	0	1	0	1	4	4

d)

groundwater level change [cm]	0	2.5	0.5	1	1.5	2	2.5	3
-60	0	0	0	0	0	0	3	5
-40	0	0	0	0	0	0	4	4
-20	0	0	0	0	0	0	4	4
0	0	0	0	0	0	0	5	5
20	0	0	0	0	0	0	4	6
40	1	1	1	1	0	4	5	5
60	1	1	2	2	0	3	5	6

Figure 4.8. a) Number of example cases per groundwater level-and-salinity change combination (summed over all 40 polygons' time series of 89 years (2011-2099); total number of cases = 3560). Lookup tables of adjustment times [years] with b) our expectations (the darker, the longer adjustment time), and c) results of the resilience analysis in step 1 for *L. perenne* and d) *S. maritimus* (intensive grassland; see **Fig. C1.6** for tables of all five habitats). The bold frames in c) and d) mark cases which occur in our example data, cf. a). White arrows in c) and d) mark the example case used in **Fig. 4.5** and **4.7**.

In our example, we found 363 cases of abrupt one-year changes (10 % of all 3560 potential cases, i.e. 40 polygons × 89 years; for the first and the last year of the time series our conditional definition could not be checked) ranging from a 60 cm groundwater level decrease to 40 cm increase, and up to 0.5 g l^{-1} salinity increase (**Fig. 4.8a**). Interestingly, mapping how often in 89 years (2011-2099) abrupt groundwater level changes occurred in each hydrotope (**Fig. 4.9a**) revealed a positive relationship between the number of changes and elevation. The highest numbers of changes were found in elevated hydrotopes, while the low-lying hydrotopes along the coastline exhibited the lowest number of changes (**Fig. 4.9a**). This spatial pattern is virtually inverted when mapping the goodness-of-fit of linear models fitted to the groundwater level time series of each hydrotopes (the 'smoother' the time series, the better the fit of a linear model; **Fig. 4.9b**). Here, low-lying polygons along the coast exhibited the most linear time series (R^2 close to 1). Thus, the lack of abrupt changes along the coast is not the absence of change in general, but indicates a more gradual increase of both groundwater level and salinity (however, abrupt salinity changes are confined to the low-lying coastline).

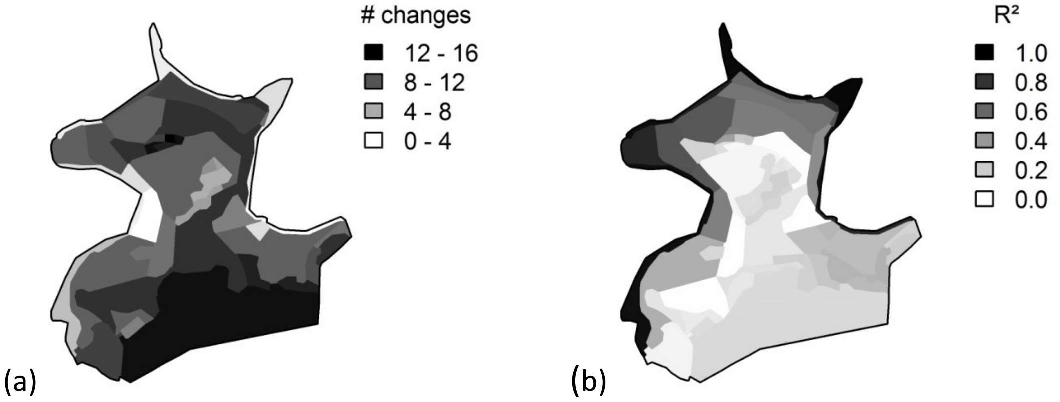


Figure 4.9. Maps of (a) number of abrupt changes in groundwater level over the entire time series (2011-2099) and (b) goodness-of-fit of a linear model (R^2) fitted to the groundwater level time series (indicating how gradual the changes are over time).

4.3.2. Resilience

Although we expected adjustment times after change events to differ between species and initial conditions (i.e. habitat types), we generally expected them to increase with the magnitude of change, i.e. with increasing (absolute) groundwater level changes and salinity increases, as shown by the shading in **Fig. 4.8b**. Despite variation, we found the expected pattern of generally increasing adjustment times with greater salinity increases (i.e. from left to right in **Fig. 4.8c** and **d**) and less so for groundwater levels (but see longer adjustment times with groundwater level increases ≥ 40 cm for *S. maritimus*, **Fig. 4.8d**). Thus, both species were more sensitive to salinity increases than to groundwater level changes (see Appendix C1, **Fig. C1.6** for lookup tables of adjustment times in all habitat types).

L. perenne was very resilient to changes as only salinity increases exceeding 2 g l^{-1} resulted in any adjustment time (**Fig. 4.8c**). *S. maritimus* exhibited a similar pattern with only very high salinity increases resulting in adjustment times which in turn were generally lower than for *L. perenne* in the same habitat type and combination of groundwater level and salinity change (but see difference between initial conditions in **Fig. C1.7**, Appendix C1). The longest adjustment time in our example cases (see bold frames in **Fig. C1.6**) were 6 years for *L. perenne* (wet meadow) and 11 years for *S. maritimus* (salt marsh).

4.3.3. Correction of statistical model predictions

Of the 363 occurring cases of environmental change, by far the most led to no response in either PBM or SDM (68 % *L. perenne*, 67 % *S. maritimus*, **Fig. 4.10**). In 22 % of the cases, the SDM underestimated the resilience of both species by predicting positive or negative peaks unconfirmed by the PBM (**Fig. 4.10**). The respective SDM peaks in the time series of predicted occurrence probability were smoothed out. In contrast, the SDM overestimated the resilience of the species in only 5 % and 4 % for *L. perenne* and *S. maritimus*, respectively (**Fig. 4.10**). In these cases, new positive or negative peaks were inserted into the original time series of occurrence probabilities, depending on the response predicted by the PBM. In only 4 % (*L. perenne*) and 1 % (*S. maritimus*) of all cases, both approaches predicted a positive response, and the original SDM predictions were adjusted via relative control-treatment differences. In the remaining 1 % (*L. perenne*) and 6 % (*S. maritimus*) of all cases, contrasting response predictions (SDM: negative, PBM: positive) had to be resolved by replacing the originally negative SDM peak with a positive peak drawn from the pool of correct positive peaks.

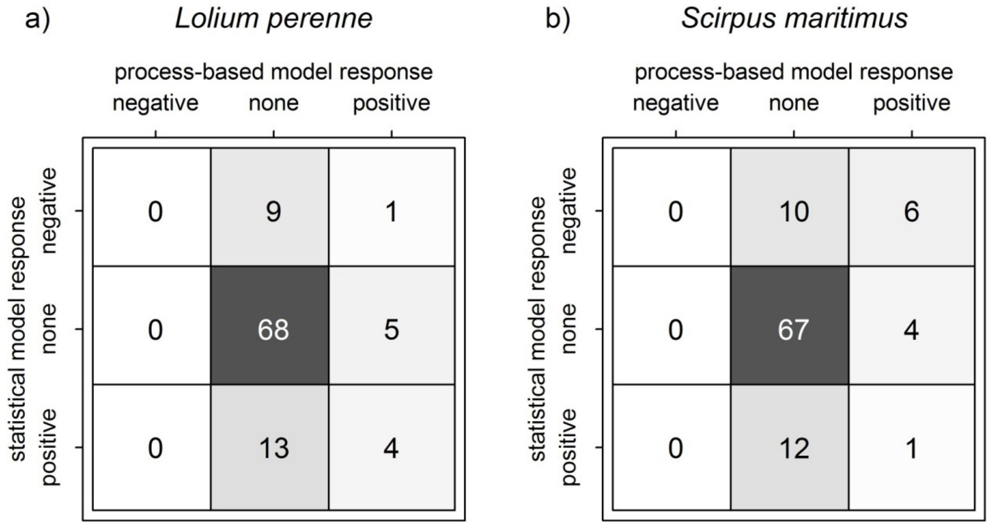


Figure 4.10. Fraction of example cases of abrupt environmental change (see **Fig. 4.8a**) per combination of predicted species response by process-based vs. statistical model (cf. **Fig. 4.6**) for both example species. Shades of grey underline the share of the total number of cases.

Thus, the corrections of the statistical predictions consisted mostly of smoothed out peaks (**Fig. 4.11**). Example hydrotope A was a case of gradual groundwater level (two abrupt changes over 89 years) and salinity (three abrupt increases) increase (**Fig. 4.11**, A). By 2050, the habitat type shifted from salt marsh to reed as salt marsh species *Festuca rubra* subsp. *littoralis* was replaced by *S. maritimus* (**Fig. C4.2**). These conditions excluded *L. perenne* from the beginning (occurrence probability = 0) and the five change events resulted in no correction, as both approaches predicted no response. However, the same changes led to improved habitat suitability for *S. maritimus* whose

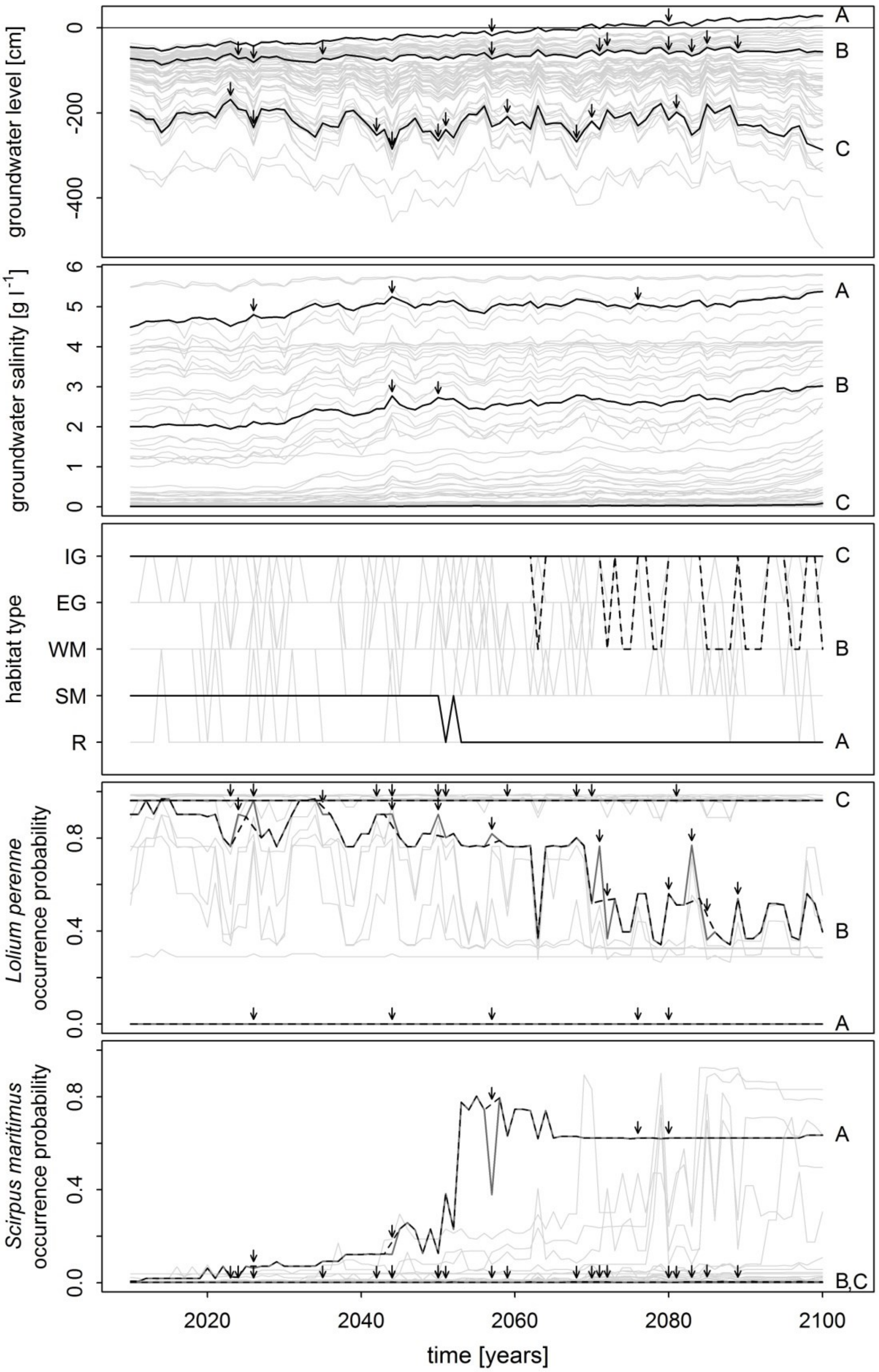


Figure 4.11. Groundwater level and salinity time series as well as classified habitat type (IG= intensive grassland, EG= extensive grassland, WM= wet meadow, SM= salt marsh, R= reed) and predicted occurrence probabilities for *L. perenne* and *S. maritimus* (dark grey= original SDM, broken line= corrected) for all hydrotopes (grey lines) with example polygons A, B, C highlighted (see map in **Fig. 4.1**). Cases of abrupt environmental changes according to our definition are highlighted by arrows.

occurrence probability increased from 0 to 0.62. The only corrections consisted of smoothing out unconfirmed responses, e.g. the omission of a negative peak predicted by the SDM in year 2057. A contrasting example was hydrotope C with ten abrupt groundwater level changes but no salinity (changes) which was continuously classified as intensive grassland due to the presence of *L. perenne*, *Trifolium repens* and *Taraxacum Sec. Ruderalia* (**Fig. C4.2**). In this hydrotope, *L. perenne* was present (constant occurrence probability = 0.96), while *S. maritimus* was absent throughout the entire time series (**Fig. 4.11**, C). The change events triggered no species responses in either SDM or PBM, and thus the original did not need any correction.

