Drivers of forest dynamics: Joint effects of climate and competition

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Wer immer nur tut, was er schon kann,

bleibt immer nur dass, was er schon ist.

Henry Ford

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Abstract

The present dissertation thesis addresses different aspects of forest dynamics and possible changes due to climate change. Various modelling approaches are used to explore joint effects of climate and competition on forest dynamics with a focus on temperate forests. Motivated by scientific interest, this thesis is aimed at contributing to the establishment of fundamental knowledge for proper ecosystem management. Each of the research projects of this thesis explores a facet of forest dynamics. It appears that for projections of forest dynamics under climate change particularly, it is critical to consider competition among trees.

In the first study, the joint effect of climate and competition on forest dynamics in a mountain forest of New Zealand was investigated. The landscape simulation model LandClim was calibrated based on empirical data and applied to reproduce a 1700 years forest succession under stationary climate at the slope of Mt. Hauhungatahi, North Island. Although designed for European temperate forests, LandClim was capable of simulating NZ´s forest dynamics.

Under non-stationary climate, forests likely remain in disequilibrium with climate for some time due to the longevity of trees and competitive prevention of establishment. This aspect was investigated in a mixed beech-oak forest in Germany, using LandClim and the forest gap model SILVA in a cooperation study. Furthermore, a possible ‘climatic turning point’ was investigated, the point at which species dominances change due to changes in competitiveness caused by climate change. Both models projected a potential climatic turning point at a mean annual temperature of 11-12 °C and precipitation sum of 500-530 mm. However, the change of species composition in existing mixed stands was much slower since the turning point also depended on inherited stand structure. Based on these projections the promotion of oak at dry sites seems advisable due to its superior resistance and resilience to drought.

The applied simulation models consider joint effects of climate and competition but no changes in species sensitivity to competition along climatic gradients. The Spanish National Forest Inventories provided a solid basis to develop a statistical model for the influence of climate and competition on tree growth. The results indicated that in Mediterranean forests the effect of competition increases with aridity potentially resulting in an additional disadvantage for drought sensitive oaks compared to pines under climate change.

Under the prerequisite that forest dynamics will be affected by climate change, different forest management strategies on adaptation are currently discussed. One option is the promotion of tree species that are better adapted to anticipated future climates (such as oak instead of beech in Germany) and also the introduction of non-local ecotypes of local species. This increase in biodiversity intuitively appears promising because it is in line with the insurance hypothesis and the portfolio effect theory. Within this thesis the effect of ecotype mixing as an increase of within stand diversity under consideration of self-thinning was assessed. It was shown that ecotype mixing in forest stands might lower the risk of yield losses and at the same time might exempt the portfolio effect from its drawback of lower chances for high yields.

Climate not only affects demographic rates of tree species but also all other ecosystem components. Disturbances are an important component of forest dynamics because they initiate successions and thereby influence species coexistence. Climate will alter disturbance regimes not only directly but also due to interactions among disturbances, for example an increased risk of insect outbreaks due to weak tree defence caused by severe drought stress. Most disturbance interactions have been observed to be positive, implying that increases of disturbances in quality and quantity due to climate change will be amplified. Furthermore, systems containing positive feedback loops are considered to be mostly unstable, which would result in forest collapse. A theoretical study on disturbance interactions showed why positive feedback loops of disturbances do not necessarily lead to a forest collapse. Disturbance interactions might cause only a minor part of disturbances, whereas direct changes due to climate change are of much higher importance.

The described studies reflect the diversity of the research field forest dynamics and innovative ecological methodology. Nevertheless, the present thesis is not an exhaustive discussion of drivers of forest dynamics under climate change. Forest dynamics and its drivers provide a range of open research questions posing a challenge for fundamental an applied research of high relevance for society.

Zusammenfassung

Diese Dissertation befasst sich mit Walddynamik und möglichen Veränderungen in Folge des Klimawandels. Verschiedene Modellierungsansätze werden verwendet, um den Einfluss von Klima und Konkurrenz auf die Walddynamik zu untersuchen. Motiviert durch wissenschaftliche Neugier soll diese Arbeit auch dazu beitragen, fundiertes Wissen als Basis für nachhaltiges Forstmanagement zu schaffen. Jede der hier vorgestellten Studien untersucht einen Aspekt der Walddynamik, mit einem Schwerpunkt auf temperaten Wäldern. Es erweist sich, dass vor allem im Hinblick auf Projektionen zukünftiger Wälder unter Klimawandel Konkurrenz berücksichtigt werden muss.

In der ersten hier vorgestellten Studie wurde der gemeinsame Einfluss von Klima und Konkurrenz entlang eines Höhentransektes in Neuseeland untersucht. Das Landschaftsmodell LandClim wurde dazu kalibriert und 1700 Jahre Waldsukzession am Hang des Mt. Hauhungatahi (Nordinsel, Neuseelands) unter stationärem Klima simuliert. Obwohl das Simulationsmodell LandClim für europäische, temperate Wälder entwickelt wurde, war es mit nur geringfügigen Anpassungen möglich, die Walddynamik in Neuseeland zu simulieren.

Unter sich veränderndem Klima bleiben Wälder wegen ihrer Langlebigkeit und durch Konkurrenzausschluss von Etablierung für mehrere Generationen im Ungleichgewicht mit dem Klima. Dieser Aspekt wurde in einem deutschen Buchen-Eichen Mischwald unter Verwendung von LandClim und SILVA untersucht. Es wurde nach einem „Klimatischen Wendepunkt“ (climatic turning point, CTP) gesucht, bei dem sich die Dominanz von Buche und Eiche umkehrt. Beide Modelle prognostizierten einen CTP bei Jahresmitteltemperaturen von 11-12 °C und Jahresniederschlägen von 500-530 mm. Ein Artwechsel in bereits bestehenden Beständen fand jedoch nicht sofort statt. Die Studie zeigte, dass es schon heute sinnvoll erscheint auf relativ trockenen Standorten die Eiche gegenüber der Buche zu fördern.

Die angewendeten Simulationsmodelle berücksichtigen den gemeinsamen Einfluss von Klima und Konkurrenz auf die Walddynamik, nicht aber eine Veränderung des Einflusses von Konkurrenz entlang eines Klimagradienten. Die spanischen Nationalen Waldinventuren boten die Möglichkeit ein statistisches Modell für den Einfluss von Klima und Konkurrenz auf das Baumwachstum zu entwickeln. Die Ergebnisse zeigten, dass die Bedeutung von Konkurrenz mit zunehmender Aridität größer wird. Dies könnte zu einem zusätzlichen Nachteil für

schattentolerante aber dürre-sensitive Arten wie die (sub-) mediterranen Eichen gegenüber Kiefern unter Klimawandel bedeuten.

Angesichts des Klimawandels werden aktuell verschiedene Möglichkeiten des Managements diskutiert. Eine vielversprechende Möglichkeit ist die Förderung und auch eine Neu-Einführung von Arten und Ökotypen, die besser an zukünftige Bedingungen angepasst sind. Diese Steigerung der Biodiversität erscheint vielversprechend, da sie im Einklang mit der „Versicherungs-Hypothese“ (engl. insurance hypothesis) und der Portfolio Effekt Theorie ist. In einer Studie konnte gezeigt werden, dass „Ecotype Mixing“, d.h. der Anbau von verschiedenen Ökotypen der selben Art in einem Bestand, das Risiko von Verlusten unter unsicherer Zukunft vermindert. Dabei war der Portfolio Effekt sogar von seinem Nachteil einer geringeren Wahrscheinlichkeit hoher Erträge befreit. „Ecotype Mixing“ erscheint daher eine aussichtsreiche Möglichkeit zur Anpassung an den Klimawandel zu sein.

Das Klima beeinflusst nicht nur die demographischen Prozesse der Arten sondern auch alle anderen Ökosystemkomponenten. Störungen machen einen wichtigen Teil der Walddynamik aus, weil sie Sukzessionen initiieren. Dadurch beeinflussen sie die Koexistenz von Arten. Der Klimawandel verändert Störungsregime aber nicht nur direkt sondern auch indirekt, zum Beispiel durch ein erhöhtes Borkenkäfer-Risiko durch vermehrte Dürre und eine dadurch verringerte Widerstandsfähigkeit der Bäume. Die meisten Studien finden positive Interaktionen zwischen einzelnen Störungen, so dass ein Anstieg der Qualität und Quantität von Störungen durch den Klimawandel noch verstärkt würde. Außerdem sind Systeme, die positive Rückkoppelungen enthalten, sehr oft instabil, was zum Zusammenbruch der Wälder führen könnte. Eine theoretische Studie über Störungsinteraktionen zeigte, warum positive Rückkoppelungen zwischen Störungen nicht zum vollständigen Rückgang der Wälder führen müssen. Außerdem zeigte die Studie, dass Störungsinteraktionen möglicherweise nur einen geringen Anteil an Störungsregimen bedingen und Veränderungen im Zuge des Klimawandels weitaus bedeutender sind.

Die vorgestellten Studien spiegeln die Vielfalt des Forschungsfeldes „Walddynamik“ und der ökologischen Methodik wieder, es was aber unmöglich das Thema umfassend im Rahmen dieser Dissertation abzuhandeln. Es bleiben daher eine Vielzahl von offenen Fragen zu Walddynamik und den beteiligten Prozessen, deren Erforschung eine Herausforderung darstellt und von großer Bedeutung für die Gesellschaft ist.

Introduction

Background

Facilitation of sustainable forest management is a crucial task to protect biodiversity, to reduce carbon emissions from deforestation and forest degradation while preserving the socio-economic value. Trees as the key organisms of forests provide shelter and food for animals such as large herbivores and smaller mammals, birds, insects, as well as for understorey plants, epiphytes, mosses, fungi and, notably, to a rich biodiversity of soil organisms. Estimates of global tree species richness range from 60,000 (Grandtner 2005) to 100,000 taxa (Oldfield et al. 1998). Besides the intrinsic value of biodiversity (Lindenmayer et al. 2000) and its role for ecological stability, forests provide very important goods and services to society such as watershed and air quality protection, soil erosion control, food and timber production, and recreational and cultural functions (Schroter 2005, Sunderlin et al. 2008, Turner and Daily 2008).

Current climate change is anticipated to affect forest productivity, composition and distribution considerably (Allen et al. 2010, Köhl et al. 2010, Hanewinkel et al. 2012). Besides alterations in mean climate, increasing temporal variability and more frequent occurrences of extreme weather events such as droughts pose challenges for ecosystem management (Jentsch 2007, Jentsch and Beierkuhnlein 2008). Notably, projected impacts of climate change on forests differ among bioclimatical regions (Rivas-Martínez et al. 2004, Scholze 2006). Temperate and boreal forests, for example, are less vulnerable in regard to productivity losses than Mediterranean forest ecosystems, where growth is already water limited (Lindner et al. 2010).

The management of long-lived ecosystems such as forests has to deal with uncertain future growing conditions while long term decisions have to be made (Hildebrandt and Knoke 2011). Particularly in the face of climate change, management decisions that are only based on experience but lack profound understanding cannot cope with dynamic changes of ecosystem processes provisioning biotic interactions (Korzukhin et al. 1996). This is based on the assumption that future conditions have no equivalent in the past (Williams and Jackson 2007). Under such novel conditions forest community responses cannot simply be projected by means of extrapolating regression functions (Veloz et al. 2012). A mechanistic understanding of natural forest dynamics is required for projections as basis for proper ecosystem management.

Forest dynamics primarily emerge out of the main demographic processes: Dispersal, establishment, growth and mortality (Nakashizuka 2001, Petit and Hampe 2006). Climate, soil, relief and exogenous disturbances are important abiotic drivers. Competition among neighbouring trees and all other organisms is one of the most important biotic drivers. Whereas spatial species distributions (altitudinal and latitudinal gradients) are primarily influenced by abiotic factors such as climate and soil properties (Jump et al. 2009), forest succession is influenced more strongly by competition, mainly competition for light (Finegan 1984). Current climate change confounds effects of a climatic gradient with forest succession. This renders assessments of climate change impacts on forests a special case compared to investigations on spatial distributions.

Motivated by the need to prepare forests for the future aiming at maintaining biodiversity and ecosystem services, this thesis intents to deepen the understanding of key processes of forest dynamics. A focus lies on temperate forests and the influence of climate on forest growth considering competition among neighbouring trees. The processes and interactions that shape natural communities are often difficult to trace. One of the obstacles is the richness of processes in ecosystems that furthermore appear at different temporal and spatial scales. For some ecological processes such as forest succession the temporal scales are larger than the human lifespan. To gain insights in such processes there is need for abstraction from real ecosystems and reduction of complexity. Within this thesis modelling techniques addressing different levels of complexity were applied to explore the following research questions with respect to forest dynamics:

- How do temperature and precipitation influence tree growth and forest composition (**Manuscripts 1-3**)?
- How does competition interact with climate in shaping forests (**Manuscripts 1-3**)?
- Which role plays intraspecific diversity for climate change adaptation in forests (**Manuscript 4**)?

- Does positive feedback among forest disturbances pose a threat to current forests (**Manuscript 5**)?

Natural forest dynamics

The main demographic processes dispersal (Howe and Smallwood 1982), establishment (Urbieta et al. 2008), growth (Kunstler et al. 2011) and mortality (Franklin et al. 1987) together with biotic interactions shape species distributions at spatial and temporal scales (Nakashizuka 2001, Petit and Hampe 2006). The geographic distribution of species is highly correlated with climate (Thuiller et al. 2003, Rodríguez-Sánchez et al. 2010, Michelot et al. 2012, García-Valdés et al. 2013) and can be assessed best along strong climatic gradients. Research on the climatic niche is intense but still largely based on presence-absence data (e.g. Araújo and Guisan 2006). Commonly, the two-dimensional temperature-precipitation niche of tree species is used for forest management, particularly in the face of climate change (Kölling 2007, Falk and Mellert 2011). Yet, competition modifies species abundances and can even cause competitive exclusion of one species due to the presence of another within its physiological range (Huston and Smith 1987, Loehle 1998, Franklin et al. 2002). Competition among neighbouring trees and all other organisms is one of the most important biotic interactions and a main driver of forest succession (Finegan 1984).