Hydrotope B was an intermediate case with also ten abrupt groundwater level changes, but two additional abrupt increases of salinity, which increased from a level of 2 g l^{-1} (**Fig. 4.11**, B). Consequently, the habitat type started changing from intensive grassland to wet meadow in 2063 when *L. perenne* started to vanish due to deteriorating habitat conditions (**Fig. C4.2**). *L. perenne* was present at the beginning of the time series (occurrence probability > 0.9), but its occurrence probability decreased to approx. 0.4 by the end of the century. High biomass removal (80 %), rather than unsuitable moisture and salinity conditions excluded *S. maritimus* on this site from the beginning. The corrections consisted again of smoothed out positive (8) and negative (4) SDM peaks (e.g. in year 2083).

In summary, corrections of SDM predictions by the PBM were rare and mostly consisted of smoothing out unconfirmed SDM peaks in individual years. Thus, the potential errors of unassisted SDMs in our case study were short-term, and the coupled model did not yield fundamentally different predictions considering the entire time series.

4.4. Discussion

4.4.1. Resilience of coastal vegetation

4.4.1.1. Illustrative example: *L. perenne* and *S. maritimus*

In our illustrative example, we found cases of abrupt and gradual environmental change. We did not investigate gradual changes as we assumed them to be less problematic when using statistical models. The vegetation can keep pace with its slowly changing surroundings, and thus no adjustment times need to be taken into account. Instead, habitat suitability slowly increases or decreases, and species response appears instantaneous at least in annual time steps. Abrupt environmental changes, on the other hand, can lead to suddenly adverse or suitable habitat conditions which species often do not respond to instantaneously or triggering long-term changes in the species community, neither of which can be handled by statistical models. Concerning abrupt environmental changes of one-year duration, our example study revealed high resilience of both *L. perenne* and *S. maritimus* occurrence which can be explained by the ecology of the two species:

L. perenne is a fast-growing, strong competitor, sensitive to droughts (low resistance in a glasshouse experiment by Davis et al. 1994) but highly resilient with respect to e.g. trampling, as it persists even under intensive grazing with high stocking rates (Cosgrove 2011). According to the plant strategy theory (Grime 1977), *L. perenne* is classified as ruderal/ competitive strategist (Pierce et al. 2013, Campbell and Grime 1992). The ruderal strategy focuses on reproductive processes, e.g. seed production and the establishment of a viable seed bank (Grime 1977). It thus increases resilience by enabling plants to establish quickly after disturbance events (Lepš et al. 1982).

S. maritimus is an emergent macrophyte and facultative halophyte (Hroudová et al. 2007) which tolerates water levels up to 90 cm above soil surface (Dykyjová 1986) and survived four months of 18 ‰ S (= 18 g l^{-1}) in a chronic salt stress experiment (60 % mortality, Hootsmans and Wiegman 1998). The species responds to saline conditions by accumulating chloride and sodium which comes at the cost of reduced growth and leaf necrosis (Krüger and Kirst 1991). In anaerobic conditions, *S. maritimus* grows long shoots and spacers (to emerge from water-logged conditions) as well as tubers (storage for overwintering, Clevering and Hundscheid 1998). Thus, the strategy of *S. maritimus* according to Grime (1977) is stress tolerance which is an important resistance mechanism (Lepš et al. 1982).

We found high resilience (or resistance, see *section 4.4.1.2*) of the occurrence of *L. perenne* and *S. maritimus*. Experimental studies investigating the effect of salinity on *S. maritimus* survival confirm its high resistance to salinity and deep water. Only salinities exceeding 15 ‰ S (= 15 g l^{-1}) severely affected *S. maritimus* survival in an experiment by Lillebø et al. (2003). Salinities as high as this did not occur in our example data (max. 5.8 g l^{-1} in 2099, **Fig. 4.1**), and in our simulation experiments we investigated only changes of salinity resulting in not more than 7.6 g l^{-1} (**Fig. C1.3**). Coops et al. (1996) planted *S. maritimus* at different water depths and found it to survive even in 80 cm deep water after two growing seasons. In our example data, the highest mean annual groundwater level was 37.2 cm in 2100 (**Fig. 4.1**, polygon A). But in our simulation experiments we did explore abrupt groundwater level increases resulting in final groundwater levels of up to 40 cm (wet meadow and salt marsh) and even 74 cm (reed) (**Fig. C1.3**; in intensive/extensive grasslands, initial groundwater levels were much lower, thus final groundwater levels did not exceed 20 cm). And indeed, the adjustment times of *S. maritimus* in reed, salt marsh or wet meadow for 60 cm groundwater level increase were longer than in intensive/extensive grasslands, especially in combination with salinity increases (**Fig. C1.6** and **Fig. C1.7** in Appendix C1). Thus, the survival and our related occurrence measure of *S. maritimus* were only affected by the extreme cases of groundwater level and salinity changes investigated here, which is supported by experimental studies.

4.4.1.2. Resilience vs. resistance

Temporal resolution matters when distinguishing between resilience and resistance. For example, in their salt stress experiments, Hootsmans and Wiegman (1998) found aboveground biomass of *S. maritimus* seedlings to grow back quickly to the control level after temporary salt stress (three weeks, 18 g l^{-1}). They hypothesized that *S. maritimus* had recycled carbohydrates accumulated in response to previous salt stress to create high osmotic pressure. Thus, considering weekly time steps this could be considered resilience, while on the annual scale this would be considered resistance (no difference from control in this year).

In our example of annual time steps, we cannot distinguish between short-term resilience and resistance. *L. perenne* may be highly resilient, thus returning to the pre-disturbance level of occurrence within one year, while *S. maritimus* might be highly resistant, not even responding to the disturbance in the first place. Both, resistance and resilience, result in the same PBM prediction: adjustment time = 0 year. For the purpose of correcting annual SDM predictions, it is irrelevant whether the missing PBM response is due to resistance or resilience. Here, we abandon process detail provided by the PBM (in the modeled weekly resolution) when upscaling to match the SDM's temporal resolution (i.e. annual).

4.4.2. Model coupling framework

4.4.2.1. Novelty and flexibility of the proposed model coupling approach

Including biotic interactions into SDMs is pivotal to improve predictions of future species distribution (Anderson 2017, Wisz et al. 2013). Currently, several model coupling approaches ('hybrid models', Dormann et al. 2012) link SDM-derived habitat suitability maps with e.g. cellular automata simulating dispersal (Engler and Guisan 2009, Iverson et al. 2004, Carey 1996) or (meta)-population models (Zurell et al. 2012b, Söndgerath and Schröder 2002, Akçakaya 2000). However, hybrid model approaches linking SDMs with community-level models considering biotic interactions such as inter-specific competition are much rarer (but see BioMove, Midgley et al. 2010). Here, we present a novel approach to include biotic interactions in SDMs which goes beyond the simple inclusion of species co-occurrences as additional predictors (Giannini et al. 2013).

In BioMove, Midgley et al. (2010) scaled the competitive ability of different plant functional types in a process-based community-level succession model using SDM-derived habitat suitability. Thus, the temporal and spatial resolution of model application and consequently computation time for model runs were determined by the PBM. In our study, on the other hand, we focused on minimizing computational effort by adopting a two-step procedure. We simplified the results of the first step, i.e. the resilience analysis by PBM simulation experiments, into two measures: adjustment times and relative annual differences between *control* and *treatment* after simulated disturbance events. These two measures were static output of step 1 used in step 2, similar to the static habitat suitability maps derived from SDMs which then provide input for PBMs in a next step in current hybrid model approaches. Once step 1 with its considerable effort related to PBM parameterization and run time of various simulation experiments including replicates was completed, the PBM application was finished. Thus, the resolution of application was determined by the SDM, i.e. annual (instead of weekly) time steps and areas of entire hydrotopes (instead of 130 × 130 cm^2). The considerable advantage of simplifying PBM outputs and classifying change events was that looking up the same species reactions for similar change events recurring in the time series of different hydrotopes saved computational time in a large-scale, long-term application, while at the same time conserving the important process details of community reactions to disturbance.

While most hybrid model approaches focus on spatial patterns via using habitat suitability maps (e.g. Fordham et al. 2013, Anderson et al. 2009, Akçakaya 2001), we here use temporal patterns, i.e. development of *control*- *treatment* differences over time, to link process-based and statistical models. As a comparison of different model approaches revealed, hybrid models such as ours are not only superior to classic SDMs in environmental change applications, but they are still among the best available methods for predicting species responses to climate change (Zurell et al. 2016).

4.4.2.2. Statistical vs. process-based model predictions

In our example change event (40 cm groundwater level and 2 g l^{-1} salinity increase) used in **Fig. 4.5** and **4.7**, SDM and PBM both agreed on the direction of response (negative for *L. perenne*, positive for *S. maritimus*), but differed in temporal development. SDM response curves (**Fig. 4.2**) confirmed the responses modeled by the PBM. However, in most cases of abrupt changes that triggered any species response, SDM and PBM disagreed (**Fig. 4.10**).

The most common modification of SDM predictions in our illustrative example was smoothing out unconfirmed peaks in individual years. Thus, the corrected SDM predictions were less variable than the original SDM predictions which implausibly suggested that species vanish completely from a site in one year only to suddenly reappear in the next. Instead the species would either resist or be decimated in abundance, but not removed completely (Lavorel 1999) in most cases. Similarly, it is implausible that one year of suitable conditions on an otherwise unfavourable site leads to the sudden establishment of a species as it has to compete with already present competitors in the existing community. Thus, the correction of the SDM resulted in ecologically more plausible predictions.

Discrepancies between SDM and PBM (**Fig. 4.6** and **4.10**) do not indicate that one of the two models does not work. Instead, they demonstrate the different nature of the two model approaches: SDMs predict the habitat suitability based on environmental predictors, assuming that the predictor values represent a long-term equilibrium of the environmental conditions of a site. A one-year increase of groundwater level and salinity (e.g. **Fig. 4.7a**) is thus ‘perceived’ by the SDM as an alternative site with long-term average of higher groundwater level (-50 cm, **Fig. 4.7a**) and higher salinity (6.5 g l^{-1}) which would indeed be unsuitable for *L. perenne* as the respective response curves show (**Fig. 4.2**), hence, the greatly reduced occurrence probability in this example (**Fig. 4.7a**). In the following year, the conditions suggest again a completely different site with drier (-90 cm), less saline (4.5 g l^{-1}) equilibrium conditions more suitable for *L. perenne*, hence the immediate return to high occurrence probability after disturbance (**Fig. 4.7a**). The PBM on the other hand, simulates the detailed response of *L. perenne* and all other species in the model to wetter, more saline conditions: in some of the replicate model runs *L. perenne* disappears from the model patch (hence the decrease in the PBM response variable). In the following years, *L. perenne* has to establish anew in these model patches and compete with species that were better adapted and thus less affected by the disturbance until finally, after 15 years, being back to its previous level of occurrence in all 50 replicates. The discrepancy between PBM and SDM is thus due to the specific modeling by the PBM of processes like competition between plant individuals of different species, mortality, dispersal and establishment that create transient dynamics (Reeg et al. 2017). This also explains why adverse conditions per se, which prompt a negative response in the SDM, can lead to an ultimately positive response in the PBM: while conditions may be unsuitable for e.g. *L. perenne*, they may be even less suitable for its competitors, reducing their abundance and thus the competitive pressure on *L. perenne*, ultimately improving its growing conditions and resulting in a positive PBM response. In their theoretical experiments, Allesina and Levine (2011) found that compositional shifts among competitors following an initial reduction of a focal species (e.g. due to a disturbance) favours the recovery of the focal species (intransitive competition, Gallien 2017).

4.4.2.3. Further research and potential applications

We used abrupt one-year changes as an illustrative example to demonstrate this novel model coupling approach, focusing on the methodological aspects. Further simulation experiments are currently under progress but would go beyond the scope of this paper. For example, in our time series we find cases of abrupt changes that have not returned to the previous conditions after just one but after several years (e.g. groundwater level of hydrotope C in 2063, **Fig. 4.11**). Simulations for these cases will likely reveal that adjustment times after more severe disturbances (longer duration) will be longer than after one-year events.

For multiple events in close succession which did occur in our time series (e.g. groundwater level of hydrotope B in years 2071/72, **Fig. 4.11**), we assumed that the reaction of the vegetation would be the same to each single event (**Fig. C1.4**, Appendix C1), whereas in fact a community already recovering from a prior disturbance is likely to be less resistant to a new change event and thus already respond to disturbances of smaller magnitude, or to be less resilient and need longer to recover. For example, Zedler et al. (1983) found that the burning of Californian chaparral in two consecutive years much reduced the otherwise characteristic resilience of the vegetation to fire in the second year.

So far, we have discussed only temporary changes of different magnitude or duration which can be described as disturbances, e.g. rainwater flooding affecting the mean annual groundwater level of one particular year or a storm surge that increases the salinity for a certain time. A different type of environmental change is abrupt and permanent, i.e. an abrupt change of conditions which do not return back to the previous level. A hypothetical example from the COMTESS project is the creation of polders in an alternative land management option at the North Sea. Here, drainage pumps are turned off from one year to the next in the hydrological model, and consequently groundwater levels increase abruptly and permanently. The proposed framework can be used in the same manner as described in this paper for temporary change to investigate species responses to permanent changes and adjustment times to new conditions.

Similarly, response variables other than occurrence of individual species can be investigated with our framework. For example, experimental studies investigating species performance (rather than mere survival) under different disturbance or stress treatments suggest that plant growth and fitness may already be affected by lower levels of disturbance. Common proxies for plant performance are morphological traits such as shoot length, number of leaves and tubers as well as aboveground and belowground biomass (Hroudová et al. 2014, Hootsmans and Wiegman 1998, Clevering and Hundscheid 1998). Hootsmans and Wiegman (1998) found *S. maritimus* seedlings to be very resistant to most treatments in terms of survival, while their total biomass was negatively affected by long-term salt stress (4 months, 18 g l^{-1}). Similarly, Clevering and Hundscheid (1998) observed that clonal growth was severely reduced in water depth of 20 and 30 cm after 11 weeks. These characteristics may well differ in resilience, and depending on the study question, they may be more relevant than individual species occurrence.

4.5. Conclusion

We demonstrated a novel framework to couple a statistical and a process-based model that transfers the condensed results of a resilience analysis by the PBM to SDM predictions. The resulting model combines the advantages of both model approaches: the convenient applicability of the statistical model and the process detail of the process-based model where it is relevant, i.e. in situations of abrupt environmental change. The two focal species proved to be very resilient to the disturbances investigated. Modifications by our framework consisted mostly of smoothing out SDM peaks unconfirmed by the PBM, thus correcting the SDM's underestimation of resilience. The flexible framework can be applied to any SDM predicting time series of occurrence probabilities and any PBM capable of dynamically simulating species responses to disturbances. Different definitions of disturbances and even permanent environmental shifts can be readily implemented and tested with this framework.

Acknowledgements

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Additional supplementary material on CD

Appendix C2. Description of individual-based model IBC-grass_coast (ODD protocol)

Appendix C3. Validation of individual-based model IBC-grass_coast

Appendix C1

Additional details on data and results

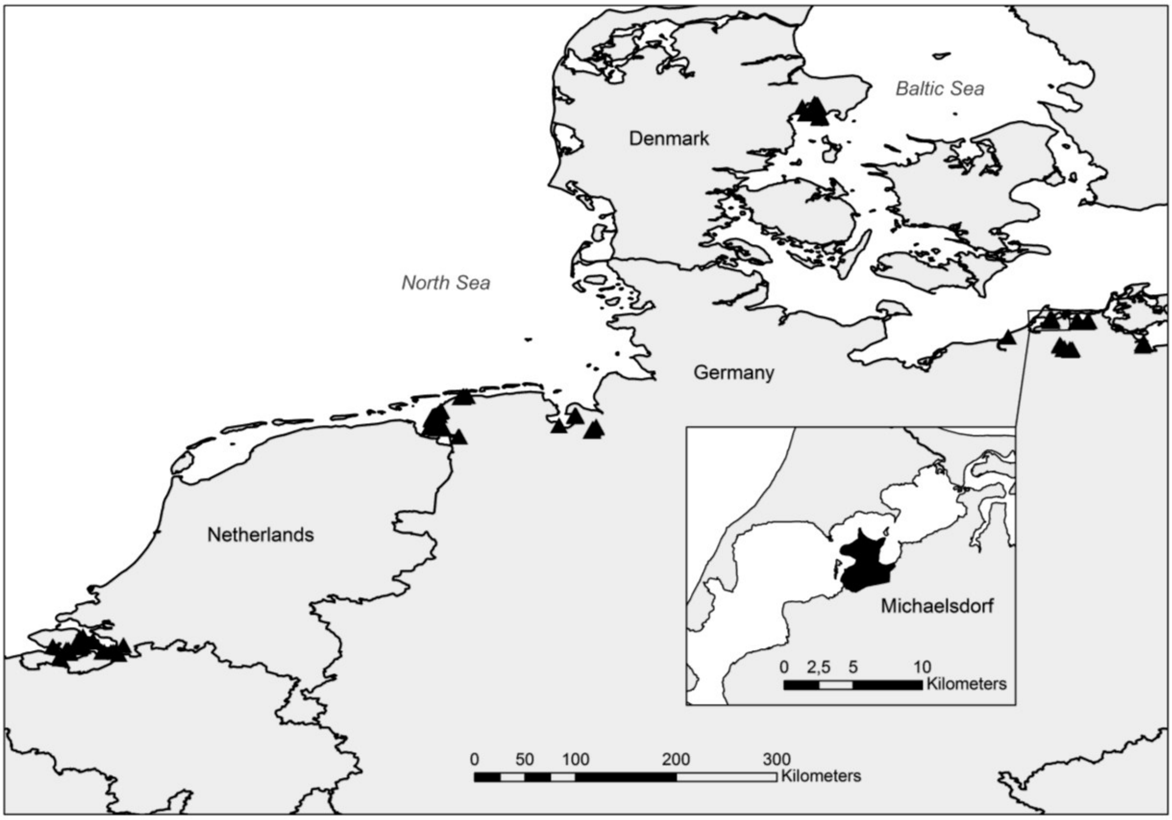

Figure C1.1. Location of data collection sites within the COMTESS project along the German, Danish and Dutch coastline of the Baltic and North Sea coast. Inset map shows the location of study region Michaelsdorf for which spatio-temporally explicit simulations of hydrological conditions and vegetation response were conducted.

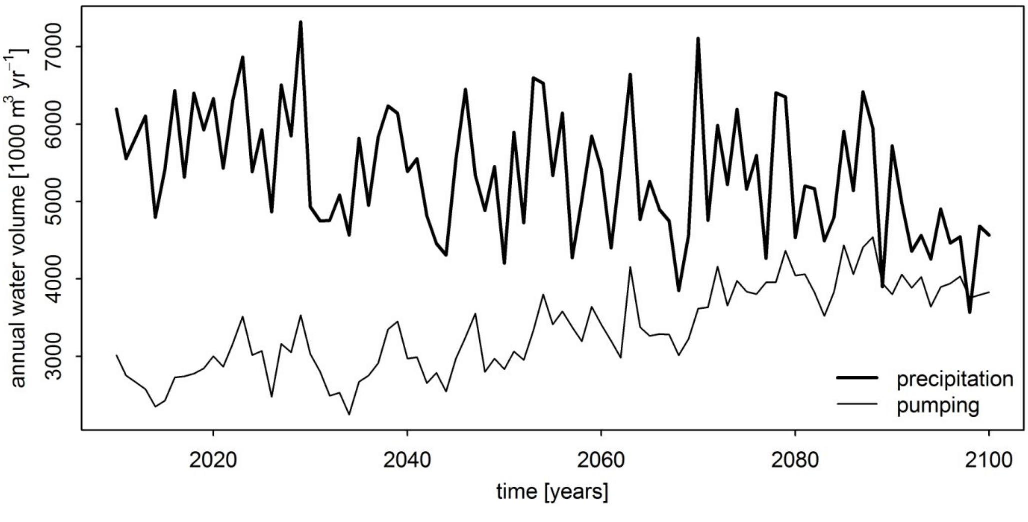

Figure C1.2: Time series of precipitation (WETTREG, realization 5a; Enke et al. 2005) and pumping rates (Kliesch et al. 2016) for Michaelsdorf.

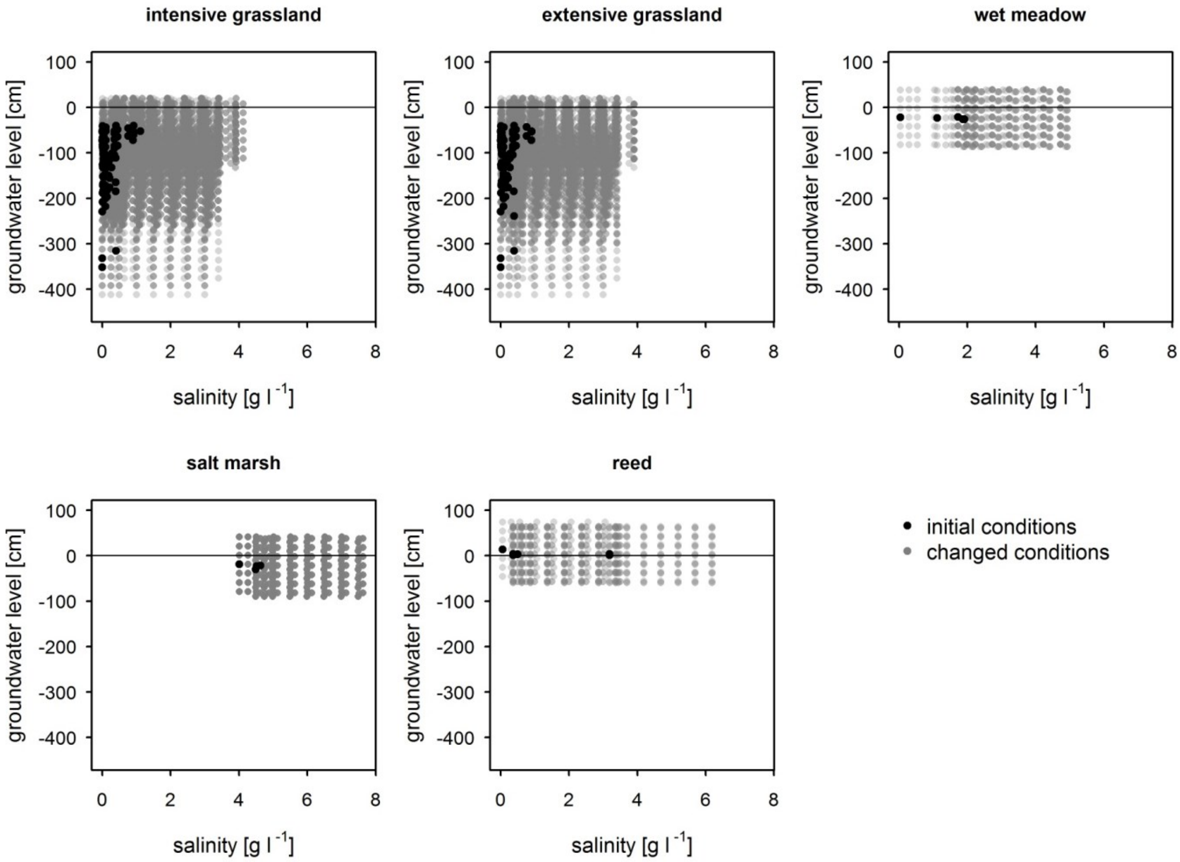

Figure C1.3. Comparison of groundwater level and salinity conditions before (black) and after (grey) simulated change events per habitat type.