Besides demographic processes, natural abiotic and biotic disturbances are fundamental components of forest dynamics (Jentsch 2007). Disturbances remove biomass which in turn provides space for establishment. The main forest disturbances are wind storms, wildfires and insect outbreaks all of which are expected to change in quality and quantity due to climate change (Dale et al. 2000, Dale et al. 2001). Since many forestry practices involve disturbance-like impacts, forestry will inevitably have effects on forest dynamics particularly in Europe and other regions with high population densities. For example, it has been estimated that more than 80% of temperate broadleaved forests are under strong anthropogenic influence (Hannah et al. 1995). However, sustainable forest management can also be used as an option for climate change adaptation (Noss 2001, Bengtsson et al. 2000, Temperli et al. 2012, **Manuscripts 2 & 4**).

Demographic processes

Dispersal

Demographic rates of trees are known to be correlated with average climate but are also influenced by forest disturbances and extreme weather events. Yet, dispersal as the initial colonization step is mainly controlled by the medium which carries seeds or propagules: Dispersal by animals such as birds, ants and migrating ungulates, wind dispersal, down stream water dispersal and also self-dispersal with subsequent secondary dispersal (Howe and Smallwood 1982, Manzano and Malo 2006). Some tree species are also able to reproduce by vegetative propagules even more successfully than by sexual reproduction (Leakey 1985, Koop 1987, Del Tredici 2001).

Rapidity of species range shifts after past climatic changes (e.g. Quaternary glaciation cycles) and current anthropogenic climate change is determined by yearly dispersal distances into previously uncolonised regions. Yearly dispersal distances of about 100 m have been estimated for tree species, however a high variability exists between species (Davis 1983, Higgins and Richardson 1999, Svenning and Skov 2007). Besides dispersal distances of seeds and propagules, reproductive maturity plays an important role for the rapidity of range expansion (Kozłowski 1992, He 1999). Dispersal limitations result in species distribution that is out of equilibrium with the climate. This poses a challenge in estimations of environmental niches (Svenning and Skov 2007, Thuiller et al. 2008, Jump et al. 2009).

Establishment

Establishment is considered to be a bottleneck for species distributions (Urbieta et al. 2008), particularly in the context of naturalization and invasion of neobiota (Kowarik and Boye 2003). Species can only establish within certain abiotic limits which are similar to those controlling growth (**Manuscripts 1 & 2**). Yet, ontogenetic changes in species traits lead to different habitat requirements for seedlings, saplings and adults. For example, young trees are often more sensitive to drought than mature trees (Cavender-Bares and Bazzaz 2000) and establishment is therefore only possible under favourable conditions (Urbieta et al. 2008).

Despite the climatic regeneration niche, establishment is strongly influenced by biotic interactions (Kellman and Kading 1992, Kobe et al. 1995, Calder and St. Clair 2012). Competition among tree individuals leads to considerable self-thinning during the establishment phase and also later on (Pickard 1983, Lonsdale 1990). Individuals are selected according to their performance which might lead to survival of the best adapted (**Manuscript 4**). Besides adaptation to the abiotic environment, shade tolerance strongly determines survival of self-thinning (Kobe et al. 1995). Similarly to drought tolerance, shade tolerance can differ between ontogenetic life stages, usually in support of seedling survival (Lusk 2004, Niinemets 2006). Some pioneer tree species can only establish in forest gaps (e.g. caused by single tree death) or after disturbances, i.e. at low competition levels (Whitmore 1989, **Manuscripts 1**). Furthermore, most tree species are very sensitive to herbivory during their early life stages (rodents, deer, insects, below and above ground herbivory). Regrowth can even be prevented completely if herbivore population is too large (Meiners 2000, Cierjacks and Hensen 2004, Côté et al. 2004).

Growth

Tree growth is considered as a good proxy for vitality and whole plant carbon balance (Dobbertin 2005) and has been studied intensively (Loehle 1998, Sánchez-Gómez et al. 2008, Gómez-Aparicio et al. 2011, Kunstler et al. 2011, Babst et al. 2013). Absolute growth, for example measured as diameter increment, is to a large part determined by tree size and can be expressed through allometric relations (Zeide 1993, Weiner and Thomas 2001). Two ecological principles underlie the sigmoid allometry of tree growth and size: The Malthusian law of exponential growth (Malthus 1798) and the existence of an upper limit adopted from population ecology (Berryman 1999, Turchin 2001).

Climate and competition (and further environmental factors such as nutrient supply) modify individual growth and determine the competitiveness of species in a given environment (**Manuscripts 1-3**). Statistical analysis of tree growth found that competition can even have a stronger effect on growth than climate (Gómez-Aparicio et al. 2011, Kunstler et al. 2011), particularly competition for the resource light (**Manuscript 3**).

Mortality

Tree death is the result of complex interactions among multiple factors and less understood than growth and other demographic processes (Franklin et al. 1987). The particular reasons that a tree dies are difficult to separate. Different mortality agents might be dominant during different ontogenetic stages of trees (Franklin et al. 1987, Kozlowski 1991). Usually, regular growth-dependent mortality causes such as senescence, competition, climate effects and weak pathogens are distinguished from external growth-independent mortality due to fire, windthrow, and severe epidemics. Abrupt mortality due to extreme weather events and disturbances such as fire, windthrow and insect epidemics often remove entire stands (**Manuscripts 1 & 5**).

Regular tree mortality is closely related to growth (Bigler and Bugmann 2003, Wunder et al. 2006, Wunder et al. 2008) and can be predicted by statistical models. This correlation is widely used in forest simulation models (Keane et al. 2001, Bigler and Bugmann 2004, Manusch et al. 2012, **Manuscripts 1 & 2**). One major reason for growth reduction and subsequent tree death is competition and subsequently tree mortality is very high during the early phase of self-thinning (Pickard 1983, Lonsdale 1990, **Manuscript 4**). Occurrence of age dependent mortality, i.e. mortality due to senescence, in terms of changes in gene expression that might indicate genetically controlled ageing mechanisms (Diego et al. 2004) is discussed but an intrinsic physiological alteration has not been proven to date.

The most prominent causes of tree death currently discussed are increased aridity and severe drought due to climate change (Allen et al. 2010, **Manuscript 2**). Increased mortality in temperate forests and even die-backs are attributed to increased aridity (Gitlin et al. 2006, van Mantgem and Stephenson 2007, Worrall et al. 2008, Rehfeldt et al. 2009, Carnicer et al. 2011). Water scarcity over longer time periods leads to carbon starvation and subsequent growth reduction (McDowell and Sevanto 2010, Sala et al. 2010). During times of prolonged drought, trees reduce evapotranspiration by closing their stomata (McDowell et al. 2008). Since plant respiration is thereby also reduced, closing the stomata essentially means that the plant starves itself by blocking carbon uptake for photosynthesis. Very severe drought additionally reduces phloem conductance or even causes cavitation which might lead to starvation (Wortemann et al. 2011). Hydraulic failure occurs when drought intensity is sufficient to push a plant past its threshold for irreversible desiccation (Sala et al. 2010).

Drought can further indirectly deteriorate tree defence and facilitate insect calamities and other diseases (Hebertson and Jenkins 2008, **Manuscript 5**). Slowly progressing tree diseases such as root rot and herbivores can cause starvation by lowering water and nutrient uptake in case of root damage or hinder photosynthesis in case of defoliation. Furthermore, semi-parasites such as mistletoe can intensify drought stress extracting water and nutrients from the phloem of its host (Dobbertin and Rigling 2006).

Data sources

Tree response to climate can be assessed best along wide climatic gradients preferably covering the entire physiological range of the species. For the analysis of tree growth, datasets with at least two measurements of tree size at different points of time are required (e.g. Gómez-Aparicio et al. 2011, Kunstler et al. 2011). The analysis of growth dependent mortality requires as many as three measurements of tree size (e.g. Wunder et al. 2008). In Europe, the collection of national forest inventory data represents a valuable source of information on forest resources and a promising base for the analysis of tree growth (**Manuscript 3**) as well as regrowth (Ruiz-Benito et al. 2012) and mortality (Ruiz-Benito et al. 2013). The first EU wide analysis based on harmonized databases is currently being conducted (Winter et al. 2008, Ferretti 2010).

Alternatively, dendrological data can be used (Briffa et al. 1998, Bigler and Bugmann 2004, Rossi et al. 2006, Čufar et al. 2008, **Manuscript 2**). This data provides a much higher temporal resolution and longer time series than forest inventories. It allows for assessments of tree reactions on an annual or even sub-annual scale when combined with high resolution climate data. Time lags in reactions to climatic events and recovery times can thereby be assessed (Meinardus and Bräuning 2011). In making use of the correlation between climate and tree growth, the reverse research approach is also chosen, i.e. reconstructions of climate and of insect calamities based on tree ring analysis (Briffa et al. 2001, Luterbacher 2004, Martinelli 2004, Campbell et al. 2007).

Another source of data on demographic rates are experimental studies (Underwood 2009). In manipulative experiments environmental variables are controlled while the target variable, e.g. growth, is measured (**Manuscript 4**). This approach facilitates separating the effects of variables that are largely correlated in the field (such as temperature and precipitation, stand density and precipitation; **Manuscript 3**). Additionally, by manipulative experiments the responses of an organism or ecosystem to conditions of interest can be assessed systematically through manipulative experiments. Consequently, experiments are very common in climate change research (Bart 2006, Jentsch et al. 2007, Pretzsch et al. 2010, Kreyling et al. 2012). However, slow processes such as tree growth and regular mortality result in the need for long-lasting experiments (Benson et al. 1992, Pretzsch et al. 2010). Since it is not always feasible to wait for the entire life-span of a tree to get results, alternative model organisms are often used. To assess the growth reaction of tree species and ecotypes to different climatic conditions, saplings are commonly used and findings are transferred to mature trees (Thiel et al. 2012, **Manuscript 4**). Aside from the problem of transferability, the need for replicates to enable hypothesis testing poses a main challenge (Oksanen 2001).

Forest disturbances

Disturbances constitute an important component of forest dynamics (Jentsch 2007). Their occurrence is rather sporadic or can re-initiate forest successions at broader scales. On a global scale, the main non-anthropogenic forest disturbances are wind storms, wildfires and insect outbreaks (Dale et al. 2000, Dale et al. 2001, **Manuscript 5**). Further examples of natural disturbances are herbivores, extreme weather events such as drought (Ayres and Lombardero 2000, White and Jentsch 2001, Weisberg and Bugmann 2003) and extreme disturbances such as volcanic eruptions affecting entire landscapes (‘large infrequent disturbances’ sensu Turner et al. 1998, **Manuscript 1**).

Generally, in forest ecology disturbance is an event that involves the removal of biomass or causes death of individuals (Grime 1977, Sousa 1984) and can be characterized by its frequency, size, severity, intensity and residuals (White and Pickett 1985, Turner et al. 1998). Temporal scaling of disturbances, i.e. their frequency, has to be interpreted with regard to the generation time of the population of interest, i.e. the life span of trees in the case of forests. The same applies to the spatial scaling which is relative to the organism size or its range of activity, for trees dispersal distances. In forests, severity usually includes not only biomass removal and tree mortality but also the disruption of ecosystem structure: Erosion due to exposure of mineral soil and loss of soil nutrients, death of advance regeneration and seed banks (Peterson and Pickett 1995). The sum of all disturbances affecting an ecosystem is called its disturbance regime.

Disturbances are considered to affect biodiversity and species coexistence (Nakashizuka 2001, Papaik and Canham 2006). According to the predictions of the intermediate disturbance hypothesis (Connell 1978, Huston 1979), diversity is high at intermediate disturbance levels due to the coexistence of colonizers and competitors (Hubbell 1999, Stueve et al. 2011, **Manuscript 1**). The underlying mechanism is biomass removal from the community. Thereby, competitive species are prevented from rapidly occupy the entire area (**Manuscript 2**; but see also Tilman 1994 for the spatial competition hypothesis). As a result, the community remains in an early to intermediate successional phase. In the climate change context, disturbances can be considered as catalysts of vegetation changes based on their effect to re-initiate successions with unknown successional pathways (Sykes and Prentice 1996, Soja et al. 2007, **Manuscript 2**).

Disturbance regimes will likely alter due to climate change (Dale et al. 2000, Dale et al. 2001), either because they are directly related to climate such as drought or wind storms (Jentsch et al. 2007) or because they are indirectly influenced by climate such as wildfires by ‘fire weather’, and insect outbreaks due to temperature control of the organisms life cycles (Wermelinger 2004, Bigler et al. 2005, Carnicer et al. 2011). Furthermore, disturbances can exert a feedback on vegetation properties such as fuel load for fires and stand age and composition for insects such as bark beetles (Veblen et al. 1994, Cumming 2001). Disturbances also interact among each other and thereby complicate predictions of disturbance regimes under changed environmental conditions (White and Jentsch 2001, Buma and Wessman 2011, **Manuscript 5**).

Forest succession

Forest succession is the process of change in species structure and composition of a forest community over time (Finegan 1984, Pickett et al. 1987). Succession pathways differ between climates, soils and regional species pools (Kupfer and

Runkle 1996, **Manuscripts 1 & 2**). Species replacements during forest succession are primarily influenced by changes in light conditions (Finegan 1984, Franklin et al. 2002). Furthermore, soil (i.e. nutrient cycling) and other factors change with time (Guariguata and Ostertag 2001, Burga et al. 2010). In an ideal case, succession begins uninfluenced by pre-existing communities (primary succession). First colonizers can usually be described as light demanding pioneer species (such as *Betula pendula*, *Pinus sylvestris*, *Sorbus aucuparia* in temperate forests) with high dispersal potential and fast growth rates (Grime 1977). These early successional species will be replaced over time by competitive species that are more shade tolerant, growing at slower pace and have longer live span (e.g. *Fagus sylvatica*).