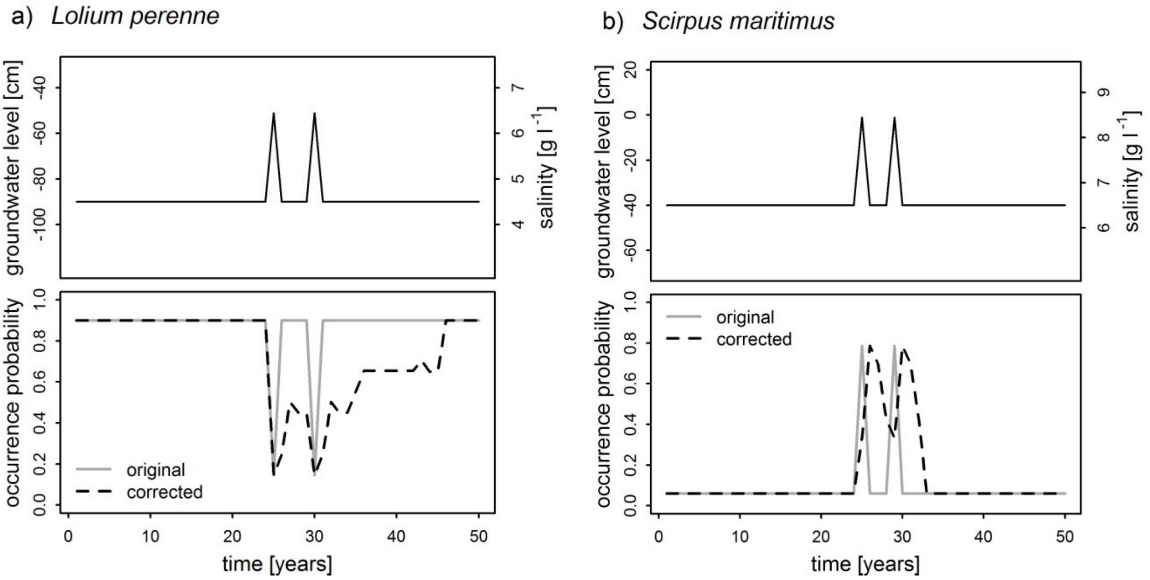

Figure C1.4. Examples of a series of abrupt one-year changes of groundwater level (+ 40 cm) and salinity (+ 2 g l^{-1}) for a) *Lolium perenne* and b) *Scirpus maritimus.* The final correction is the absolute maximum of all corrections.

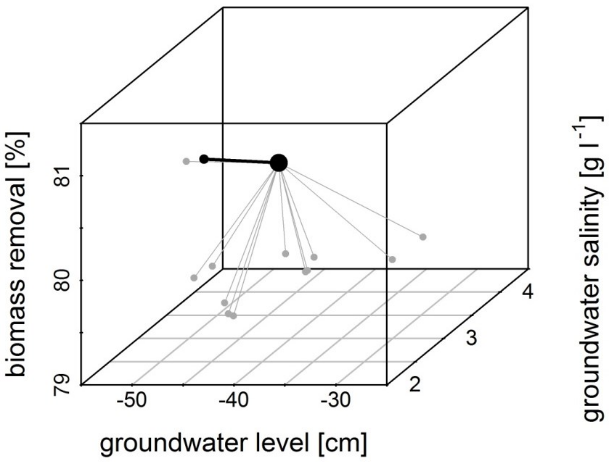

Figure C1.5. Example of finding the closest match concerning groundwater level, salinity and biomass for a positive *L. perenne* peak (grey). The small black dot is the closest case to the example case (big dot) for which the SDM predicted no response, and for which a peak had to be drawn from the pool of 13 cases for which the SDM 'correctly' predicted positive peaks.

Figure C1.6. See next page.

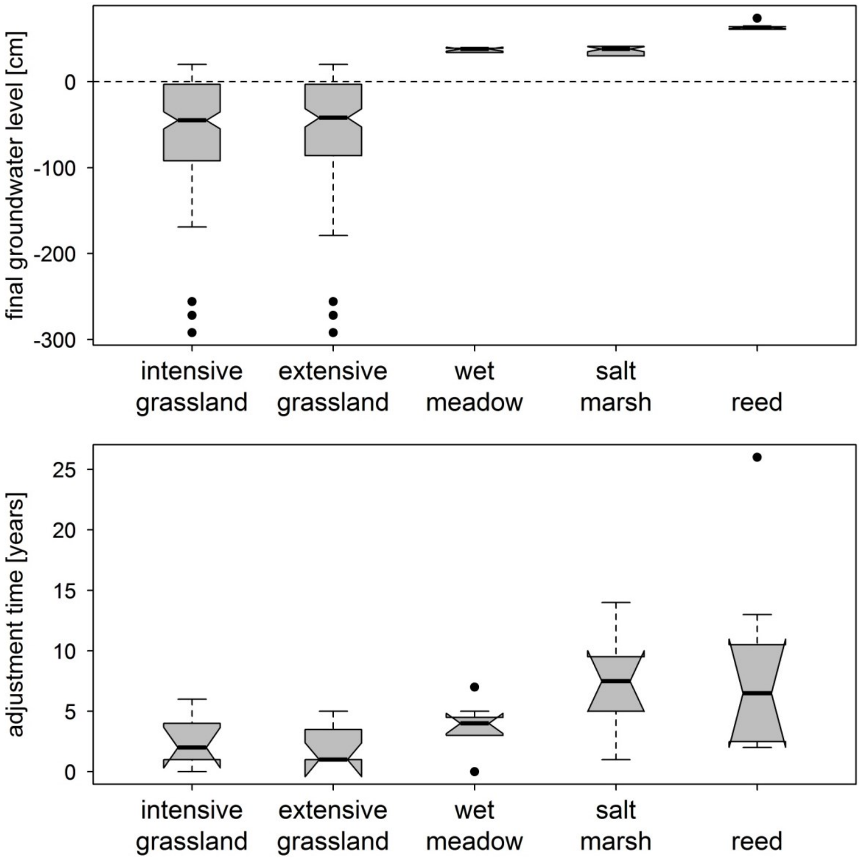

Figure C1.7. For each habitat type, the final groundwater levels (i.e. after the change) and resulting adjustment times for *S. maritimus* are given for groundwater level change + 60 cm. The variation in the upper panel stems from the conditions of different successful parameterizations from which cases are drawn for the simulation experiments (cf. **Fig. C1.3**); the number of values making up the boxplots differs between habitat types. The variation in the lower panel stems from eight different salinity changes investigated in combination with + 60 cm groundwater level increase (cf. last row in each lookup table, **Fig. C1.6**).

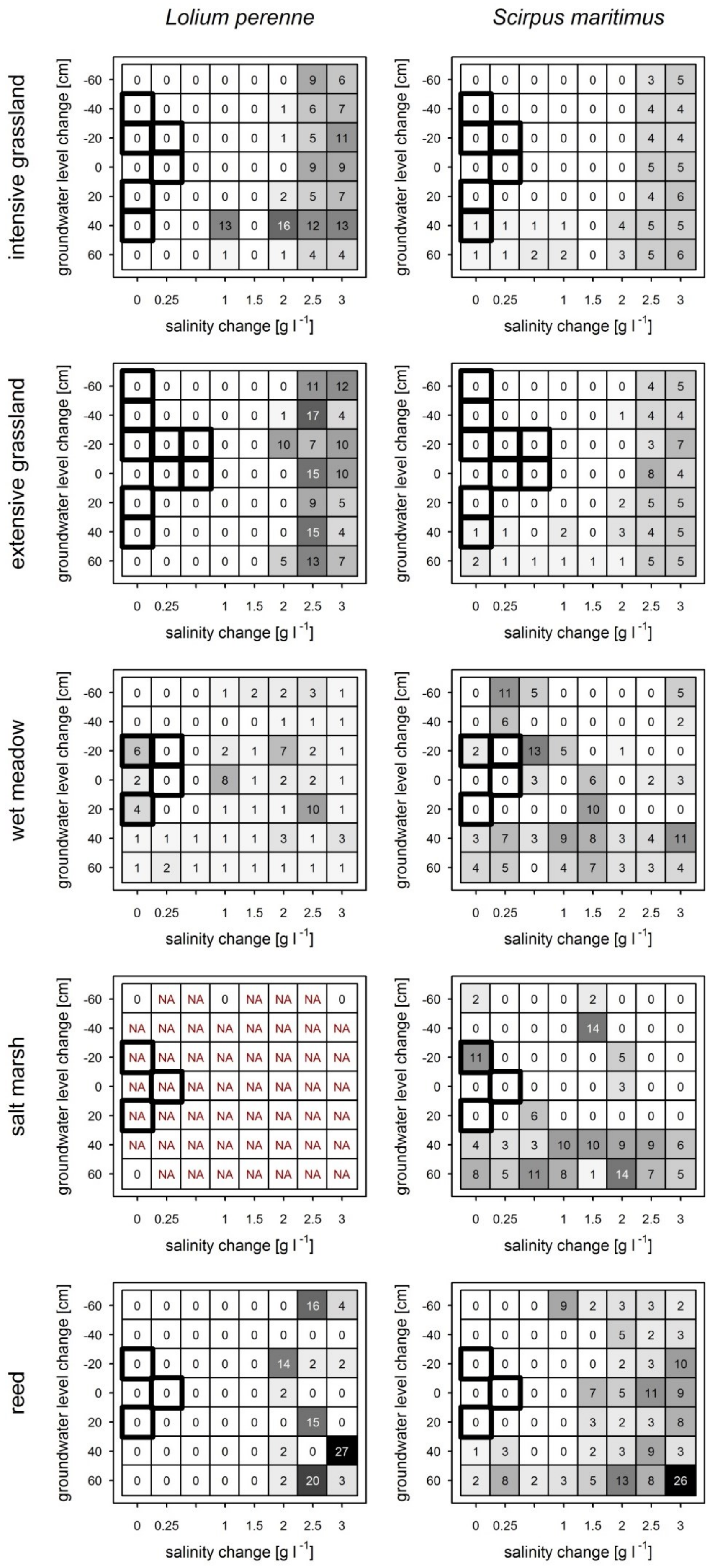

Figure C1.6. Species-specific lookup tables of adjustment times per habitat type. Bold frames mark occurring cases in our example data set. NAs mean that this species was never present in any model simulation of that habitat (here: *L. perenne* never occurred in most salt marsh simulations).

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	0	0	0	0	0	9	6
-40	0	0	0	0	0	1	6	7
-20	0	0	0	0	0	1	5	11
0	0	0	0	0	0	0	9	9
20	0	0	0	0	0	2	5	7
40	0	0	0	13	0	16	12	13
60	0	0	0	1	0	1	4	4

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	0	0	0	0	0	3	5
-40	0	0	0	0	0	0	4	4
-20	0	0	0	0	0	0	4	4
0	0	0	0	0	0	0	5	5
20	0	0	0	0	0	0	4	6
40	1	1	1	1	0	4	5	5
60	1	1	2	2	0	3	5	6

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	0	0	0	0	0	11	12
-40	0	0	0	0	0	1	17	4
-20	0	0	0	0	0	10	7	10
0	0	0	0	0	0	0	15	10
20	0	0	0	0	0	0	9	5
40	0	0	0	0	0	0	15	4
60	0	0	0	0	0	5	13	7

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	0	0	0	0	0	4	5
-40	0	0	0	0	0	1	4	4
-20	0	0	0	0	0	0	3	7
0	0	0	0	0	0	0	8	4
20	0	0	0	0	0	2	5	5
40	1	1	0	2	0	3	4	5
60	2	1	1	1	1	1	5	5

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	0	0	1	2	2	3	1
-40	0	0	0	0	0	1	1	1
-20	6	0	0	2	1	7	2	1
0	2	0	0	8	1	2	2	1
20	4	0	0	1	1	1	10	1
40	1	1	1	1	1	3	1	3
60	1	2	1	1	1	1	1	1

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	11	5	0	0	0	0	5
-40	0	6	0	0	0	0	0	2
-20	2	0	13	5	0	1	0	0
0	0	0	3	0	6	0	2	3
20	0	0	0	0	10	0	0	0
40	3	7	3	9	8	3	4	11
60	4	5	0	4	7	3	3	4

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	NA	NA	0	NA	NA	NA	0
-40	NA	NA	NA	NA	NA	NA	NA	NA
-20	NA	NA	NA	NA	NA	NA	NA	NA
0	NA	NA	NA	NA	NA	NA	NA	NA
20	NA	NA	NA	NA	NA	NA	NA	NA
40	NA	NA	NA	NA	NA	NA	NA	NA
60	0	NA	NA	NA	NA	NA	NA	NA

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	2	0	0	0	2	0	0	0
-40	0	0	0	0	14	0	0	0
-20	11	0	0	0	0	5	0	0
0	0	0	0	0	0	3	0	0
20	0	0	6	0	0	0	0	0
40	4	3	3	10	10	9	9	6
60	8	5	11	8	1	14	7	5

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	0	0	0	0	0	16	4
-40	0	0	0	0	0	0	0	0
-20	0	0	0	0	0	14	2	2
0	0	0	0	0	0	2	0	0
20	0	0	0	0	0	0	15	0
40	0	0	0	0	0	2	0	27
60	0	0	0	0	0	2	20	3

groundwater level change [cm]	0	0.25		1	1.5	2	2.5	3
-60	0	0	0	9	2	3	3	2
-40	0	0	0	0	0	5	2	3
-20	0	0	0	0	0	2	3	10
0	0	0	0	0	7	5	11	9
20	0	0	0	0	3	2	3	8
40	1	3	0	0	2	3	9	3
60	2	8	2	3	5	13	8	26

Appendix C2

Description of individual-based model IBC-grass_coast (ODD protocol) ► see CD

Appendix C3

Validation of individual-based model IBC-grass_coast

► see CD for full description and **Figures C3.1** – **C3.5**

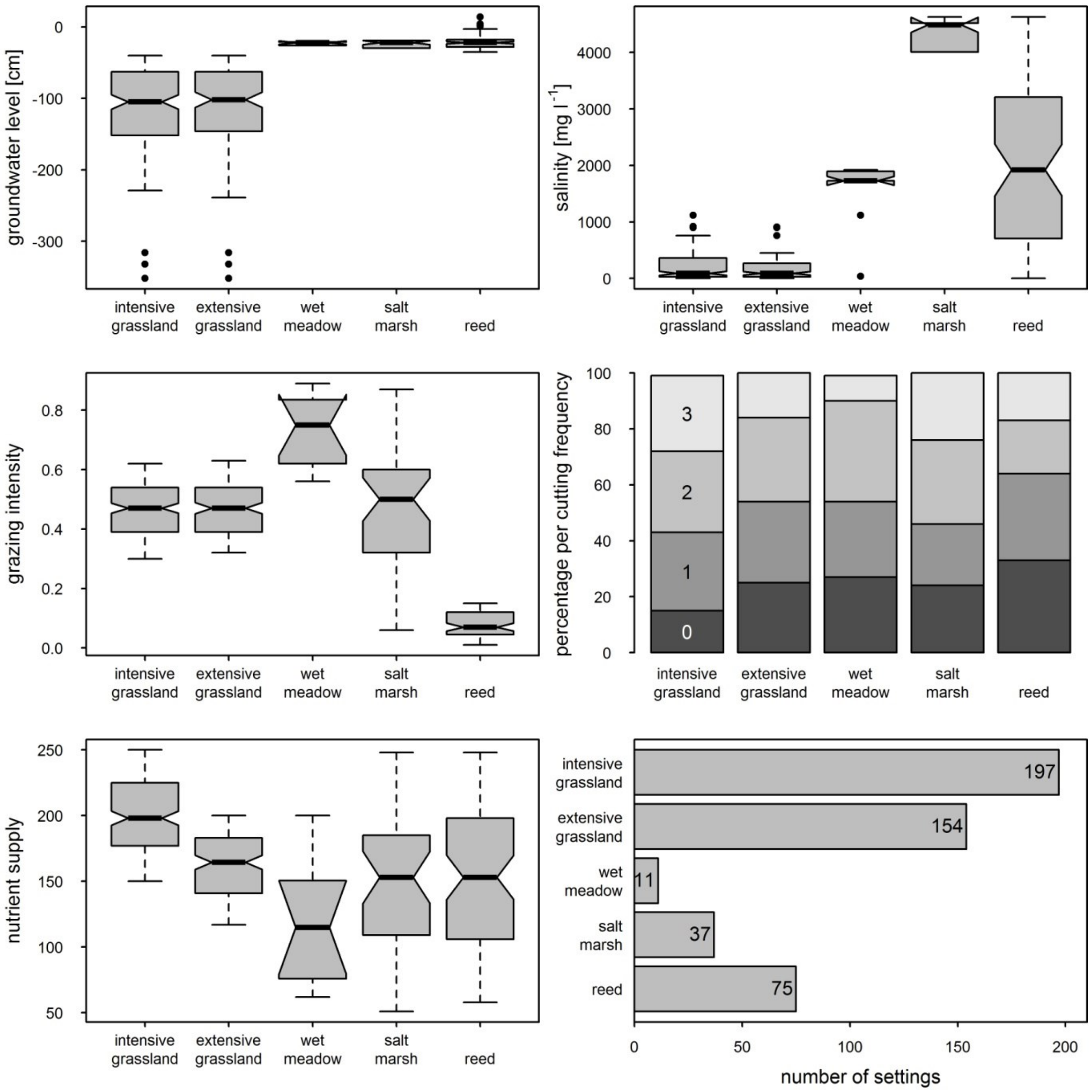

Figure C3.6. Overview of environmental conditions for each of the five habitat types in the simulation experiments by the individual-based model. Boxplots show the variation of environmental variables among different settings per habitat type (see number of settings per habitat type in the last panel).

Appendix C4

Habitat type classification

The simulations of the individual-based model were run for each of five habitat types which were the basis for parameterization (see **Appendix C3**, CD). Thus, for the application of lookup tables in the model coupling, we needed to assign each hydrotope in each simulation year one of the five habitat types (**Table C4.1**). To this end we analyzed the SDM-predicted species community for the presence of species characterizing each habitat type (**Table C4.2** and **Fig. C4.1**).

Table C4.1. Assignment of species groups (see **Table C4.2**) to each habitat type based on ecological knowledge. Last column gives the number of plots for each habitat type in our data.

habitat type	description	present	allowed	absent	n
intensive grassland (**IG**)	grazing (cattle and horses), up to 5 cuts, high nutrient input	IG		EG, WM, SM, R	33
extensive grassland (**EG**)	lower grazing intensity, up to 2 cuts, lower nutrient input	EG	IG	WM, SM, R	42
wet meadow (**WM**)	no nutrient input, 1 cut	WM	IG, EG, R	SM	34
salt marsh (**SM**)	coastal marshlands	SM		IG, EG, WM, R	124
reed (**R**)	reed species dominant, no grazing, no cutting	R	WM, SM	IG, EG	83

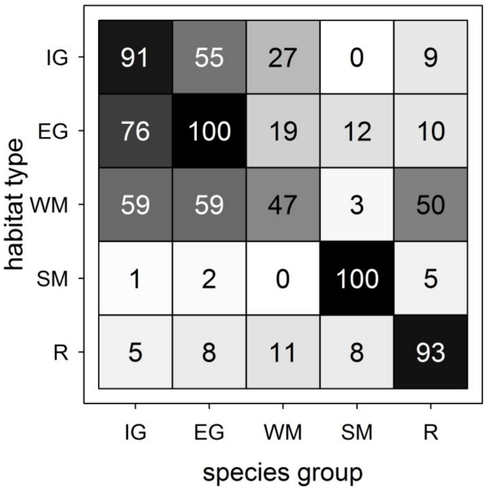

Figure C4.1. Distribution of species groups among habitat types from the observations. Numbers are share of the plots of a given habitat type on which any species of a given species group was present (IG = intensive grassland, EG = extensive grassland, WM = wet meadow, SM = salt marsh, R = reed). E.g. on all extensive grasslands species of the respective groups were present (100 %), but only 91 % of the plots classified as intensive grassland also contained species of the intensive grassland species group.

Predicted occurrence probabilities were classified as present if they exceeded the species-specific classification threshold κ_{MAX} (**Table C4.2**). The resulting sets of present species were then sorted into the respective species groups (**Table C4.2**). Rule-based queries applied to the number of species in each group then determined the habitat type in two steps (first, **Table C4.3a**, then **Table C4.3b**). For example, intensive grasslands (IG) were classified if the number of species in the IG group was greater than in any other group (**Table C4.3a**, row 1) and if the sum of all IG species was greater than the sum of all other groups (**Table C4.3b**, row 2). Reeds (R) were classified if at least one of the two R species (*Phragmites australis* and *Scirpus maritimus*) was present, but no IG species were (**Table C4.3a**, row 6), and other classifications were overridden if both R species were present (**Table C4.3b**, row 1). If none of the characteristic species were present (but instead other species of the 61 modeled), we assumed the most common habitat type in our landscape, extensive grassland.

Table C4.2. Sorting of 33 COMTESS species into species groups used to define habitat types (see **Table C4.1**), the performance of each species' occurrence model (mean ± SE of AUC and explained deviance [%] from 10-fold cross-validation) and the classification threshold κ_{MAX} (Allouche et al. 2006) above which occurrence probabilities were classified as present.

habitat type	#	species	model performance		classification threshold κ_{MAX}
			expl. dev.	AUC	
intensive grassland (IG)	1	*Alopecurus pratensis*	39.7 ± 7.4	0.92 ± 0.02	0.53
	2	*Bellis perennis*	24.3 ± 11.1	0.89 ± 0.04	0.20
	3	*Lolium perenne*	56.2 ± 6.7	0.95 ± 0.01	0.40
	4	*Phleum pratense*	18.5 ± 7.6	0.79 ± 0.05	0.32
	5	*Taraxacum Sec. Ruderalia*	36.8 ± 4.6	0.89 ± 0.02	0.56
	6	*Trifolium repens*	30.0 ± 4.7	0.84 ± 0.03	0.28
extensive grassland (EG)	7	*Agrostis capillaris*	19.6 ± 10.6	0.83 ± 0.06	0.41
	8	*Anthoxanthum odoratum*	11.9 ± 13.6	0.85 ± 0.05	0.35
	9	*Cerastium fontanum s. vulgare*	25.2 ± 4.3	0.83 ± 0.04	0.30
	10	*Cynosurus cristatus*	9.7 ± 6.9	0.71 ± 0.09	0.20
	11	*Elymus repens*	22.6 ± 5.5	0.82 ± 0.05	0.40
	12	*Festuca rubra* subsp. *rubra*	30.9 ± 5.8	0.88 ± 0.02	0.26
	13	*Holcus lanatus*	35.4 ± 6.2	0.86 ± 0.03	0.36
wet meadow (WM)	14	*Alopecurus geniculatus*	38.8 ± 7.8	0.94 ± 0.02	0.35
	15	*Deschampsia cespitosa*	34.3 ± 9.5	0.87 ± 0.06	0.35
	16	*Galium palustre*	18.4 ± 9.6	0.82 ± 0.06	0.53
	17	*Juncus conglomeratus*	20.2 ± 11.8	0.78 ± 0.10	0.31
salt marsh (SM)	18	*Juncus gerardi*	20.7 ± 8.1	0.83 ± 0.06	0.42
	19	*Artemisia maritima*	22.0 ± 9.3	0.88 ± 0.05	0.25
	20	*Aster tripolium*	38.8 ± 5.7	0.90 ± 0.02	0.49
	21	*Atriplex littoralis*	23.3 ± 5.0	0.92 ± 0.02	0.43
	22	*Elymus pycnanthus*	59.4 ± 3.6	0.97 ± 0.01	0.29
	23	*Halimione portulacoides*	44.9 ± 5.9	0.92 ± 0.02	0.39
	24	*Limonium vulgare*	18.7 ± 8.7	0.93 ± 0.03	0.41
	25	*Puccinellia maritima*	47.1 ± 6.3	0.94 ± 0.02	0.42
	26	*Salicornia europaea*	24.4 ± 6.8	0.87 ± 0.03	0.26
	27	*Spartina anglica*	22.2 ± 7.7	0.89 ± 0.03	0.27
	28	*Spergularia media*	31.7 ± 6.1	0.93 ± 0.03	0.49
	29	*Suaeda maritima*	32.4 ± 5.3	0.92 ± 0.02	0.22
	30	*Triglochin maritima*	17.7 ± 5.9	0.86 ± 0.03	0.23
	31	*Festuca rubra* subsp. *littoralis*	18.4 ± 3.7	0.80 ± 0.02	0.17
reed (R)	32	*Phragmites australis*	46.2 ± 3.8	0.92 ± 0.02	0.46
	33	*Scirpus maritimus*	30.8 ± 6.5	0.88 ± 0.02	0.34