Until recently, a stable climax community was considered to be the end point of succession (Mueller-Dombois and Ellenberg 1974). Over the course of time, though, a stand is likely to be affected by disturbance events. Currently, the climax theory is supplemented by the acknowledgement that ecosystems change continuously and that in many cases a climax state is never attained due to regular small scale disturbances (Pickett 1980, van der Maarel et al. 1995, Yamamoto 2000).

Climatic gradients

Climatic gradients can be of spatial (latitude, continentality, altitude) and temporal nature (‘climate change’). Tree species performance (e.g. rates of demographic processes) and thereby community assembly change along climatic gradients is mainly due to differences in energy and water supply (O'Brien et al. 2000). There is a fundamental difference between spatial and temporal gradients for sessile organisms such as plants, particularly for long-lived organisms. Under rapid (temporal) climate change individual trees might be subject to different climates. Thereby, current climate change mixes effects of a climatic gradient with forest succession (as in **Manuscript 2**) whereas effects of spatial climatic gradients are mixed with alterations of other site properties such as soil properties (as in **Manuscripts 1 & 3**).

Relative species competitiveness is determined by performance and therefore changes with climate (despite e.g. nutrient limited sites). Community responses to climate are hence a combination of single species responses and interactions among species. A number of studies shows that the nature of competition changes along ecological gradients (Kunstler et al. 2011, Zang et al. 2012, **Manuscript 3**).

Changes in species competitiveness cause rank reversals in species performance and thereby result in non-linear changes in community structure (Sánchez-Gómez et al. 2008, Gómez-Aparicio et al. 2011, Scharnweber et al. 2011, **Manuscript 2**).

Spatial climatic gradients

Global circulation causes global climatic zones (Flohn 1957, Salmond and Smith 1996). Generally, higher latitudes comprise cooler climates since the amount of solar radiation gets dispersed over a larger area than in the central latitudes. This pattern is mainly modified by planetary wind systems transporting latent energy. Moreover, cool or warm ocean currents transport energy from lower to higher latitudes (e.g. the warm Gulf Stream). Smaller currents influence temperatures close to the coast (e.g. the cold Canary Stream). Precipitation is strongly influenced by the global and local wind systems, land-water distributions and relief (Street-Perrott et al. 1983, Trenberth 1999).

At the continental scale, latitudinal climatic zones are modified by the effect of continentality (distance from the sea). Regions close to large water bodies are usually moister and comprise a lower temperature variability. In contrast, regions within land surfaces have larger temperature amplitudes and less precipitation. This difference is a consequence of much lower effective heat capacities of land surfaces as well as of their reduced evaporation rates compared to large water bodies.

Altitudinal gradients provide the opportunity to assess vegetation patterns within small areas but with large environmental differences (Beals 1969, Jump et al. 2009). Similar to latitudinal gradients, species distribution along altitudinal gradients is primarily controlled by climate, particularly the upper limits (Wardle 1964, Druitt et al. 1990, **Manuscript 1**). Lowland environments are usually warmer and drier and maintain a higher site productivity. Temperature falls with increasing altitude due to adiabatic cooling and relief rainfall usually leads to higher precipitation. In addition to the climatic gradient other factors such as soil properties change with altitude and should to be considered in the interpretation of species and community zonation (Brzeziecki et al. 1993, Burga et al. 2010).

Climate change

Major climatic changes have occurred several times throughout the past millennia (Petit et al. 1999). The last strong climatic change took place c. 10,000 years ago after the Quaternary glaciation cycles. In Europe, tree species expanded their distribution ranges from their refugia northwards (Taberlet et al. 1998). Contemporary forest communities are considered to be the result of this post-glacial colonization which is most likely still in progress.

Current climate change can be observed best in mountain regions in terms of upward shifts of species ranges since the dispersal distances of species coincide with the rate of climate change (Cannone et al. 2008, Harsch et al. 2009, Jump et al. 2009). In contrast, horizontal species range shifts are dispersal limited, due to large distances and landscape fragmentation.

The rate of previous climatic changes during the Quaternary was smaller than the rate of current anthropogenic climate change. Migration rates of tree species have been estimated from 50 to 2000 m per year (Davis 1983 for *Fagus grandifolia* and Dennis 1993 for *Picea spp.*). Many species have the potential in terms of dispersal rate to keep up with moderate climatic changes and are likely to shift their distribution ranges in the future. Moreover, given sufficient time, evolutionary adaptation might occur, i.e. genetic changes generating better adapted ecotypes or even new species. In contrast, it is unclear if current fast-paced climatic change exceeds the limits of adaptability for some species possible resultung in local and global extinctions (Jump et al. 2009; refere to Kreyling et al. 2011 for assisted migration). Mountains and their unique biota are disproportionately vulnerable to climate change (Theurillat and Guisan 2001, Engler et al. 2011, Dullinger et al. 2012). On major reason is that species cannot escape the upward shift of climatic zones once the mountain summit is reached. New sites with suitable environmental conditions for mountain species are often very distant and outside the range of natural dispersal.

Current climate change is faster than forest succession due to the longevity of trees. Thereby, forests will likely remain in non-equilibrium with climate. In forest stands, effects of climate change might be observable with a time lag in the order of life-span of a tree (Kienast and Kräuchi 1991, Sykes and Prentice 1996, **Manuscript 1**).

Forest modelling

Ecological models serve as tools to extend conceptual ideas and learn about interrelationships in ecosystems. From an ecologists view models can be used for

- testing hypotheses about the functioning of ecosystems (**Manuscripts 1-3**),
- exploring system behaviour under different (climatic) conditions (**Manuscripts 2, 5**),
- investigating scenarios which are impossible to test in real ecosystems (**Manuscripts 1, 2, 4, 5**),
- supplementing and motivating field experiments and further data collection (**Manuscripts 4 & 5)**, and
- identifying knowledge gaps and developing new hypothesis (**Manuscripts 4 & 5**)

(e.g. Caswell 1988, Wissel 1992, Dislich 2011).

Like every scientific endeavour, model building follows the basic principles of science (Grimm 1994, Jackson et al. 2000). Observations of the natural world should be foundation of all ecological research, including model building. Additionally, ecological knowledge and system understanding are the basis for developing new ecological theory and hypotheses (preferably but not exclusively testable ones; Caswell 1988). Yet, understanding systems and processes is crucial, an incomplete understanding of the system should not prevent model building (Starfield 1997). For model building there is need for abstraction from real ecosystems and reduction of complexity with respect to the formulated hypotheses (Wissel 1989, Grimm 1999). Structures and processes of interest must be defined and decisions about spatial and temporal scales as well as the type of model must be taken. By means of combining models with empirical data, the system behaviour can be explored and hypotheses can be tested. Finally, as modelling is an iterative process, the results must be evaluated. Modifications of the model and its underlying theory should be discussed and new data surveys or experiments might be designed.

In the following sections three main types of models are introduced which can be used to explore forest dynamics and its drivers (**Manuscripts 1-5**). Each type of model comprises different advantages and limitations essential to acknowledge.

Statistical models

In natural resource planning, models are typically used to project how resource dynamics will develop in the future and to guide decision making. A traditional method to project forest growth and yield is the use of regional and site-specific yield tables which interpolate past observations of stand growth under given climatic, soil and management conditions (e.g. Assmann and Franz 1972). Contemporary statistical models (empirical models) of tree species distributions, site suitability, growth and productivity are more flexible than yield tables and are fitted to much larger datasets.

There are many different types of statistical models but all of them base on the principle of drawing conclusions from data that is subject to random variation. Statistical models aid in the exploration of the effect of variables on observed patterns and thus give phenomenological descriptions of vegetation responses (Wissel 1992, Dormann et al. 2012). Prediction accuracy is mostly an implicit objective of statistical modelling, particularly when used as management support. Prominent examples of applications are species distribution models (SDMs; Araújo and Guisan 2006, Falk and Mellert 2011), models on demographic processes of trees (Kunstler et al. 2011, Ruiz-Benito et al. 2012, Ruiz-Benito et al. 2013, **Manuscript 3**) and also statistical down-scaling of global circulation models in climate change research (e.g. WETTREG; Enke et al. 2005a, Enke et al. 2005b).

Since statistical models often perform better than process-based models in terms of predictions, it is advisable to use them for management questions. However, management based on SDMs ignores abundant information available from forest inventories (e.g. Kölling 2007, Falk and Mellert 2011). Species range limits are without doubt strongly influenced by climate and soil properties, but other factors might be of similar importance (Sexton et al. 2009), depending on the considered scale (Pearson and Dawson 2003). Firstly, species presence in Europe is strongly influenced by management resulting in a logical cycle when calculating site suitability based on species presences and absences (Hannah et al.

1995). Secondly, dispersal limitation might limit distributions more than abiotic site suitability (Svenning and Skov 2007). Thirdly, distribution is influenced by biotic interactions such as competition (which might be reduced by management; e.g. Pretzsch et al. 2013). Therefore, species niches and site suitability inferred from current range limits might not represent the actual physiological potential of a species. The analysis of demographic processes might help to overcome these limitations.

In any case, statistical models do not readily allow for insights into processes leading to the observed pattern as they follow the general concept of correlation. Consequently, effect and response might be mixed and false correlations might lead to misinterpretations. Moreover, correlative approaches only work well in constant environments but not under non-analogous conditions triggered by climate change (Bossel 1991, Williams and Jackson 2007).

Simulation models

Simulation models have advantages over statistical models when considering projections outside known environments and consequently gain importance in forest management applications (Pretzsch et al. 2008, Muys et al. 2010). Forest simulation models are based on the current understanding of biomass, energy, water, nutrients and competition relations as other biotic interactions. Ecosystem structure and processes can be implemented based on mechanistic understanding (Tilman 1987, Bossel 1991). Single-tree models with an emphasize on either morphology or physiology are very detailed models. Morphological models aim at simulating the spatial structure of a plant (Kurth 1994) while physiological models (process-based models) simplify the spatial configuration but start with biochemical representations of photosynthesis and respiration controlled by resource availability in high temporal resolution (Grote and Pretzsch 2002). Furthermore, there have also been efforts to combine the advantages of both model approaches (Perttunen 1996).

As the scale of interest becomes coarser and larger systems are considered, smaller components are generally aggregated to maintain a manageable complexity within models (Levin 1992, Rastetter et al. 1992, Elkin et al. 2012). Forest gap models are at intermediate spatial and temporal scales and simulate forest stands for one generation or rotation period (Botkin et al. 1972, Shugart and West

1981, Bugmann 2001). With this approach physiological processes are aggregated and empirical (correlative, statistical) functions are used to relate demographic processes to the environment. Competition among neighbouring trees is considered morphologically simplified. Gap models have a high potential for application in management questions as they can be used to explore the stand-level implications of management regimes, changes of atmospheric CO_2 concentrations, nitrogen deposition, or climate change (Mäkelä et al. 2000). The forest growth simulator SILVA, for example, was primarily developed as a management tool, but can also be applied to ecological questions concerning climate change (Pretzsch et al. 2002, Muys et al. 2010, **Manuscript 2**).

LandClim is an example of a forest model simulating climate and competition-driven forest dynamics and disturbance regimes at a landscape-scale (Schumacher et al. 2004, Schumacher et al. 2006, **Manuscripts 1 & 2**). Forest simulations at such larger scales need further aggregation of ecosystem processes compared to gap models. LandClim uses a grid based approach with a spatial resolution of c. 25 x 25 m per grid cell being detailed enough to capture local variation in soil conditions and topography. This model simulates species-level forest dynamics by tracking species age cohorts (not individual trees) at 10-year time steps under natural disturbances (e.g. Colombaroli et al. 2010, Henne et al. 2012). Similar to LandClim, LANDIS is a spatially explicit, stochastic, raster-based landscape model which facilitates the study of the effects of natural and anthropogenic disturbances, vegetational succession, management strategies and their interactive effects on forest landscapes (Mladenoff et al. 1999). LANDIS is a powerful tool for evaluating alternative forest management strategies at a landscape-scale (He 1999, Mehta et al. 2004, Xu et al. 2009, Yao et al. 2012).

Dynamic Global Vegetation Models (DGVMs) simulate the global distribution of forests and other vegetation types under historic, present and simulated future climates (Prentice et al. 2007, Purves and Pacala 2008). Accurate representation of the structure and processes of natural systems is necessary for reliable ecological models. Yet, for DGVMs generalization of unneeded detail is required to increase model efficiency. In DGVMs, biomes, vegetation types or plant functional types are reduced to their biomass or net primary productivity (Peng 2000, Bonan et al. 2003, Sitch et al. 2008). Applications of such models include global risk assessments for ecosystems under projected climate change (Scholze 2006), the effect of forest carbon uptake on climate (Purves and Pacala 2008) and the role of agriculture within the global climate-vegetation system (Bondeau et al. 2007).

Mathematical models

Complex simulation models of ecological systems are as a rule incomprehensible and the behaviour of the model cannot be fully explored. In contrast, simplistic mathematical models (conceptual/strategic mathematical models; May 1976, Grimm 1994) offer analytically tractable solutions and the possibility to examine the underlying model properties. This allows for understanding the parts of the model which determine the resulting pattern. Mathematical models thus 'sacrifice detail for generality' and thereby serve to demonstrate the 'consequences of what we believe to be true' (Levins 1966, Grimm 1994, **Manuscript 5**).

Models of population dynamics, the main field of mathematical modelling in ecology, are often expressed in terms of differential or difference equations, which describe how system components change over time. The most widely known mathematical models stem form the Lotka-Volterra equations describing an ecological predator-prey (or parasite-host) system (e.g. Berryman 1992). The model is largely phenomenological, combining simple 'laws' of exponential growth of populations not limited by resources (Malthus 1798) and of mass action kinetics borrowed from chemistry (Murray 2002). The logistic model of population growth integrates the concept of negative density dependence. As populations grow, resources decline, so that fitness of any population member is negatively correlated to population density (cf. Berryman 1999). This principle was transferred to tree growth as growth-size allometry (Zeide 1993). Another example is the principle of competitive exclusion which was assessed by another descendent of the Lotka-Volterra model (Cushing et al. 2004).

Limits

As modelling has become a frequently used tool in ecology, it is important to be aware of problems which models cannot resolve. Models are imperfect representations of real ecosystems, by definition and purpose, and due to limited system understanding and computation power. They always contain errors in assumption, formulation and parametrization (Grimm 1999). Levins (1966) points out that modelling is essentially a trade-off between generality, realism and precision. To describe general ecological principles, it is usually necessary to sacrifice realism and precision. To describe a particular ecosystem, it is usually necessary to sacrifice generality. A general model that will represent an ecosystem completely and answer to all questions posed is practically impossible due to the complexity of natural systems, nor is such complex model desired – because of the lack of comprehensibility (Wissel 1992, Starfield 1997). Hence, adequacy and usefulness of any particular model has to be evaluated in respect to its purpose.

One might ask how much confidence can be placed in the results of a model. Particularly when model outcomes are used for predictions/projections (cf. Peterson et al. 2003), uncertainty must be considered. The uncertainty of an ecological model is caused by both the lack of knowledge (in data for parametrization, mechanistic understanding and also scenario planing) and the variability among models and their parameters (Cheaib et al. 2012, Dormann et al. 2012, Grimm and Railsback 2012). There are various ways to deal with uncertainty: Sensitivity analysis, Bayesian uncertainty analysis, ensemble modelling and scenario analysis (e.g. Cacuci 2003, Webster et al. 2003, van Oijen et al. 2005, Cariboni et al. 2007, Harper et al. 2011, Makler-Pick et al. 2011, van Oijen et al. 2013). In climate change modelling particularly, and more recently in vegetation modelling, ensemble modelling is applied as a means of evaluating uncertainties of projections (Littell et al. 2011). With this method of evaluations, it is important to consider if the models used in the ensemble are really independent (Dormann et al. 2012).

Plurality in modelling can help, as each model type has some disadvantages, making it more difficult to capture some features of reality relative to others. The choice for a modelling framework should be primarily driven by its adequacy for the specific task and not by the researchers habits and convictions, because interesting aspects will likely remain unnoticed – or as Abraham Maslow said in 1966, ‘I suppose it is tempting, if the only tool you have is a hammer, to treat everything as if it were a nail.’

Conclusions

This thesis provides new insights into processes governing forest dynamics with a special focus on possible impacts of climate change. The underlying assumption is that effects of climate and competition on tree establishment, growth and mortality mediate changes in species performance and cause species distributions and community assemblies. Each of the research projects composing this thesis explores a facet of forest dynamics. It appears that for projections of forest dynamics under climate change particularly, it is critical to consider competition among trees.

Forest dynamics and its drivers provide a range of open research questions posing a challenge for fundamental and applied research. In this context, basic ecological questions on species coexistence and community assemblies along various environmental gradients can be assessed, leading to the specification of risks and opportunities for ecosystem management. For example, current harmonization of European wide national forest inventories together with improved climate interpolations and projections will enable enhanced statistical analysis on demographic rates of trees along continental gradients as well as proper calibrations of dynamic forest simulation models. Ecological processes such as ontogenetic changes in shade or drought tolerance can thereby be quantified and later implemented into forest simulation models. Similarly, consideration of intraspecific variability comprising adaptation potential of a species might lead to changes in forest projections, to name but a few examples.

However, apart from physical site factors (climate, soil) and biotic interactions, direct human impact on forests in terms of land use change has a major influence on forest biomes trajectories (Dellasala et al. 2012). Land use change is the main cause of global forest decline today (Houghton 1994). The global deforestation rate for the past decade (2000-2010) averaged 13 million ha annually (FAO 2010). Global deforestation, forest degradation, and also land abandonment and regrowth are not only fundamental in the context of biodiversity conservation and sustainable ecosystem management but also regarding feedbacks within climate systems (Bonan 2008). Reducing carbon emissions caused by deforestation and forest degradation and increasing carbon uptake through afforestation and sustainable forest management highlight the essential role of forests in climate change mitigation. On the opposite side, forests have low surface albedo and can mask the high albedo of snow, which contributes to planetary warming through increased solar heating of land. Ultimately, conclusive estimates on future forests can only be made under consideration of both, natural and anthropogenic influences on forests, not only in terms of sustainable forest management and adaptation but also regarding changes in land use due to fluctuations in the demands of human societies.

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Manuscripts

Summary of the following manuscripts

The first study was realized in a mountain forest of New Zealand along an altitudinal gradient. In **Manuscript 1 'Long-term vegetation dynamics in New Zealand',** forest succession after a catastrophic volcanic eruption at the slope of Mt. Hauhungatahi, North Island, was simulated using the forest simulation model LandClim. The study explored climate and competition as drivers of observed forest dynamics and calibrated LandClim for the first time for New Zealand´s temperate mountain forest.

Manuscript 2 'Climatic turning point for beech and oak' directly addressed the of question whether contemporary forests will change during the next decades. The study region was located in south-western Germany in a climatically dry region. Employing two different forest simulation models (SILVA and LandClim), the response of a mixed beech-oak stand was assessed under non-stationary climate. The results showed that a 'climatic turning point' in terms of species dominance might be passed during the present century. Inherited stand structure, however, might lead to a considerable time delay of observable forest response in undisturbed stands.

The combined effect of climate and competition on tree growth was investigated in more detail in a study based on the Spanish National Inventories. In **Manuscript 3 'Symmetric and asymmetric competition',** changes of competition intensity and importance along the aridity gradient throughout the Iberian Peninsula were assessed. Symmetric and asymmetric competition were distinguished and integrated within a statistical model. The study exhibited that the negative effect of competition on tree growth increased with aridity.

Manuscript 4 'Ecotype mixing as climate change adaptation' deals with the question how to adapt forests to climate change. One management strategy might be to introduce non-local ecotypes in order to increase biodiversity. Thereby, future yield is assumed to be more stable, according to the portfolio effect theory. However, forest stands differ from common economic products by the natural process of self-thinning. A consideration of self-thinning in the evaluation of ecotype mixing is important and could exempt the portfolio effect from its drawback of lower chances for high yields.

In **Manuscript 5 'Disturbance interactions',** forests disturbances – particularly their interactions – were assessed. Disturbance interactions were found to be positive resulting in a system containing positive, closed feedback loops. From a theoretical perspective it is likely that such a system is unstable, i.e. that forest disturbances will increase until forest collapse. In **Manuscript 5,** a framework of disturbance interactions was developed and translated into a strategic mathematical model. The model showed that although all interactions might be positive, forests do not necessarily need to collapse. Furthermore, disturbance interactions might cause only a minor part of overall disturbances regimes and direct alteration in climate is of much higher importance.

Manuscript 1: Long-term vegetation dynamics in New Zealand

Simulating long-term vegetation dynamics using a forest landscape model: The post-Taupo succession on Mt. Hauhungatahi, North Island, New Zealand

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Abstract

Forest dynamics in New Zealand (NZ) are shaped by catastrophic, landscape-scale disturbances (e.g. volcanic eruptions, landslides, windstorms and fires). The long return-intervals of these disturbances, combined with the longevity of many of NZ's tree species, restrict solely empirical investigations of forest dynamics. In combination with empirical data (e.g. descriptions of past vegetation via palaeoecological reconstructions), simulation modelling provides a way to address these limitations and to unravel complex interplays between disturbances, biotic interactions, and abiotic constraints such as climate, soil, and topography. Here we adapt the established forest landscape model LandClim to address complex interacting processes across the large spatio-temporal scales relevant for NZ's forest landscape dynamics.

Using the well-investigated western slope of Mt. Hauhungatahi in the central North Island as a case study, we examine forest succession after large scale disturbances, in this case the Taupo eruption of c. 1700 BP, and the subsequent emergence of altitudinal species zonation. We derived a set of life-history parameters that agreed with those described in the ecological literature by applying a pattern-oriented parametrization approach for the traits 'maximum growth rate' and 'shade tolerance'. With this parameter set, LandClim was able to reproduce similar spatio-temporal patterns in the vegetation structure as seen in pollen reconstructions and contemporary vegetation studies along the altitudinal transect. The modelled successional sequence displayed a major shift in forest composition between simulation years 400 to 700, when the dense initial stands of conifers (dominated mainly by *Libocedrus bidwillii* – pāhautea or kaikawaka) were progressively replaced by the angiosperm *Weinmannia racemosa* (kamāhi) in the montane forest. From around year 1000 onwards, the currently observed altitudinal species zonation was attained. Light-competition controlled the major successional trends and, together with temperature-limitation,explained the observed altitudinal species zonation.

Although designed for European temperate forests, LandClim is capable of simulating NZ's landscape dynamics and forest response to catastrophic disturbances such as the Taupo eruption. We suggest that LandClim provides a suitable framework for investigating the role of spatial processes, in particular disturbance, in NZ's forest landscapes.

Keywords: LandClim, inverse modelling, disturbance regime, long-lived tree species, gap model, succession

Introduction

Climate, soil, relief and exogenous disturbance are important abiotic drivers of the spatial distribution of forest types (Leathwick and Mitchell 1992). Along altitudinal gradients, temperature and other parameters of climate are the primary controls of species distribution, in particular their upper limits (Wardle 1964, Druitt et al. 1990). Large-scale disturbances are another key driver of the long-term dynamics of forests in New Zealand (NZ) (Ogden and Stewart 1995). A number of studies have demonstrated the long-lasting impact of large, infrequent disturbances, such as earthquakes, landslides, volcanic eruptions and windstorms, on NZ's forests (Clarkson 1990, Wells et al. 2001, Lecointre et al. 2004, Martin and Ogden 2006). The effect of disturbances also plays a central role in the long-standing questions surrounding the nature of conifer-angiosperm interactions in NZ's mixed forests (Veblen and Stewart 1982, Wells et al. 2001, Ogden et al. 2005). Contrasting traits of conifers and angiosperms are considered key in structuring forest communities over time (McKelvey 1963, Ogden and Stewart 1995, Coomes et al. 2005, Kunstler et al. 2009). Conifers are generally slower growing than angiosperms on productive sites (i.e. rich in nutrients and water, warmer temperatures) and therefore tend to be outcompeted by angiosperms over the long term (Bond 1989, Becker 2000, Coomes et al. 2005, Brodribb et al. 2012). In NZ, and other parts of the southern hemisphere, 'long lived pioneer' conifers (e.g. *Agathis australis*, *Dacrydium cupressinum*, *Libocedrus bidwillii*) can however be observed to persist alongside angiosperm competitors (Ogden and Stewart 1995). Large, infrequent disturbances are considered key for mediating the competition between both groups (Ogden and Stewart 1995).

The dynamics of forests dominated by long-lived tree species and shaped by the infrequent occurrence of large disturbances are particularly intractable to study (Enright et al. 1999) as time-scales up to the millennial need to be considered (Ogden and Stewart 1995). Palaeoecological reconstructions, for example via fossil pollen records, provide descriptions of long-term successions after large disturbances (McGlone et al. 1988, Horrocks and Ogden 1998). However, palaeoecological records are challenging to interpret due to the influence of a multitude of confounding factors such as climate, disturbance, dispersal lags, and biotic interactions (Anderson et al. 2006, Brewer et al 2012). Therefore, while such records provide invaluable descriptions of temporal dynamics, they are by themselves seldom sufficient to draw general conclusions about the processes that underlie the patterns they show.

Process-based simulation models are well-suited for the exploration of forest dynamics over extended spatio-temporal scales and provide a valuable complement to empirical studies (Henne et al. 2011). So-called ‘forest gap models’ are widely used to address diverse questions regarding global change impacts on long-term forest dynamics (Bugmann 2001, Perry and Millington 2008), but have received surprisingly little application in NZ. In an early attempt to implement a forest gap model in NZ, Develice (1988) developed the non-spatial FORENZ model for Fiordland, South Island. Currently, LINKNZ (Hall and Hollinger 2000, Hall and McGlone 2006) and SORTIE/NZ (Kunstler et al. 2009) are the forest gap models best established for New Zealand’s forests. For example, McGlone et al. (2011) used the forest gap model LINKNZ to explore how decreased seasonality in the early Holocene in NZ might account for the patterns found in pollen records.

Traditional forest gap models are not designed to represent large and heterogeneous landscapes with areas of differing climate, topography and soils (Mladenoff 2004). Rather, forest gap models simulate successional processes in small gap-sized forest patches (less than one ha), often without interactions between the patches (Bugmann 2001). At the landscape level, however, interactions between patches are important, in particular with respect to seed dispersal and larger disturbance events. Since traditional gap models focus on tracking the development of individual trees in a complex representation of their physical competitive environment, they are computationally expensive (Mladenoff 2004). Therefore, individual to stand-scale gap models tend to consider spatial extents of a few tens of hectares. Furthermore highly mechanistic, spatially explicit gap models such as SORTIE require considerable parametrization effort (Uriarte et al. 2009).

While, promising approaches have been developed to overcome these computational limits, such as the PPA model for SORTIE (Strigul et al. 2008) or upscaling approaches (Hartig et al. 2012), these remain in their infancy. Forest models suitable for investigating interacting processes across large landscapes need to fulfil three important prerequisites: (i) reduced complexity in the representation of stand-scale processes, while retaining structural realism, (ii) an ability to represent spatio-temporally heterogeneous landscapes at extents of up to 1000s of hectares over centuries to millennia, (iii) the incorporation of ecological processes important at larger scales (e.g. landscape-level disturbance) (Mladenoff 2004, Schumacher 2004).