We applied this rule-based procedure to observed species presences and compared the result with observed habitat types (as classified manually based on ecological knowledge of the data collectors in the field; plot data, n= 318). On average, 83 % of the habitat types were correctly classified using our method (**Table C4.4a**) compared to 76 % when predicted species presences were used (**Table C4.4b**, added error of species predictions). However, the classification success varied greatly among habitat types: Salt marshes (n=124) were easiest to classify (98 % classification success) as salt marsh species were rare in other habitat types (**Fig. C4.1**). Wet meadows on the other hand, were often mistaken for extensive grasslands (**Table C4.4**) as all other species groups (but salt marsh) were common on wet meadow plots (**Fig. C4.1**).

We considered the procedure detailed above fit for classifying predicted species occurrences into habitat classes. **Fig. C4.2** shows the predicted species time series for the three example polygons and the resulting habitat type. In polygon A, *Festuca rubra* subsp. *littoralis* is replaced by *S. maritimus* in 2050, tipping the species balance from salt marsh to reed. In polygon B, the loss of *Lolium perenne* starting in 2063 turns intensive grassland into wet meadow. In polygon C, three intensive grassland species constantly dominate.

Table C4.3a. Rule-based definition of habitat types based on the number of species present in a given hydrotope that belong to each species group (**Table C4.2**).

condition 1	condition 2	condition 3	condition 4	result
IG > EG	IG > WM	IG > SM	IG > R	intensive grassland (IG)
EG ≥ IG	EG > WM	EG > SM	EG > R	extensive grassland (EG)
WM ≥ IG	WM ≥ EG	WM ≥ R	SM == 0	wet meadow (WM)
SM > IG	SM > EG	SM > WM	SM > R	salt marsh (SM)
SM > 1	R == 1			
R > 0	IG == 0			reed (R)
sum(IG, EG, WM, SM, R) == 0				NA
> 1 of the above rules == TRUE				ambiguous
all other cases				missing rule

Table C4.3b. Rules queried after rules in **Table C4.3a** to resolve ambiguity, missing rules and NAs resulting from first set of rules (= habitat type before). The new habitat types (= habitat type after) were the final result of the rule-based classification.

habitat type before	conditions			habitat type after
any	R == 2			R
IG			sum(EG, WM, SM, R) > IG	most common group (≠ IG)
ambiguous	EG > 0	R > 0		WM
ambiguous	SM > 2	R ≤ 1	sum(IG, EG, WM) == 0	SM
ambiguous	R == 1	WM == 1	sum(IG, EG, SM) == 0	R
ambiguous	EG == WM	SM == 0		WM
ambiguous	EG == 2	R==1		EG
missing rule	IG == R		sum(EG, WM, SM) == 0	WM
NA	without character species, assume most common type:			EG

Table C4.4. Plot-based habitat type classification success of rule-based query for observed (a) and predicted (b) species presences. (IG = intensive grassland, EG = extensive grassland, WM = wet meadow, SM = salt marsh, R = reed, ambig = ambiguous, miss = missing rule).

a) observed species	predicted habitat type (% of plots with observed type)						
observed type	IG	EG	WM	SM	R	ambig	miss
intensive grassland	**76**	18	6	-	-	-	-
extensive grassland	2	**94**	0	-	-	2	2
wet meadow	8	18	**65**	-	7	2	-
salt marsh	-	-	-	**98**	1	1	-
reed	1	8	2	1	**83**	5	-

b) predicted species	predicted habitat type (% of plots with observed type)						
observed type	IG	EG	WM	SM	R	ambig	miss
intensive grassland	**62**	26	6	3	-	-	3
extensive grassland	2	**81**	11	2	2	-	2
wet meadow	5	20	**60**	3	5	5	2
salt marsh	-	-	-	**98**	1	1	-
reed	-	4	11	6	**77**	2	-

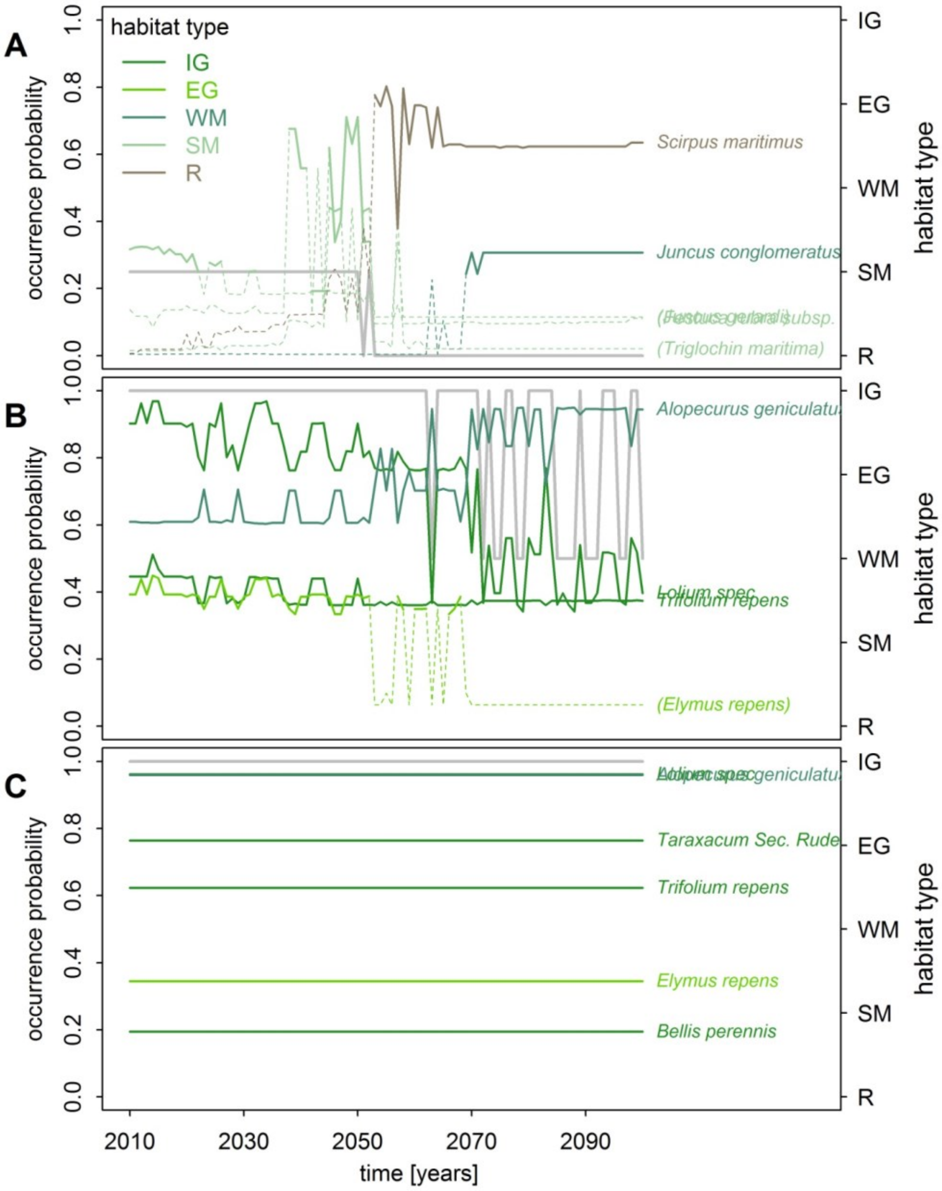

Figure C4.2: Time series of all species being present in any year (2010-2100) in example polygons A, B, C (see map in **Fig. 4.1** and groundwater level and salinity time series in **Fig. 4.11**). Species that were absent for the entire time series are not shown. Solid lines mean the predicted occurrence probability is > κmax (species-specific classification threshold, see **Table C4.2**), i.e. the species is classified as present; broken lines mean the opposite, i.e. classified absence. The colours sort species into groups characteristic for each habitat type (IG = intensive grassland, EG = extensive grassland, WM = wet meadow, SM = salt marsh, R = reed). The grey line is the time series of the classified habitat type (axis on the right).

5. Synthesis

5.1. Summary of this thesis' results

In this thesis, I applied and compared existing statistical (**chapter 2**) and process-based approaches (**chapter 3**) to predict species distributions, and I discussed their respective limitations, specifically for applications in changing environments. As a potential solution, I added a new approach (**chapter 4**) to the repertoire of existing hybrid models linking statistical and process-based models to combine their respective advantages.

5.1.1. Statistical models have their limits…

In **chapter 2**, we applied a sophisticated statistical method with two objectives going beyond a mere mapping exercise: (i) understanding the driving factors that determine the current position of one of the most prominent biome boundaries (boreal treeline) and thereby assessing its sensitivity to ongoing climate change; and (ii) examining the spatial and temporal transferability of the resulting models to evaluate whether they are able to predict future distributions.

We were fortunate to obtain large sets of abundance data from 1978 and 2003 which we additionally classified into presence-absence records. Thus, our data basis exceeded that of many recent climate change impact studies using presence-only records (Yackulic et al. 2013). The two data sets allowed us to assess environmental change over a 25-year interval during which the climate had warmed and precipitation patterns had shifted. We, thus, had the opportunity to *observe*, not hypothesize about, the performance of statistical models trained on historical data (1978) in an application to future climate data (2003) by assessing the temporal transferability of our models (see also Araújo et al. 2005b).

We employed a complex method (Boosted Regression Trees) which captures non-linear relationships as well as interactions among predictors and frequently outperforms other SDM methods in comparative studies (Mainali et al. 2015, Valle et al. 2013, Bahn and McGill 2013, Revermann et al. 2012). We carefully accounted for methodological issues such as zero inflation (Martin et al. (2005); which we counteracted using a conditional model, Fletcher et al. (2005)), overfitting (which we controlled by cross-validation, Elith et al. 2008) and spatial autocorrelation (Dormann et al. 2007; specific testing in model residuals revealed none).

Based on studies which recommend the inclusion of more meaningful predictors into SDMs (Petitpierre et al. 2017, Mod et al. 2016), we added non-climatic, abiotic factors such as edaphic and topographic characteristics as well as biotic interactions (abundance of co-occurring species) to the commonly used climatic predictors. We additionally used more complex temperature indices capturing seasonality for more process detail. Thus, climate sensitivity was not inherent in our models, as it is in SDMs based exclusively on climatic predictors. Indeed, we identified non-climatic predictors site fertility and biotic interactions as very important factors in the models, thus reducing their sensitivity to climatic changes. We compared the relative importance and response curves of predictors between occurrence and abundance models, between spatial and temporal data subsets as well as among species. The results accurately revealed ecological processes described in the literature: (i) competitive exclusion of *P. sylvestris* by the stronger competitor *P. abies* on fertile soils despite nutrient-limited growth of *P. sylvestris*; (ii) easing of temperature limitation of *P. sylvestris* in the north due to climate change; (iii) edaphic, not climatic, limitation of *P. abies*, supporting the hypothesis that the Lapland Granulite Belt functions as dispersal barrier to this species' northward migration after the last glaciation.