LandClim (Schumacher et al. 2004, Schumacher and Bugmann 2006), as a landscape simulation model, meets these three requirements and can help to assess processes at larger scales. In LandClim individual species are represented in terms of their ecological traits (among them longevity, growth rate, temperature requirements, shade tolerance) which determine the species ability to establish, grow and survive. Due to its structural realism, simulation outcomes of LandClim can be evaluated against various empirical patterns of forest composition and age structure, thereby facilitating pattern-oriented modelling (POM; Grimm et al. 2005, Hartig et al. 2011, Hall et al. 2001, Grimm and Railsback 2012). Pattern-oriented parametrization, a subset of the broader POM framework, infers realistic parameter ranges from observed system behaviour by comparing model outputs with multiple observed patterns and thereby filtering the parameter space. Pattern-oriented parameterization therefore provides a promising approach to overcome the difficulties and limitations of direct parameterization (Hall et al. 2001). LandClim, as do most other forest gap models, contains species parameters that are difficult to quantify directly, in particular the crucial species traits of ‘shade tolerance’ and ‘maximum growth-rate’ (relative biomass growth rate per year). Growth rates measured in the field are always influenced by the abiotic environment and biotic interactions and can not therefore be assumed as equivalent to the growth potential of a species. Shade tolerance is similarly difficult to quantify in the field due to interactions with other growth limiting factors and its dependency on ontogeny (Valladares and Niinemets 2008).

Here we make use of the rich spatio-temporal dataset describing forest structure and dynamics on the western slope of Mt. Hauhungatahi to apply LandClim to a NZ situation for the first time and parametrize the traits ‘shade tolerance’ and ‘maximum growth-rate’ of dominant canopy species by means of a pattern-oriented parameterization approach. The location of Mt. Hauhungatahi in the volcanic area of Tongariro National Park offers an ideal study site to investigate the effects of landscape-level disturbance on forest succession following the cataclysmic c. 1700 BP Taupo eruption (Wilmshurst and McGlone 1996, Horrocks and Ogden 1998). High-resolution pollen data collected along an altitudinal transect at Mt. Hauhungatahi by Horrocks and Ogden (1998), together with contemporary vegetation studies (Druitt et al. 1990, Ogden et al. 2005) provide key patterns describing the dynamics and structure of the forest ecosystem. The integration of both spatial and temporal data on forest dynamics allows us to improve the robustness of the species parameterization and strengthens the reliability of the model. We consider our approach as complementary to previously established forest gap models such as LINKNZ and SORTIE/NZ. No single model can entirely represent reality, therefore using multiple models enable us to explore the significance of different system representations and so increase the robustness of model-based inferences.

Besides being the first adaption of LandClim to NZ´s forests the aims of this study are to increase the understanding of drivers of species organisation following a catastrophic disturbance event and to contribute to the ongoing discussion over the long-term dynamics of mixed angiosperm-conifers forests. Our expectations are that: (i) species current altitudinal distribution will emerge from climatic preferences, in particular temperature requirements and (ii) the post-Taupo eruption forest succession can be explained by trade-offs and interactions between species shade tolerance, growth rate and longevity.

Methods

LandClim

LandClim is a spatially explicit forest landscape model that was originally developed to investigate the importance of climatic effects and disturbance processes for forest dynamics in the European Alps (Schumacher 2004, Schumacher et al. 2004, Schumacher and Bugmann 2006). The LandClim model structure comprises two main parts, one tracks stand-structure processes, such as establishment, growth and death, at annual time steps, while the other is concerned with landscape-level dynamics at a decadal time step. LandClim tracks individual trees in the aggregated form of cohorts. Cohorts are groups of same-aged trees within a grid cell (25 × 25 m), and all individuals in a given cohort are assumed to have the same biomass. Trees might establish in grid cells if propagules are available and environmental conditions are suitable. Tree growth is represented by a maximum growth rate (representing growth under optimum conditions) which is reduced as a function of limiting environmental factors and biotic interactions. Despite the problem of determining the maximum potential growth rate (parameter 'Rmax', see Tab. 1), this down-weighting approach is found in most forest gap models, such as JABOWA (Bugmann 2001). Tree mortality is a function of three factors: Growth-dependent stress, density-dependent stress and an intrinsic, age-related component. Detailed descriptions of the formulation of stand-scale processes in LandClim are given in Supplement S1.

LandClim represents the effects of disturbance on forest composition and structure reciprocally, which, in turn, allows for studies of past and future changing environments (Schumacher and Bugmann 2006, Henne et al. 2011). Environmental input variables are topography, soil water capacity and 'land-type' (a user-defined map assigning specific establishment rates and disturbance regimes to distinct areas), as well as temperature and precipitation at monthly resolution. Spe-

Tab. 1: Species life-history parameters. Tolerance-classes range from 1 (lowest) to 5 (highest tolerance). Abbreviations: EG: Evergreen, BL-EG: Broadleaf-evergreen. A brief explanation as well as references and basis for the parameter choice are given in Supplement, S2 and S3. The parameters 'shade tolerance' and 'Rmax' were determined via a pattern-oriented parameterization. The parameter 'minDD' was calibrated to fit species upper altitudinal limits described in Druitt et al. (1990), see also Supplement S2 for further details. Drought-, fire- and browsing-tolerance were not relevant in the present study, therefore, a default value of 3 was assigned to all species. Parameters are discussed in more detail in Schumacher (2004).

Parameter name	**Parameter description**	***Dacrydium cupressinum***	***Libocedrus bidwillii***	***Podocarpus unninghamii***	***Tree fern***	***Weinmannia racemosa***
maxAge	Maximum age (years) that an individual can reach	800	1000	650	150	400
Kmax	Maximum aboveground tree biomass (tons) a species can reach	12	8	7.73	0.5	6.32
leafHabit	Leaf habit (form)	EG	EG	EG	BL-EG	BL-EG
foliageType	Shading potential of a species canopy	3	3	4	5	5
minTemperature	Minimum temperature (°C) for establishment	-8	-13	-13	-8	-8
shadeTolerance	Species shade tolerance	4	2	2	5	4
droughtTolerance	Species drought tolerance	3	3	3	3	3
minDD	Minimum annual degree day sum	1400	1200	1280	1550	1300
Rmax	Maximum above-ground biomass growth rate (per year)	0.07	0.12	0.11	0.10	0.13

cies environmental responses are defined by traits such as drought tolerance, shade tolerance and temperature requirements. LandClim operates over long time scales (hundreds to thousands of years) and large spatial extents (100s to 10000s of hectares) at a relatively fine scale (grid cells of 25 by 25 m). It has previously been tested in and adapted to the European Alps, the North American Rocky Mountains and Mediterranean forests (Schumacher and Bugmann 2006, Colombaroli et al. 2010, Henne et al. 2011, Henne et al. 2012, Briner et al. 2012, Elkin et al. 2012).

This study is the first application of LandClim to the Southern Hemisphere. The model structure of LandClim was kept unchanged; the only differences from the previous studies were a new allometric relationship for calculation of NZ's species biomass to DBH, an increase in the maximum stand biomass from 300 t/ha to 1000 t/ha (see Supplement S1 for details) and the parameterization of tree species.

Study site

Our simulations focused on the western slope of Mt. Hauhungatahi, which has been intensively studied previously (Druitt et al. 1990, Horrocks and Ogden 1998, Ogden et al. 2005). Mt. Hauhungatahi is located in the Tongariro National Park in the central North Island of New Zealand (Fig. 1) where forests have been subject to recurrent volcanic events throughout the Quaternary, with therhyolitic Taupo eruption of 1718 ± 5 cal. BP (Hogg et al. 2012) particularly significant (Horrocks and Ogden 1998). Druitt et al. (1990) distinguished three main belts of forest

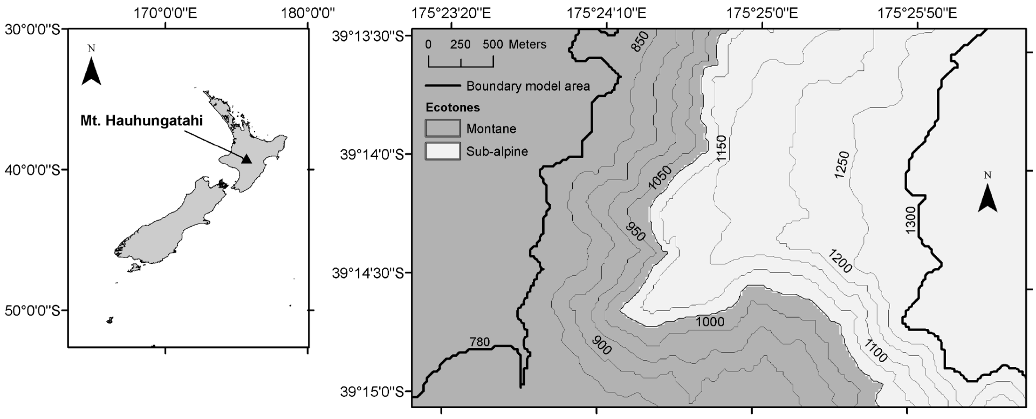

Fig. 1: Map of study area on the western slope of Mt. Hauhungatahi in the Tongariro National Park, New Zealand.

using the importance value as a measure of species dominance (species nomenclature follows Landcare Research 2011b):

(i) A montane forest from 850 to 1000 m a.s.l. with the canopy dominated by angiosperms, in particular *Weinmannia racemosa* (kamāhi). Scattered old conifer individuals (e.g. *Dacrydium cupressinum* – rimu) are present and constitute an important part of the total basal area, but younger conifer individuals are mostly absent. Tree ferns (e.g. *Cyathea smithii* – katote) are important components of the sub-canopy layer.

(ii) A transitional zone ranging from 1000 to 1050 m a.s.l., where several species (including *W. racemosa*, *D. cupressinum* and tree ferns) reach their upper limit. Conifers, and in particular *Podocarpus cunninghamii* (formerly *P. hallii*, Hall's totara), are prominent in this belt.

(iii) A sub-alpine zone (from 1050 m to the treeline), which is largely dominated by the conifer *Libocedrus bidwillii* (pāhautea). The treeline (formed by *L. bidwillii*, together with *Halocarpus biformis*) is highly discontinuous, varying between altitudinal limits of 1100 to 1250 m a.s.l.

Ogden et al. (2005) reported the highest densities and most vigorous regeneration of *L. bidwillii* in the sub-alpine zone, with densities and regeneration declining towards the transition zone at around 1050 m. This decline coincided with an increase in angiosperm densities, with *W. racemosa* becoming dominant in the upper montane zone.

Horrocks and Ogden (1998) outline the effect of the Taupo eruption on forest succession at Mt. Hauhungatahi using detailed pollen diagrams collected along the altitudinal transect described by Druitt et al. (1990). The two dominant patterns seen in Horrocks and Ogden's pollen diagrams are: (i) the initial increase and spread of *L. bidwillii* immediately following the eruption, and (ii) the progressive spread of the angiosperm *W. racemosa* in the montane forest in the centuries following the eruption, resulting in the present vegetation zonation.

Simulation experiments

The western slope of Mt. Hauhungatahi was represented in LandClim on a grid of cells (25 × 25 m) describing topography and soils. Topographic parameters (elevation, aspect and slope) were derived from a digital elevation map of the area

(DEM25, Land Information New Zealand 2011). Areas below 780 m were excluded since they are currently deforested and could not, therefore, be compared with empirical data. The widespread peatland area above the treeline (> 1300 m) was also excluded.

Soil characteristics on the slopes of Mt. Hauhungatahi are spatially heterogeneous and are a function of volcanic activity and a suite of secondary processes (Druitt et al. 1990). Due to the generally high water-holding capacity of volcanic soils (Scheffer and Schachtschabel 2002), a high soil water capacity (bucket size of 200 mm) was assigned uniformly to all grid cells (the model was not sensitive to this assumption, results not shown). The climate record (1930-2000 AD) from the nearby Chateau climate station at Mt. Ruapehu (12 km east of Mt. Hauhungatahi, 1097 m a.s.l.) was used as the climatic input data for the model (data source: NIWA 2011). Because the temperature reconstructions available for the site (Palmer and Xiong 2004) do not span the full 1700 year succession that we consider, the simulation was carried out under a present climate to provide a parsimonious baseline scenario. While climate reconstructions suggest the existence of some warm- and cold-periods in the past centuries, these are only of the order of less than 0.5 °C (Palmer and Xiong 2004). Since climate change is generally considered to be small in the post-Taupoperiod compared to the millennium before the eruption (McGlone 1989, Rogers and McGlone 1989) and the fossil pollen data do not show evidence of climate-related vegetation change after the eruption (Horrocks and Ogden 1998), we considered our assumption as reasonably realistic. The 70 year climate record was resampled (with replacement) to generate a 1700 year climate sequence; this randomisation was repeated for every simulation.

The four dominant canopy species that characterise the altitudinal belts on Mt Hauhungatahi were represented in the model: The angiosperm *Weinmannia racemosa* (kamāhi) and the conifers *Dacrydium cupressinum* (rimu), *Podocarpus cunninghamii* (Hall’s totara) and *Libocedrus bidwillii* (pāhautea). A tree fern life-form was included due to their high abundance in the montane forest (especially *Cyathea smithii* ;Druitt et al. 1990) and their structural importance for forest dynamics (Coomes et al. 2005). The tree-fern life-form was implemented as a shade tolerant understory species (resembling the behaviour of *Cyathea smithii* as reported by Bystriakova et al. 2011) and treated by the model in the same way as the other tree species.

Species life-history traits were assigned from the New Zealand Eco-Trait database (Landcare Research 2011a), the ecological literature, including the Flora of New Zealand, and expert-knowledge. Details about the life-history traits and reasoning for the choice of parameters are provided in Supplement S2. The parameter 'minDD' (minimum degree days) was calibrated to fit the upper altitudinal limits described in Druitt et al. (1990), assuming that the species upper elevation limit is controlled by temperature (see Supplement S2 for further information). The parameters 'shade tolerance' and 'Rmax' (maximum relative biomass growth rate per year) were determined in a pattern-oriented parametrization approach, described in the following section.

It was assumed that the Taupo eruption removed all vegetation from the study area, since the actual degree of forest destruction remains unknown. Horrocks and Ogden (1998) noted that the effect of the Taupo eruption (including the shock wave, air fall of tephra and subsequent fires) was presumably considerable at Mt. Hauhungatahi (ca. 75 km distance from the vent), although fossil pollen indicate some surviving forest in the area. The simulations started from 'bare ground', initiated by a spatially homogeneous seed rain with the same amount of seed across all species, as is often assumed in forest landscape and gap models, particularly in the absence of detailed species-specific empirical data describing the seed rain. Although this approach neglects the possible influences of prior vegetation and heterogeneous seed rain, it provides a baseline assumption to cope with complex and unknown initial conditions. For the same reason, global seed dispersal was assumed. Succession was simulated and tracked over 1700 years, representing the time since the Taupo eruption. No further disturbance events were simulated over this succession. To ensure direct comparability with the measurements of forest structure by Ogden et al. (2005), only individuals with a DBH (diameter at breast height) larger than 10 cm were considered in the analyses of the simulated altitudinal transect (although LandClim is capable of tracking smaller individuals).

Pattern-oriented parameterization

In order to identify plausible parameter combinations for 'maximum growth-rate'(Rmax) and 'shade tolerance' that reproduce the expected system behaviour, a pattern-oriented parameterization approach was chosen.

First, a complete parameter space with both traits for all five species was created. Each parameter was given five possible values (for shade tolerance from 1 (low) to 5 (high) and 'Rmax' from 0.03 to 0.15 (in steps of 0.03)). This parameter space was reduced by discarding ecologically unreasonable parameter combinations a priori from the analysis, using the criteria below:

(i) Maximum growth rates of angiosperms (*W. racemosa*) should be higher than those of conifers (Ogden and Stewart 1995). (ii) Shade tolerance of conifers *L. bidwillii* and *P. cunninghamii* should be in the range from low to intermediate due to their characterisation as light-demanding pioneer species (Clayton-Greene 1977, Ebbett and Ogden 1998). (iii) Shade tolerance of *D. cupressinum* and *W. racemosa* should range between intermediate to high (Lusk and Ogden 1992, Lusk et al. 2009). (iv) Shade tolerance of the tree fern life form (resembling the ecology of *Cyathea smithii*) was defined as high (see Supplement S3 for further details about the tree fern life form).

The model was run for all possible parameter combinations that fulfilled these criteria (in total 23364 scenarios). The simulations for the pattern-oriented parameterization were performed on a small area (covering the length of the entire altitudinal gradient but reducing the width to only 4 cells, i.e. 100 m) in order to reduce computation time for each simulation, under a randomized present climate scenario in the absence of further disturbance events.

The simulation outputs were filtered according to spatio-temporal patterns described in the pollen records of Horrocks and Ogden (1998), using a Boolean filter. These patterns were (i) an initial dominance of conifers (in particular *L. bidwillii*) in the first centuries after the Taupo eruption which was defined as the criterion that conifer species should reach > 60% of total forest biomass in the first 300 years of succession; (ii) a progressive spread of *W. racemosa* in the montane area during later stages of succession, represented by the criterion that *W. racemosa* should reach > 60% of total forest biomass during the years 1000-1700 in the area up to 1050 m altitude. Additionally, parameter combinations resulting in unreasonably low total stand biomass were discarded. Based on the carbon stock estimates for podocarp-hardwood forests in NZ (Horrocks and Ogden 1998), a minimum biomass of 100 t per ha was estimated (under the assumption that biomass consist of 50% carbon). Further parameter combinations for which tree species had disappeared at the end of succession (i.e. species biomass dropped below < 1% of total biomass) were also discarded. These criteria narrowed down the parameter space substantially.

Finally, a refined sensitivity analysis was performed to determine optimized ‘Rmax’ values for each species. ‘Rmax’ values were assigned from within the range determined by the previous analyses and sampled in steps of 0.01. Shade tolerance values were assigned according to the results of the previous analysis. For the filtering of these results, stronger criteria were applied: *L. bidwillii* should dominate the early successional stage with > 75% of total standing biomass, and *W. racemosa* should dominate the late successional stage in the montane forest with > 75% biomass. Furthermore, simulated mean annual DBH-growth of species (at year 1700) should be in the range of mean annual growth rates reported by Ogden et al. (2005) for *L. bidwillii*, Smale and Smale (2003) for *P. cunninghamii*, Lusk and Ogden (1992) for *D. cupressinum* and *W. racemosa* (see Supplement S2). For the tree fern life form, height-growth estimates from Ogden et al. (1997a) were used (see Supplement S3).

The final parameter set was used to simulate the spatio-temporal forest dynamics of Mt. Hauhungatahi (Tab. 1). Simulations were repeated 50 times with a randomized present climate to account for stochastic variation between model realisations under the same parameter conditions.

Analyses and visualization of model results were conducted using R.2.15.2 (R Development Core Team 2012). The pattern-oriented parameterization was carried out on a high-performance computer cluster at the University of Bayreuth, Germany.

Results

Species traits

In the pattern-oriented parameterization, the application of the filter criteria (see previous section) narrowed down the parameter space from 23364 to 129 possible combinations. The shade tolerance ranges defined a priori proved suitable, as most model results from the given range were accepted by the filter criteria (Fig. 2, black bars). The specific ‘Rmax’ values substantially influenced the successional sequence and the biomass of individual species. ‘Rmax’ values below 0.06 typically resulted in low species biomass and therefore tended to be discarded by the filter criteria. The refined sensitivity analysis showed that the observed successional dynamic was reproduced within a rather narrow constellation of ‘Rmax’ values. *L. bidwillii* and *W. racemosa* (as the main components of the simulated forest ecosystem) displayed a strong successional differentiation between pioneer and later successional species once the parameter constellation was set as shown in Fig. 2. With increasing advantage in growth rate of *W. racemosa* over *L. bidwillii*, the pattern still prevailed but the initial dominance of *L. bidwillii* became less pronounced at the expense of *W. racemosa* in the lower montane forest.

Within the parameter ranges explored, *P. cunninghamii* and *D. cupressinum* were present with only low biomass. Variations in their parameter sets consequently had a minimal effect on the gross successional trends.

Species zonation

LandClim reproduced the actual species zonation described by Druitt et al. (1990) at the end of succession (year 1700) once all species (with traits as in Tab. 1) were included in competition with each other. The species upper elevation limits were controlled by their specific temperature (‘minimum degree day’) requirements. Notably, the observations of Druitt et al. (1990) were used in the calibration of the ‘minimum degree day’ parameter, therefore they cannot be con-

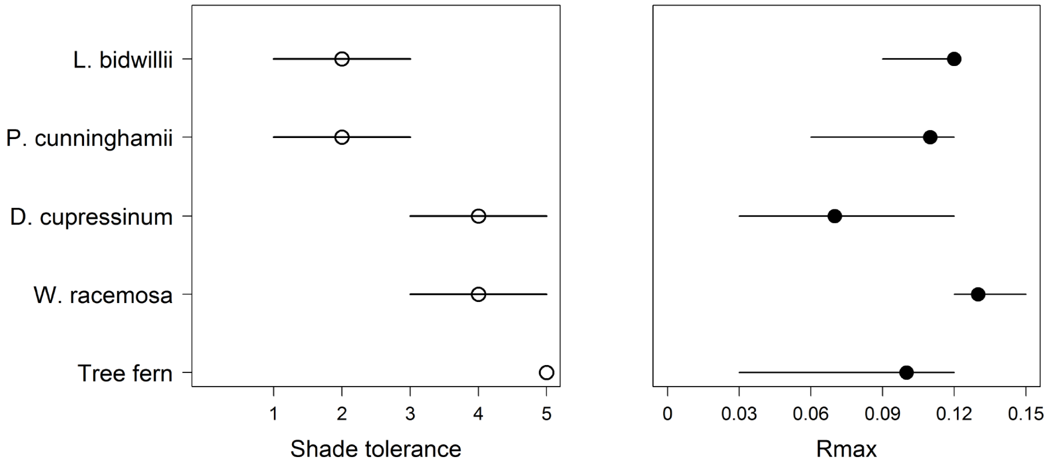

Fig. 2: Results of the pattern-oriented parameterization for the parameters ‘shade tolerance’ (left) and maximum growth rate - ‘Rmax’ (right). The range of accepted parameters is indicated by the black line, parameter values occurring with highest frequencies are indicated by a circle (filled circle indicates result of refined sensitivity analysis of ‘Rmax’).

sidered as independent data for model evaluation. In simulations of monocultures each species occurred across the altitudinal transect from the lower boundary (780 m a.s.l.) to its specific upper elevation limit. Once all species were included (and thus interspecific competition occurred), conifer species largely disappeared from lower altitudes.

The lower elevation forest band (780-950 m) was dominated by *W. racemosa*. Tree ferns occurred up to an altitude of around 880-900 m, but with a low basal area (< 1m^2 / ha) and density (< 50 stems/ha, data not shown). *D. cupressinum* occurred up to an altitude of 1000 m, but only as a very few, scattered individuals. Above 950 m a.s.l., the basal area of *W. racemosa* steadily declined to its upper altitudinal limit at around 1050 m. As *W. racemosa* declined, the forest gradually shifted in composition with the conifer species becoming increasingly important. *P. cunninghamii* reached its maximum basal area and stem density between altitudes of 950 to 1050 m. Altitudes above 1000 m were dominated by *L. bidwillii* in terms of basal area and stem density until the treeline at around 1220 m.

The simulated basal area and stem density of the species peaked at the same altitudes as those described by Ogden et al. (2005), but the model under-represented basal area for all species and over represented stem density for *L. bidwillii* (Fig. 3). The deviation between observed and simulated forest structure was particularly evident for *D. cupressinum* and *P. cunninghamii*, which achieved only very low values of basal area and stem density in the simulated year 1700.

Forest succession

The simulated post-Taupo succession resembled the general patterns described by Horrocks and Ogden (1998) once species life-history traits were assigned following a rigorous and thorough pattern-oriented parameterization process (Tab. 1). The succession was characterised by three main stages, one from simulation years 0-400, a second from years 400-700, and a third from year 700 onwards. During the early phase of the succession (simulation years 0 to 400), *L. bidwillii* dominated the study area in terms of biomass (Fig. 4). In the following centuries (simulation years 400-700, Fig. 4), the biomass of *L. bidwillii* declined, whereas that of *W. racemosa* steadily increased. From around simulation year 1000 onwards, conditions were generally stable and similar to the contemporary composition on Mt. Hauhungatahi. Both *D. cupressinum* and *P. cunning-*

hamii were only present with low biomass throughout the succession. The tree fern life-form occurred across the entire succession, but at lower biomasses than the other four tree species.

The spatial distribution of the tree species shifted over time such that there was a progressive upward expansion of *W. racemosa* in the montane forest, accompanied by a retraction of *L. bidwillii* and *P. cunninghamii* into the higher sub-alpine forest. The early successional stage (simulation years 0 to 400) was characterised by the widespread dominance of *L. bidwillii* (Fig. 4). In the montane forest, the dominance of *L. bidwillii* was associated with occasional occurrence of *P. cunninghamii* and *D. cupressinum*. *W. racemosa* occurred only in a few scattered grid cells during the early succession. During the mid-succession (simu-

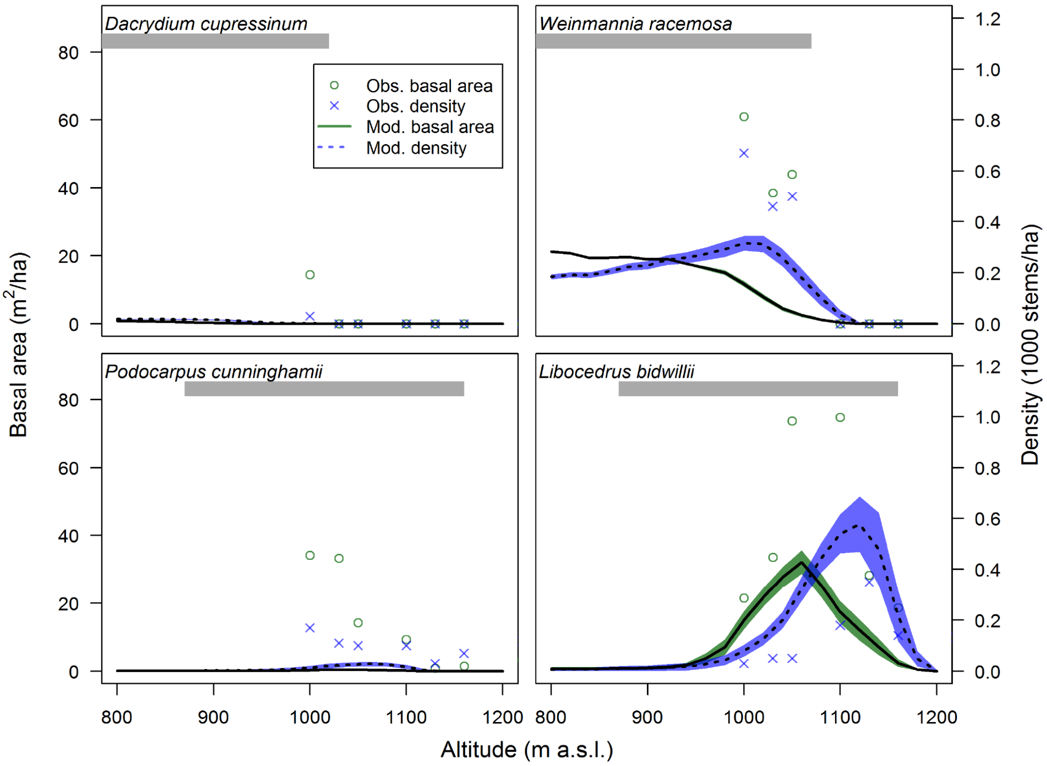

Fig. 3: Altitudinal distribution of species as described by Druitt et al. (1990) (shown as grey bar) and forest structure (basal area and density) as reported by Ogden et al. (2005) (shown as observation points) alongside model outcomes after 1700 simulation years. For model outcomes, the mean of 50 model realisations is shown together with the standard error of the mean. Only individuals with DBH > 10 cm were considered in the model in order to assure comparability with the empirical data. On the basis of their low abundance and the lack of empirical data reporting their stand structure, tree ferns were excluded.

lation years 400 to 700) *W. racemosa* began to increase in abundance, starting from the lowest elevations and spreading upslope over the following centuries. *W. racemosa* prevailed in most parts of the montane forest below 1000 m by the simulation year 700 and attained dominance in almost all of the montane forest around the simulation year 1000. The later stages of succession (simulation years 700 to 1700) were characterised by the decay of old, scattered stands of *L. bidwillii* in the montane forest and the development of the altitudinal vegetation zonation described above.