We rigorously examined the resulting models with respect to their predictive performance and transferability. As AUC alone has proven to be an unreliable measure of model performance (Mainali et al. 2015, Lobo et al. 2007), we additionally reported explained deviance from a tenfold cross-validation (internal evaluation). The resulting models were good (regarding AUC and explained deviance) and successfully reproduced observed patterns of presences and absences as well as general abundance patterns. However, autocorrelation in hold-out internal validation results in overly optimistic performance measures (Araújo et al. 2005a). Therefore, external evaluation on spatially segregated data is much more meaningful (Bahn and McGill 2013). We applied a transferability index (Dobrowski et al. 2011, Randin et al. 2006) to quantify the expected loss of performance on external datasets. Spatial model transfer between models trained on northern and southern data subsets proved to be more successful than temporal transfer between 1978 and 2003 models. However, in all external applications we found considerably loss of predictive accuracy. By visualizing the environmental space of training and application data (via environmental overlap masks, Zurell et al. 2012a) we demonstrated that the sampled environmental space differed between 1978 and 2003 as well as for northern and southern regions. Thus, the model transfer often meant extrapolation to novel predictor space which violates basic assumptions of SDMs and is a plausible explanation for poor model transferability.

In our SDM application, we used data of high quality, made careful choices regarding methodology as we built on results of former studies in order to estimate the best possible models, and we compared our model relationships to ecological knowledge as plausibility test. The resulting models provided valuable insights into the processes limiting boreal trees and were successful within their training data boundaries. Model transfer, however, revealed critical limitations and we consequently would not trust our SDMs with climate change projections.

5.1.2. … but so do process-based models.

As an alternative modelling approach, we applied the established, widely used 'fitted' process-based model (Dormann et al. 2012), LPJ-GUESS (Sitch et al. 2003, Smith et al. 2001), to the same data, i.e. the same spatial extent, time periods and species in **chapter 3**. It is a regionalized version of the DGVM LPJ (Sitch et al. 2003) which models vegetation dynamics at a greater level of detail similar to gap models. Because process-based models function in a mechanistic way, they are expected to be better transferable and thus more appropriate than statistical models in changing environments (Gustafson 2013, Cuddington et al. 2013). The European parameterization of LPJ-GUESS used in **chapter 3** successfully reproduces general present-day vegetation patterns across Europe (86 % of the area correctly classified in broad vegetation types, Hickler et al. 2012). Among the discrepancies between model simulations and potential natural vegetation map, Hickler et al. (2012) noted the transition of hemiboreal mixed forest to boreal forest in Southern Finland. This transition is a fine distinction based on the composition of understorey species (not modelled in LPJ-GUESS, Hickler et al. 2012). In contrast, the boreal treeline is a very important and clear pattern which we expected LPJ-GUESS to reproduce even if the exact biomass pattern would not be matched perfectly. However, our application revealed a systematic mismatch between observed and simulated biomass values. The range of biomass values simulated for northern Finland matched observations for *P. sylvestris* and *B. pubescens*, although the spatial pattern was not captured correctly. *Picea abies*, however, was greatly overestimated in terms of both, range of simulated biomass and spatial distribution, i.e. LPJ-GUESS simulated *P. abies* to occur far north of its current treeline. A second important finding was species imbalance indicated by single-species vs. multi-species model runs: *P. abies* was far too competitive in the model and consequently suppressed *P. sylvestris* and *B. pubescens*. Both, the overestimation of *P. abies* and species imbalance were also reported in studies of previous LPJ-GUESS applications.

Letting our knowledge about important factors from **chapter 2** guide us, we examined the implementation of competition between species in LPJ-GUESS via species-specific shade and drought tolerance, fire resistance, disturbance susceptibility and nutrient limitation more closely. In addition, we reviewed processes missing in our model version, but implemented in alternative LPJ-GUESS versions, i.e. nitrogen limitation, dispersal, pest calamities, storm damage, forest management. It is important to note that the LPJ-GUESS community is very active with 20-30 publications per year (2012-2016), and ongoing model development in different working groups leads to disparate model versions which are all promising (e.g. Jönsson et al. 2015, Smith et al. 2014, Snell et al. 2014). However, a model version combining all process additions for boreal ecosystems is not yet available.

We identified important areas for model development in LPJ-GUESS that are also recognized for DGVMs, in general (Bachelet et al. 2015, Quillet et al. 2010). For example, Bachelet et al. (2015) listed dispersal, CO_2 fertilization, nitrogen limitation, land management and lateral cell-to-cell water flow as missing processes in a similar DGVM (MC1). LPJ-GUESS reproduces the CO_2 effect (Hickler et al. 2008), and nitrogen limitation (Smith et al. 2014), dispersal (Snell et al. 2014) as well as forest management (Jönsson et al. 2015) are implemented in alternative LPJ-GUESS versions. However, other issues with MC1 (Bachelet et al. 2015) and DGVMs, in general (Quillet et al. 2010), equally apply to LPJ-GUESS: soil data uncertainty, the modelling of potential natural vegetation in the absence of human interactions, and more realistic representation of disturbances. Two issues identified by Quillet et al. (2010) are more relevant to our case study are: first, many DGVMs (including LPJ-GUESS in cohort mode as applied in **chapter 3**) model single average individuals instead of many heterogeneous individuals of a plant functional type (PFT) or species. This promotes dominance of the most competitive PFT (here: *P. abies*) instead of co-existence of different PFTs. Second, Quillet et al. (2010) stress that bioclimatic limits should be replaced by causal physiological constraints which are able to respond dynamically to climate change (as Arora and Boer (2005) did for leaf phenology). We demonstrate the limitations of static relationships by comparing the bioclimatic limits currently implemented in LPJ-GUESS with thresholds from our response curves in **chapter 2**. These thresholds had shifted between 1978 and 2003 due to the delayed response of trees to climate change, exemplifying the inherent problem of using correlational thresholds to parameterize process-based models. As long as bioclimatic limits are used in 'fitted' process-based models, they cannot be expected to be much more reliable in climate change applications than statistical SDMs.

5.1.3. Combining the two approaches is one way forward.

After identifying limitations of statistical and process-based approaches in **chapters 2** and **3**, we introduced a new method to combine the two in **chapter 4**. We propose a two-step procedure that is similar to existing hybrid model approaches (see **Table 1.3**) in using the output from one model type to feed into the other. Unlike most of the existing hybrid models, which transfer SDM-derived habitat suitability, we transfer temporal patterns of species responses. The temporal pattern emerges from dynamically modelled individual-level processes of population and community dynamics. We, thereby, condense the complexity of the PBM into one pattern, the development of species after disturbance events. This is the relevant process-detail in our specific application which SDMs lack. The application of the coupled model consists of looking up simulated species responses for similar cases occurring in the application data, thereby minimizing computational effort, which is a limiting factor in long-term, large-scale applications.

The proposed framework to link PBM and SDM via condensed process knowledge from PBM experiments overcomes the limitations of SDMs (missing process detail to capture transient dynamics following disturbances) and PBMs (computational effort). While we still require detailed species data for the parameterization of the PBM (persisting limitation), we avoid combining the two approaches' weaknesses. Because our direction of knowledge or information transfer is from PBM to SDM (contrary to current approaches), we neither transfer the SDM's weakness of low transferability to the PBM, nor do we face circularity problems (Schymanski et al. 2013). Circularity refers to the fact that SDMs are based on real-world observations, the result of processes such as biotic interactions, population dynamics and dispersal. These processes are thus implicitly (not explicitly!) included in SDM predictions and may subsequently be contained twice in hybrid models linked by SDM-derived habitat suitability (circularity, Gallien et al. 2010).

Another advantage of transferring the well-defined output from one model type to the other is the flexibility of the resulting framework. This is similar to existing hybrid models in which SDMs are interchangeable as long as they estimate habitat suitability. We hope that our framework will be utilized by other modellers, as hybrid models are still promising improvements on classic SDMs in environmental change applications, although even more complex and sophisticated approaches are looming on the horizon (see *section 5.3.2*).

5.2. Lessons learned [4]

5.2.1. Don’t blame the hammer (for screwing wrong)

Statistical SDMs predict species-specific habitat suitability based on observed species distribution and concurrently observed environmental variables. Environmental input variables are often restricted to abiotic, mostly climatic, factors (Araújo and Peterson 2012, Pearson and Dawson 2003). However, the observed species distribution results from a complex interplay of abiotic and biotic limitations as well as from dynamic processes over time (see *section 1.1*). These additional processes are not included explicitly as predictor variables in SDMs, but implicitly, as they are ‘hidden’ in the observed distribution of species (Gallien et al. 2010). The observed correlation between species distribution and e.g. climate is a surprisingly good estimate of habitat suitability for all cases in which the estimated as well as hidden relationships remain constant (stationarity, Osborne et al. 2007). This is the application for which the tool SDM is made: hammering (e.g. successful SDM application within training data ranges in **chapter 2**).

Applying SDMs to cases in which the relationships of underlying processes differ (e.g. in distant regions, Osborne et al. (2007), or due to climate change, **chapter 2**) is like driving in a screw with a hammer: using a tool designed and optimized for a specific task for something else. It can be done by brute force, but it will not result in the desired quality and prompt qualified craftsmen to sadly shake their heads. In this light, SDMs do not ‘fail’ by not explicitly including factors limiting species except climatic suitability (e.g. Warren et al. 2014), but they are simply ill-equipped for the new task (Araújo and Peterson 2012, Pearson and Dawson 2003). Predicting species distributions in changing environments requires the relevant processes to be added to SDMs, e.g. by coupling them to PBMs (with explicit process representation) in hybrid models (Zurell et al. 2016, Thuiller et al. 2008).

Similarly, process-based models in which relevant processes are missing (e.g. dispersal barriers, **chapter 3**) or miscalibrated (e.g. competition, **chapter 3**) may not be expected to function satisfactorily. Global DGVMs (e.g. LPJ) need to be downscaled for regional applications (e.g. LPJ-GUESS), analogous to regional climate models which downscale general circulation models (Fowler et al. 2007). This includes adding process detail irrelevant on the more aggregated global scale (e.g. detailed soil or topography information, Bachelet et al. 2015). In conclusion, model failure in inappropriate applications (including our application of well-behaved SDMs beyond their training data range in **chapter 2** or our application of LPJ-GUESS without reparameterization in **chapter 3**) is not really a problem of the model but of the modeller ignoring inherent model limitations.

5.2.2. Knowing your model’s weaknesses is actually a strength

Especially for statistical SDMs, recent years have seen publications soaring that are dedicated exclusively to their limitations (e.g. Warren et al. 2014, Zurell et al. 2009, Jiménez-Valverde et al. 2008, Guisan et al. 2006). While this might seem daunting combined with the dizzying multitude of methods available (see overview in Beaumont et al. (2016) and Heikkinen et al. (2006)), the awareness of model limitations actually promotes more sound applications. For example, there are more tools available to detect and eliminate violations of underlying assumptions, e.g. spatial

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[4] Being worthy of a cheesy motivational poster does not mean it is without merit!

autocorrelation (Crase et al. 2012, Dormann et al. 2007, Segurado et al. 2006), non-stationarity (Hothorn et al. 2011, Osborne et al. 2007) or collinearity (Dormann et al. 2013). Available tools to better fit and interpret models include supporting R functions for BRT (Elith et al. (2008); now part of R package `dismo`, Hijmans et al. (2016)) and the detection and visualization of spurious extrapolation (Zurell et al. (2012a); used in **chapter 2**). The virtual ecologist approach (Thibaud et al. 2014, Zurell et al. 2010) allows the selection of sampling strategies and analysis of potential bias before collecting field data to estimate or validate SDMs, and to vigorously assess SDM methods themselves (Zurell et al. 2016). Several publications provide proper guidelines that help users to choose the right methodologies (Anderson 2015, Jarnevich et al. 2015, Guillera-Arroita et al. 2015, Heikkinen et al. 2006), concerning e.g. data preparation (Zuur et al. 2010), model selection (Symonds and Moussalli 2011, Ye 1998), specific model types such as BRT (Elith et al. 2008, Bühlmann and Hothorn 2007) or MaxEnt (Elith et al. 2011, Elith et al. 2010), variable selection (Petitpierre et al. 2017, Bradter et al. 2013, Austin and Niel 2011) and model performance measures (Bahn and McGill 2013).