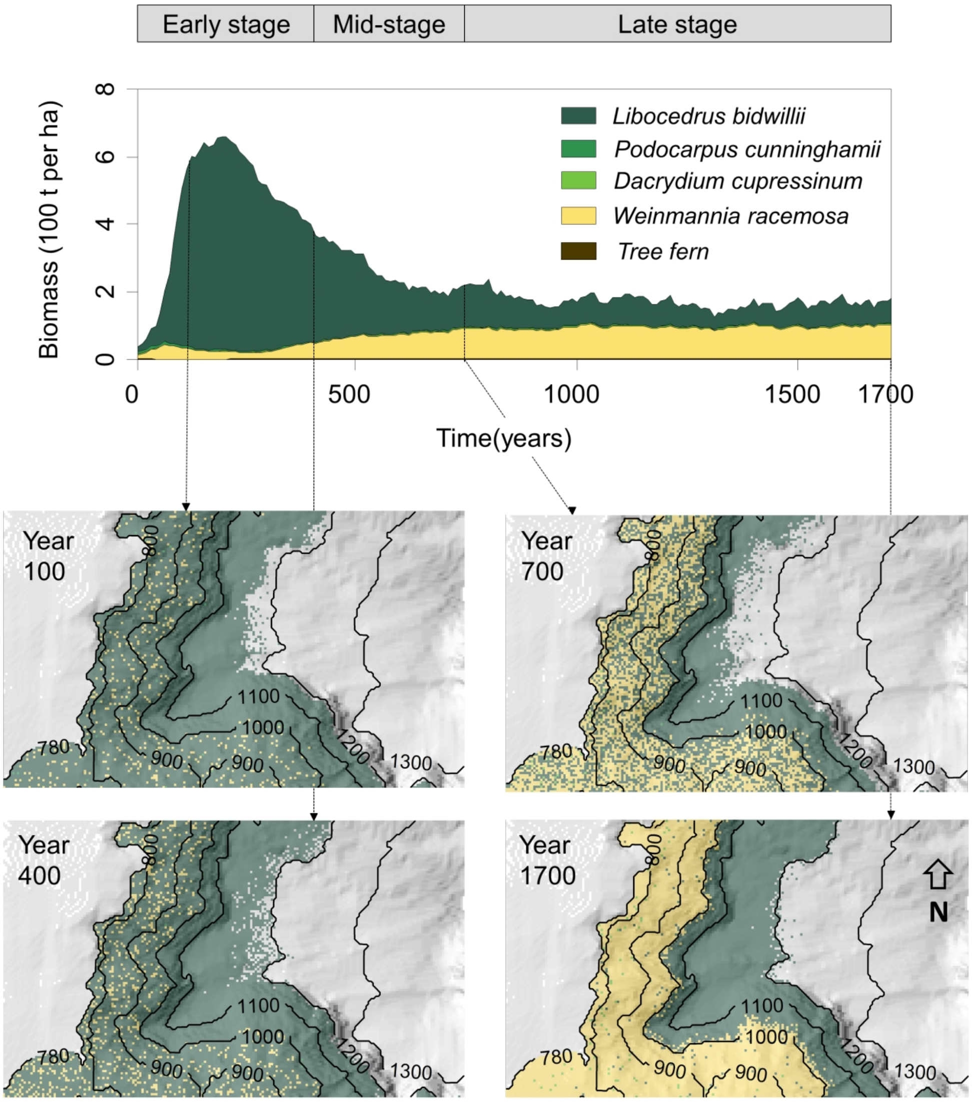

Fig. 4: Simulated succession of tree species following the Taupo eruption (c. 1700 BP) on the western slope of Mt Hauhungatahi. For the spatial distribution of vegetation, dominant tree species (in terms of biomass) of each grid cell are displayed.

While general temporal patterns of an initial spread of *L. bidwillii* and a subsequent spread of *W. racemosa* in the montane forest coincided with the palynological findings of Horrocks and Ogden (1998), patterns for *D. cupressinum* did not match well. Fossil pollen records show that *D. cupressinum* was continuously present at Mt. Hauhungatahi throughout the post-Taupo succession constituting a substantial fraction to the amount of pollen. In the simulation, *D. cupressinum* was present at all times, however with generally very low biomass. According to Horrocks and Ogden (1998), the pollen abundance of *Dacrydium* is, however, not a good predictor for basal area, which prohibits a direct comparison between model results and observation.

Discussion

LandClim proved capable of reproducing the general patterns of species zonation and successional patterns by parameterization of species traits only. The model structure itself was left unchanged. This finding is of particular interest, as NZ's temperate forests are considered to differ from their Northern hemisphere counterparts in several aspects (McGlone et al. 2010, Wilson and Lee 2012). A reproduction of key patterns by a northern-temperate forest model might, therefore, point towards a generality of underlying mechanisms that structure temperate forest landscapes worldwide.

Species upper altitudinal limits resulted from the species temperature requirements (through calibration of the 'minimum degree days' parameter), whereas biotic interactions (competition for light determined by the species shade tolerance, temperature requirements and potential growth rate) were important for species lower altitudinal limits and for structuring succession.

The outcome of interspecific competition therefore varied both spatially and temporally, since environmental conditions changed with altitude (temperature) and over time (light-transmission to the forest floor). The landscape approach presented here highlights how gradual changes in the environmental conditions affect the competitive balance between species, and results in a differentiated picture of spatio-temporal forest dynamics.

Species traits

In the trait space (Tab. 1), *L. bidwillii* and *W. racemosa* occupy different positions reflecting a trade-off in their capacity to cope with stress induced by shade and low temperatures. A frequent observation is that an adaptation to a certain climatic environment often comes at the cost of adaptation to other conditions (Hereford 2009). Similar trade-offs have been described for adaptions to shade, drought and waterlogging (e.g. Niinemets and Valladares 2006) as well as for the relationship between growth rate and survival under limited light (Lusk and del Pozo 2002, Kunstler et al. 2009), cold (Loehle 1998) or nutrient conditions (Chapin et al. 1986, Lusk and Matus 2000).

In respect to a trade-off underlying spatio-temporal vegetation dynamics, our model results are similar to the study of Smith and Huston (1989), who found that the temporal and spatial shift in species dominance can be explained by different adaptions of plants for two or more resources (in their case light and water use).

In LandClim, the *L. bidwillii* traits enable it to take advantage of well-lit, open sites at higher altitudes, where low temperature impedes the growth of its competitors (such as *W. racemosa*). An increase in shading of the forest floor in turn results in a decrease of the regeneration success of *L. bidwillii*. Under these conditions, the more shade tolerant species *W. racemosa* can outcompete the shade intolerant conifer and progressively take over its sites. Here, *L. bidwillii* loses its initial advantage (in terms of better growth performance under cooler conditions) since shade becomes the main limiting factor for growth. The strategy of *W. racemosa* proves to be more successful at this point, at least up to a certain altitude (in the model at around 1000 m) where temperature limitations turn the competition-balance again.

The evaluation of the trait shade tolerance was not, however, straightforward for all species. The results of the pattern-oriented parameterization imply that *D. cupressinum* and *W. racemosa* are both moderately shade tolerant (shade tolerance class 4, implying a minimum requirement of 5% light availability, see also Schumacher 2004, Tab. B.3). This appears to be reasonable for *W. racemosa*, which is usually regarded as a species of intermediate shade tolerance with some evidence for continuous regeneration under closed canopy (e.g. all-aged populations found by Lusk and Ogden 1992 in Horopito, near Mt. Hauhungatahi). *D. cupressinum*, by contrast, is often described as a species with pioneer behaviour on open sites (e.g. Beveridge 1973), displaying a restricted age-range, which points towards a regeneration after exogenous disturbances (Lusk and Ogden 1992). However, Lusk et al. (2009) found that seedlings of *D. cupressinum* could tolerate lower levels of diffuse light availability than *W. racemosa*. The result of the pattern-oriented parameterization (shade tolerance value 4 both species) therefore only reflects partly the ecology and the expected behaviour of both species.

Valladares and Niinemets (2008) reviewed the nature of shade tolerance and pointed out that it is a much more complex trait than often considered to be. In particular, they noted that a species shade tolerance is influenced by numerous biotic and abiotic factors and can furthermore vary with plant ontogeny. In NZ, Kunstler et al. (2009) investigated the growth and mortality of a range of podocarp-hardwood species (including *W. racemosa* and *D. cupressinum*) and found that several species changed their strategy in respect to the growth-shade tolerance trade between sapling, seedling and mature life stages of several species. In particular *D. cupressinum* displayed this phenomenon, commonly referred to as 'ontogenetic trade-off'.

Regeneration of some of NZ's tree species (and hence species position during succession) might therefore likely be influenced by more complex processes than those represented in LandClim. A closer consideration of the representation of regeneration (for example in respect to the ontogenetic trade-off) might be beneficial for further studies using LandClim in NZ.

Finally, for the incorporation of further NZ's species it might be necessary to represent more shade tolerance classes (as per Henne et al. 2012 in Mediterranean forests who considered six) to account for the possibility of species to regenerate and grow in deep shade under light levels below 1% (as for example reported for *Beilschmiedia tawa* by Lusk et al. 2009).

Species zonation

The simulated species zonation was the outcome of temperature requirements (i.e. by the species specific requirements for minimum degree days – 'minDD') controlling species upper altitudinal limits and competition determining their lower limits. It is important, however, to note that the observations of Druitt et al. (1990) were used in the calibration of the 'minimum degree day' parameter and are not, therefore, an independent dataset for the purposes of model evaluation. The species ranking in minimum degree days is, however, supported by Leathwick (1995), who found *D. cupressinum* and *W. racemosa* biased towards warmer habitats (in terms of mean annual temperature), *P. cunninghamii* growing under cooler and *L. bidwillii* under the coldest conditions. Druitt et al. (1990) discussed the effects of climate, competition, soil (and nutrient status), as well as slope steepness, in controlling the vegetation distribution on Mt. Hauhungatahi, and suggested competitive exclusion as a potentially important mechanisms for the current restriction of *P. cunninghamii* to the 'transition zone' (1000-1050 m a.s.l.). Our model-based experiments support this argument by showing a virtual exclusion of conifers from the montane forest during the late stage of succession (Fig. 3 and 4) in comparison to monoculture simulations, where conifers were abundantly present in lower altitudes as well (results not shown). While temperature is an important control on the upper altitudinal limit of *L. bidwillii*, the variable nature of the treeline at Mt. Hauhungatahi suggests that other processes, such as disturbance and previous environmental fluctuations, can also have significant, and potentially, long lasting effects (Ogden et al. 1997b, Horrocks and Ogden 1998).

LandClim was able to reproduce the broad spatial patterns of basal area and stem density reported by Ogden et al. (2005). A zone with abundant *W. racemosa* at lower altitudes (resembling the montane forest of Druitt et al. 1990) was followed by a belt of *P. cuninghamii* (i.e., the transition zone) and finally *L. bidwillii* dominating the highest altitudes (i.e., the sub-alpine zone). Basal area was, however, systematically underestimated and density of *L. bidwillii* slightly overpredicted, implying that the model produces stands with too many, too small individuals.

A notable discrepancy between model and empirical observations was found for *D. cupressinum* and *P. cunninhamii*. Conifers, including *D. cupressinum*, currently occur at low densities, and as scattered individuals, at the lower altitudes of Mt. Hauhungatahi (Druitt et al. 1990). Although some individuals of *D. cupressinum* appeared in the model, the species basal area was extremely low compared to that described by Ogden et al. (2005) (see Fig. 3). Both species, *D. cupressinum* and *P. cunninghamii*, are long-lived pioneer species (Ogden and Stewart 1995, Ebbett and Ogden 1998) and could therefore be expected to display a similar behaviour as *L. bidwillii*. This was not the case in the final model scenarios. Neither species was able to effectively compete with *L. bidwillii* or *W. racemosa*, which implies that important mechanisms in the species establishment and competition were not well represented. Horrocks and Ogden (1998) note the potentially important effect of further disturbance events at Mt. Hauhungatahi after the 1700 BP Taupo eruption (although their effect on the forest was probably far less severe). Mild volcanic activity in the post-Taupo period (around 660-600 BP, Horrocks and Ogden 1998) and increased storminess in the 1740s might have caused substantial canopy openings and thereby facilitated the establishment of secondary conifer recruits. Lusk and Ogden (1992) found a similar structure of *D. cupressinum* to that at Hauhungatahi at Horopito (15 km further to the south), with a predominance of old individuals and an absence of cohorts younger than 550 years that can likely be attributed to the same disturbance events that affected the forest of Mt. Hauhungatahi.

These observations point towards the importance of considering secondary, patchy disturbances (as caused by severe windstorms) in simulation experiments. LandClim contains a disturbance module explicitly designed to represent disturbances by windstorms. Although beyond the scope of the present study, this disturbance module offers further possibilities for exploration of the effect of various patchy disturbance regimes on the forest structure and composition.

Succession of tree species following Taupo eruption

According to Horrocks and Ogden (1998), *L. bidwillii* was dominant in the montane forest until a progressive invasion of *W. racemosa* commenced around c. 900-850 BP and culminated around c. 650 BP. In the model, the initial dense *L. bidwillii* stand persisted in the montane forest for several centuries by virtue of the species extreme longevity. The disintegration of this cohort was accompanied by the upward spread of *W. racemosa*, which reached the upper montane forest around 1000 BP and became fully established from c. 700 BP onward (Fig. 4). Therefore, the model results imply that the dense stands formed by the initial *L. bidwillii* cohort could have inhibited the spread of *W. racemosa* during the first centuries after the eruption.