5.2.3. Model failure is not a failure as long as you learn from it

Publication bias describes the fact that negative results (i.e. contradicting initial expectations, unable to reject the null hypothesis) are less likely to be submitted and accepted for publication (Coursol and Wagner 1986). Combined with the prevailing ‘publish-or-perish’ culture in academia (Fanelli 2010), scientists often abandon less successful attempts instead of trying to publish results from a failed experiment (van Hilten 2015). This bias is widely recognized, especially in medical research (e.g. Dirnagl and Lauritzen 2010, Easterbrook et al. 1991) but also in ecology (Parker et al. 2016, Jennions and Møller 2002), although Harlos et al. (2017) recently claimed no bias occurs in climate research. Publication bias mainly impacts on results of literature reviews and meta-analysis (Leimu and Koricheva 2004, Murtaugh 2002). But there is more to it: if researchers do not publish their so-called failed attempts, fellow scientists cannot benefit from their experience. This in turn wastes their time and money in unnecessary replications of the same trials (van Hilten 2015). Replication studies are only of value independently testing the reproducibility of results if these results are published (Parker et al. 2016, Thiele and Grimm 2015). As a solution, specified journals explicitly call for negative results of clinical trials (e.g. Journal of Negative Results in BioMedicine, since 2002; Journal of Pharmaceutical Negative Results, since 2010) and ecological experiments (Journal of Negative Results, since 2004; New Negatives in Plant Science, 2014-2016). An alternative attempt to promote the publication of all research results is the preregistration of studies (Parker et al. 2016).

There is a huge difference between ‘negative’ results of sound scientific experiments (which are proper results, just not the expected results) and a model’s inability to reproduce observed patterns (model failure). Model failure may be dismissed as mistakes made by the modeller (e.g. in choosing the model, preparing the data, setting the parameters etc.) and simply seen as a step of the model development process unworthy of publication. However, I argue, these model failures are of interest to fellow modellers, especially if they are further discussed (as we did in **chapter 3**). For example, when discussing our findings within the LPJ-GUESS community, we frequently learned that our problems were well-known, but as yet untackled issues within the community. Unfortunately, we were unable to find references for these insights, because they had never been published. Publishing more problematic issues (as demonstrated in the field of statistical SDMs, see *section 5.2.2*) would become the process-based modelling community[5]. In order to learn from (other researchers') model failure, less successful modelling studies need to be discussed and published, thereby serving as a starting point for further modelling attempts. How else are we supposed to stand on the shoulders of giants?

5.3. Ways forward

Bearing in mind the lessons learned in this thesis, I summarize four ways forward in species distribution modelling. These include congruent predictions by different modelling approaches, integration of process-based and statistical methods, better data for model estimation and validation as well as more transparency when reporting and communicating model results.

5.3.1. Compare predictions by different approaches

The aim of several of the studies listed in **Table 1.2** is a methodological comparison of model approaches (Cheaib et al. 2012, Webber et al. 2011, Elith et al. 2010, Buckley et al. 2010). Others focused specifically on producing congruent, robust forecasts and reducing model uncertainty (Briscoe et al. 2016, Estes et al. 2013, Morin and Thuiller 2009). Even models, which agree on current species distributions (most example studies in **Table 1.2**), frequently disagree when projecting future distributions. Similar behaviour has been reported for model comparisons among the same model type, e.g. DGVMs (Sitch et al. 2008, Cramer et al. 2001) as well as for global and regional climate and hydrological models (Teklesadik et al. 2017, Radić et al. 2014). For validation, future predictions cannot be compared to observations, and data sets of historical climate change for tests of temporal model transferability are rare (but see Araújo, Whittaker et al. (2005b) and **chapter 2**; simulated data using the virtual ecologist approach (Zurell et al. 2010) is another alternative). Thus, differences among forecasts by various models are an indication of their uncertainty (Pearson et al. 2006), whereas consistency of model predictions for current *and* future conditions (Lozier and Mills 2011, Kearney et al. 2010, Hijmans and Graham 2006) suggest robust predictions (consensus, Gritti et al. 2013). The harder the test, i.e. the greater the difference between model approaches in structure, process representation and input data, the more confidence do congruent predictions inspire. For example, BIOMOD offers different consensus algorithms to aggregate a suite of statistical models (Meller et al. 2014) which result in more robust predictions than single models (Marmion et al. 2009). In contrast, Gritti et al. (2013) covered an even wider methodological spectrum by integrating statistical and process-based model predictions into consensual maps. In most of our example cases (**Table 1.3**), the two model approaches agreed in some areas and differed in others (e.g. Briscoe et al. 2016, Webber et al. 2011), thereby marking areas of differing uncertainty.

In the case of disagreement between models, identifying the reason provides valuable insights into e.g. missing processes and inspires future model development. For example, the effect of CO_2 fertilization (missing in SDMs) explains the divergent predictions of maize and wheat in South Africa (Estes et al. 2013) as well as tree species in Spain (Keenan et al. 2011) and France (Cheaib et al. 2012). Other reasons for disagreement between model predictions include extrapolation

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[5] I do acknowledge that I may well be biased in my perspective on critical literature in ecological modelling, and there may in fact be as many critical publications about PBMs (yet unknown to me) as there are about SDMs.

behaviour (Webber et al. 2011, Pearson et al. 2006) and missing biotic interactions in ecophysiological models (Buckley et al. 2010, Morin and Thuiller 2009).

Our application of two different model approaches to the same region, species and input datasets (**chapter 2** and **3**) was originally aimed at comparing future predictions. But the results of the temporal transferability experiment of the SDM (**chapter 2**) inspired no confidence in their applicability to future climate data, and the PBM even failed to correctly reproduce current observations (**chapter 3**). Yet, while investigating the reasons of model discrepancy, we discovered spurious extrapolation (**chapter 2**) and identified missing and miscalibrated processes requiring further model development (**chapter 3**; see also learning from model failure, *section 5.2.3*). Comparing the temporal development of SDM and PBM predictions in **chapter 4** revealed discrepancies that support our expectation of the inability of SDMs to model species responses over time. This served as motivation for transferring the required process detail from PBM to SDM by linking the two model approaches.

5.3.2. Find (more) ways to integrate statistical and process-based approaches

While existing hybrid models (including the novel approach presented in **chapter 4**) are promising as they introduce more process detail to SDMs, critical limitations remain (Ehrlén and Morris 2015). For example, detailed species data are still required to parameterize PBMs, and using SDM output transfers the weakness of lower transferability and potential circularity problems along with e.g. habitat suitability (see *section 5.1.3*). A fundamentally different approach compared to hybrid models is integrating statistical and process-based methods as in e.g. dynamic range models (DRMs, Pagel and Schurr 2012). DRMs do not rely on SDM-derived habitat suitability, but instead use a hierarchical Bayesian framework to directly relate processes such as dispersal and population dynamics to environmental conditions (Pagel and Schurr 2012). Thus, they may be seen as the extension of a gradient reaching from classic SDMs (without dynamic process implementation) to hybrid models of increasing complexity, incorporating dispersal, population and/or community dynamics (see **Table 1.3**). DRMs jointly estimate and simulate these processes and, therefore, are expected to outperform not only classic SDMs but also hybrid models (Zurell et al. 2016).

Using simulated species data (virtual ecologist approach, Zurell et al. 2010), Zurell et al. (2016) compared alternative modelling approaches: classic SDMs, hybrid models of different complexity (all using SDM-derived habitat suitability to define demographic rates or patch matrix) as well as a DRM. Under current (equilibrium) conditions, DRMs indeed outperform all alternative model approaches, although differences are marginal (Zurell et al. 2016). Thus, SDMs are confirmedly successful in their designed application, i.e. predictions under equilibrium conditions (see *section 5.2.1*). Their disadvantages compared to models including dynamic processes (hybrid models and DRM) become apparent only under future (climate change) conditions. Here, SDMs are clearly outperformed by hybrid models and DRMs (among which no clear winner emerges, Zurell et al. 2016). These results highlight the importance of introducing dynamic behaviour (dispersal, population dynamics and biotic interactions) into species distribution models for climate change applications. To this end, data availability remains a crucial limiting factor.

5.3.3. Improve data basis for model estimation and validation

Further sophistication of current modelling approaches will surely improve our ability to make robust predictions, but without the respective data there is only so much you can do. Earlier, I stressed the advantage of SDMs able to use abundant data sources of varied quality, including presence-only data (see *section 1.2.1*). However, introducing more process detail into species distribution models (hybrid or integrated models) requires more detailed, often species-specific data. For example, mechanistic niche models require detailed experimental data on physiological limits, and the corresponding environmental data need to be at the appropriate temporal resolution (Kearney et al. 2012). Furthermore, Zurell et al. (2016) found uncertainty caused by structural decisions in the model building process (e.g. the form of relationships) to be much reduced if the relevant ecological knowledge was available. Schurr et al. (2012) explicitly list empirical data collection on their demographic research agenda, including the temporal development of species distribution and abundance (response variable of SDMs) as well as the relationship between environment and demographic parameters (required for DRM estimation). Independent, long-term observations of species distributions (and the corresponding environmental data) are also required to better validate SDMs and test their temporal transferability (Araújo, Pearson et al. (2005a)and **chapter 2** of this thesis).

5.3.4. Be clear about assumptions, limitations and uncertainties

In general, the community of ecological modellers (exceptions confirm the rule) is acutely aware of limitations of especially statistical modelling approaches and underlying assumptions (see *section 5.2.2*). We also widely appreciate the need to not only quantify (Wang et al. 2016, Buisson et al. 2010, Dormann et al. 2008) and account for uncertainty (Stoklosa et al. 2015, Cressie et al. 2009), but also to visualize and communicate (Gritti et al. 2013, Elith et al. 2002) uncertainty in model predictions to decision-makers (Guisan et al. 2013, Hayes et al. 2013, Ascough II et al. 2008).

To facilitate communication of model structure and uncertainty, Schmolke et al. (2010) proposed transparent and comprehensive ecological modelling (TRACE) documentation. TRACE is a standard format to document model building and application, similar to the ODD protocol for individual-based models (Grimm et al. 2006) which we used to describe IBC-grass_coast in **chapter 4** (Appendix C2, on CD). On the one hand, this protocol supports the modeller to properly document her model. On the other hand, it promotes more complete communication of key issues (model validation, sensitivity and uncertainty analysis) which end-users should consider when interpreting and using model results. Subsequent usage of TRACE documentation revealed that the diversity of models is not easily captured by standard protocols (Augusiak et al. 2014). Therefore, it has been updated and refocused on the validation and evaluation aspect (Grimm et al. 2014). In conclusion, while it is easier said than done, there are attempts to make being clear about our model’s assumptions, limitations and uncertainties easier.

5.4. Conclusions

In this thesis, I have explored the limitations of statistical and process-based modelling approaches to predict how species will respond to changing environments. Being neither a clear success, nor a definite failure, the first two modelling studies were important food for thought to move forward. With the final study, I proposed a novel approach to link statistical and process-based models in order to combine their strengths. I further argued that we already have a diverse range of modelling tools at hand, which can be refined further. But most importantly, they need to be applied more thoughtfully. Bearing their limitations in mind, combining their strengths and openly reporting the assumptions and uncertainties involved is the way forward.

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Author’s declaration

I prepared this dissertation myself and without any illegal assistance. The work is original except where indicated by references in the text and no part of the dissertation has been submitted for any other degree. This dissertation has not been presented to any other university for examination, neither in Germany nor in any other country.

Potsdam, 10 May 2017 ___________________________________ (Anett Schibalski)