Legacy effects from prior vegetation composition, climatic fluctuations and further (natural and anthropogenic) disturbances will all have influenced the forest succession since the Taupo eruption. A shift towards cooler, drier conditions

c. 3000-2000 BP (McGlone and Moar 1977, Rogers and McGlone 1989) might have meant that *L. bidwillii* was expanding at the time of the eruption. According to Horrocks and Ogden (1998), the effects of the Taupo eruption on Mt. Hauhungatahi were patchy, with some areas of forest escaping damage. Surviving patches of forest could have had a substantial impact on the vegetation composition immediately after the eruption, similar to contemporary post-disturbance succession at Mt. St. Helens (Dale 2005). Despite its simplified assumptions (succession starting from bare ground with global and uniform seed dispersal), the model results agree with the key patterns seen in the palynological record. The model analysis therefore highlights the profound and sustained effect of a catastrophic disturbance event such as the Taupo eruption for long-lived pioneer conifer species such as *L. bidwillii* (see also Ogden et al. 2005).

More differentiated patterns in the altitudinal series of pollen assemblages are, however, difficult to compare to the model results. First, the model represented only the main canopy species and did not account for other understorey species, some of which make substantial contributions to the relative abundance of pollen. Second, differences in pollen preservation and dispersal between species mean that there is not a consistent relationship between modern pollen abundance and basal area for all simulated species at Mt. Hauhungatahi (Ogden et al. 2005), which, in turn, makes it challenging to directly relate pollen assemblages to the simulated forest structure.

Application of LandClim for the NZ context

LandClim's facilities to represent disturbance processes (e.g. fires and stand-replacing windstorms) make it particularly well-suited for exploring questions about vegetation dynamics across broad-scales in space and time. This, in turn, means that LandClim can help to address the long-standing questions surrounding the role of disturbance processes in angiosperm-gymnosperm coexistence in NZ's forests (as suggested by a number of empirical studies, e.g. Lusk and Ogden 1992, Wells et al. 2001, Ogden et al. 2005). On the basis of a pattern-oriented parameterization of species traits and no other structural changes, LandClim proved capable of reproducing the altitudinal distribution of species on Mt. Hauhungatahi described by Druitt et al. (1990) and, to some extent, the patterns observed in forest structure by Ogden et al. (2005). Furthermore, the model experiments demonstrate how tree species life-history traits might explain the patterns of succession seen in the palynological record (Horrocks and Ogden 1998). On the other hand, relative to the data of Ogden et al. (2005), LandClim systematically underestimates basal area and tends to overestimate stem density for some species (Fig. 3). This mismatch suggests that the regeneration and mortality of long-lived trees is not represented adequately in LandClim. A more thorough consideration of how regeneration is represented in the model will be an important component of LandClim's development for future application in New Zealand.

Tree ferns constitute a distinctive feature of NZ's forests that have no direct equivalent in European and North American forest ecosystems. Our study provides a first attempt to incorporate these into a forest landscape model, but a more adequate representation will need to account for their distinctive growth behaviour.

Conclusion

Our approach highlights the potential for combining forest-landscape modelling with palaeoecological reconstructions in spatially complex environments. The use of simulation models to explore drivers underlying long-term dynamics observed in palaeoecological reconstructions is an area of considerable current interest. Whereas previous such studies using LandClim (Henne et al. 2011) have focused on cumulative pollen abundances over entire catchments, our study shows the model's suitability for use with locally and regionally distinct pollen assemblages. In the forest landscapes we consider, vegetation dynamics are controlled by interactions between biotic and abiotic drivers, but because they play out over long time-scales they are challenging to resolve empirically. Process-based simulation models as LandClim, when informed and supported by empirical data, have the potential to generate and evaluate hypotheses about the long-term trajectories of such forest systems.

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Supplement

S1: LandClim – model description

Detailed descriptions of the full structure of LandClim are given in Schumacher (2004), Schumacher et al. (2004) and Schumacher and Bugmann (2006). In order to explain the effect of biotic and abiotic drivers of vegetation dynamics, the following section provides a brief overview of the stand-level processes of LandClim.

The establishment, growth and mortality of trees are the three fundamental stand-scale processes considered by LandClim. The model tracks individual trees in the aggregated form of cohorts described by their biomass. Cohorts are groups of same-aged trees within a grid-cell (25 × 25 m) with all individuals having the same biomass (which can be translated into diameter at breast height using the allometric given below in section 'Growth') and survival probability, but with mortality occurring at the individual-level.

Establishment

For the representation of establishment, tree species are filtered by propagule availability and physical properties within each cell. Establishment in a cell is possible only in years where the light available at the forest floor exceeds a species-specific threshold value, winter temperature (mean temperature of the coldest month) is higher than a species-specific minimum temperature, and the sum of growing degree-days exceeds the species-specific minimum requirement. A species-specific establishment coefficient affects the probability of actual establishment. To reduce computational effort, the number and biomass of trees in any newly established cohort are calculated decadally.

Growth

Maximum growth rates are assigned to each species (representing the growth-rate under optimum environmental conditions), which are reduced by light availability, sum of degree days and drought. Actual tree growth is determined by a combination of these reduction factors under the application of Liebig's 'Law of the minimum'.

For conversion of the model biomass output into DBH, an allometric relationship was derived from individual-level data for *Weinmannia racemosa* (kamāhi) and *Dacrydium cupressinum* (rimu), reported by Beets et al. (2008):

$$d = 45.59799 \cdot b^{0.39877240} \quad \text{Eq. S1}$$

where: d = diameter at breast height (cm), and b = aboveground biomass (kg; assuming that 50% of dry trunk biomass is carbon).

Mortality

Tree mortality arises from three broad factors: 1) growth-dependent stress, 2) density-dependent stress and 3) an intrinsic, age-related component. Growth-dependent stress occurs when the annual growth rate drops below a species-specific threshold value due to unfavourable environmental conditions. Stress-related mortality probability increases after a minimum number of consecutive low-growth years accumulate. Density-dependent mortality occurs only if total stand biomass exceeds the maximum stand biomass in a given cell. Age-dependent mortality increases with tree age. The probability of an individual tree dying is given by the maximum of these three probabilities.

New Zealand's temperate forests can attain substantial amounts of standing biomass per area (Wardle 1991), exceeding those of central European forests. Therefore, the maximum stand biomass was increased from 300 to 1000 t/ha. This increased limit to standing biomass effectively reduces the probability of density-dependent mortality.

S2: Parameterization of tree species life-history traits

maxAge

The parameter 'maxAge' characterises the expected longevity of a tree species (Bugmann 1994, Schumacher et al. 2004). For the Hauhungatahi species, the maximum age was assigned based on the age-estimates of oldest individuals given by the following studies:

Ogden et al. (2005) for *L. bidwillii* (1000 years), Smale and Smale (2003) for *P. unninghamii* (650 years), Lusk and Ogden (1992) for *W. racemosa* (400 years). A value of 800 years was assigned to *D. cupressinum* since a wide range of maximum ages have been reported (500 up to 1000 years, Lusk and Ogden 1992). An estimated maximum age of 150 years was assigned to the tree fern life form.

Shade tolerance

Species shade tolerance expressed in classes between 1 and 5, with 1 denoting the least shade tolerance (following the classification given by Ellenberg 2009). These classes define species-specific minimum light requirements (see Schumacher, 2004, p.122, Tab. B.3). Shade tolerance classes for the tree species of Mt. Hauhungatahi were determined via the pattern-oriented parametrization approach.

Rmax

The parameter ‘Rmax’ determines the maximum above-ground biomass growth rate per year, and is expressed relative to the maximum biomass of a tree species. The ranges for ‘Rmax’ were determined by the pattern-oriented parameterization approach and a refined sensitivity analysis. Average growth rates were determined by a linear regression of the age-DBH data for both empirical and model data. The empirical sources for growth data were: Ogden et al. (2005) for *L. bidwillii* (mean annual growth rate of 0.125 cm/yr), Lusk and Ogden (1992) for *W. racemosa* (0.209 cm/yr) and *D. cupressinum* (0.124 cm/yr), Smale and Smale (2003) for *P. cunninghamii* (0.15 cm/yr).

Kmax

Maximum biomass of an individual tree (‘Kmax’) was estimated from an allometric relationship given in Hall et al. (2001), relating DBH and height to biomass. Unless otherwise noted, values of mean maximum tree height were taken from the New Zealand Eco-Trait database (Landcare Research 2011a), maximum DBH-values were taken from the electronic version of the Flora of New Zealand (Landcare Research 2011b). For *P. cunninghamii*, the DBH value reported in Russo et al.´s (2007) Tab. S1 was used. For *D. cupressinum*, both DBH and height values were derived from the Flora of New Zealand (Landcare Research 2011b).

Since several maximum heights were reported, the standard maximum height listed in the Eco-Traits database was assumed and the resulting ‘Kmax’ value rounded to the nearest whole number. For *L. bidwillii*, the DBH and height values given in the Flora and Eco-Trait databases (Landcare Research 2011a, Landcare Research 2011b) resulted in a ‘Kmax’ value of 3.92. Since *L. bidwilli* did not occur in the carbon stock assessment report of Beets et al. (2008), we used the maximum DBH values given by Ogden et al. (2005) as calibration targets and found that with Kmax = 3.92 LandClim significantly under-predicted DBH (with a maximum around 60 cm compared to the 100+ cm observed by Ogden et al. 2005). Therefore, ‘Kmax’ was increased to 8, which resulted in a more reasonable maximum DBH of 90-100 cm. Preliminary test scenarios using a wide range of ‘Kmax’ values for *L. bidwillii* showed that the model was reasonably robust to changes in this parameter’s value.

Leaf Habit

The ‘LeafHabit’ distinguishes between ‘Evergreen’, ‘Broadleaved evergreen’ and ‘Deciduous’ species (Schumacher 2004). Classes were assigned according to leaf morphology information given on the NZ Eco-Trait database (Landcare Research 2011a).

Foliage type

Foliage type is a parameter ranked in five classes that determines the shading potential of a tree species. An allometric function is applied which scales from foliage characteristics to the shade cast by a tree individual (via tree size expressed as DBH).We estimated the foliage type based on information about leaf morphology given in the Eco-Trait database (Landcare Research 2011a) and from expert opinion about the species canopy structure and shading potential.

Min Temperature

This parameter determines the minimum temperature (°C) for species establishment (Bugmann 1994). We used the freezing resistance reported by Sakai and Wardle (1978) to assign this trait to *L. bidwillii*, *D. cupressinum*, *P. cunninghamii* and *W. racemosa*. For the tree fern life-form the same minimum temperature (-7 °C) as *W. racemosa* was assumed.

minDD

The minimum annual degree day sum (‘minDD’) parameter expresses a species temperature requirements for growth (see Bugmann 1994 for further explanations of the degree day concept). It was assumed that upper limits of tree species of Mt Hauhungatahi were determined by temperature. Therefore, the parameter ‘minDD’ was calibrated in order to fit the observation of upper species altitudinal limits by Druitt et al. (1990). For this purpose, each species was simulated under monoculture conditions with a range of possible minimum degree day values (between 1060 and 2200, as suggested by Hall and McGlone 2006). For comparability with measurements of (Druitt et al. 1990), only individuals with a DBH > 10 cm were considered.

S3: Parameterization of the tree fern life-form

Demographic and allometric data for tree fern species are very scarce. Because tree-ferns are monocots they do not show secondary thickening, making the development of the allometric relationships that underpin forest gap models difficult. This, in turn, can have substantial effects on the simulated competition for light resources. To overcome these restrictions, tree ferns were not simulated as a specific species but as a more general life-form drawing on information provided by Beets et al. (2008), Ogden et al. (1997) and Bystriakova et al. (2011).

At Mt. Hauhungatahi, the dominant tree fern species is *Cyathea smithii* (Druitt et al. 1990). Therefore, the life-history traits of the tree fern life-form were modelled on the ecology of *Cyathea smithii*. Bystriakova et al. (2011) investigated the ecological differences between tree fern species in terms of shade tolerance and growth-rates and found that *Cyathea smithii* and *Cyathea dealbata* were the slowest-growing and most shade tolerant species. Therefore, the tree-fern life form was implemented as a slow-growing, shade tolerant species.

Growth estimates given by Ogden et al. (1997) were used to determine growth rates of the tree fern life-form. Ogden et al. (1997) report average height increments for the slowest growing tree fern (*Cyathea dealbata*) of approximately 5 cm/yr, which was used as a target for parameterization of ‘Rmax’. In order to convert Ogden et al.’s height-growth estimates into biomass-growth, a highly simplified allometric relationship was derived from the data given by Beets et al. (2008) (Eq. S3):

$$b = \frac{h}{0.289} \qquad \text{Eq. S3}$$

where: b = total aboveground biomass (kg) and h = height (m).

For the conversion function (Eq. S3), it was assumed that tree ferns maintain a constant diameter during their life span and as a result aboveground-biomass acquisition can be translated into height growth via a linear relationship.

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Climatic turning point for beech and oak under climate change in Central Europe

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Abstract

Altering growth behaviour of coexisting tree species under climate change is important from an ecological, silvicultural and economic perspective. While many studies focus on climatic limits for species existence, we are concerned with climate related shifts in the interspecific competition. A landmark that manifests these changes in competition is the ‘climatic turning point’ (short CTP) as we call the climate conditions under which a rank reversal between key tree species occurs. Here, we use a common type of temperate mixed forest in Central Europe with European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) to explore the CTP under a future climate projection of increasing aridity during the growing season. We select a dry region where the prerequisite of differential climate sensitivity in mixed beech-oak forests is fulfilled: In-situ dendrochronological analyses prove that the currently more competitive beech is also more drought sensitive than sessile oak.

Based on this premises we are able to search for the CTP from beech to oak by modelling future forest development from the WETTREG 2010 A1B projection aiming at quantifying (i) a possible rank-reversal in species dominance and (ii) the climatic turning point (CTP). We use two climate sensitive, complementary forest growth models, namely SILVA and LandClim in order to identify conclusions robust against the assumptions of a particular model.

Despite differences in underlying assumptions and stand initialization, both models predict a potential turning point at a mean annual temperature of 11-12 °C (July temperature > 18 °C) and precipitation sum of 500-530 mm. However, the change of tree species composition in already existing mixed stands is much slower since the turning point also depends on inherited stand structure.

Keywords: Climatic turning point, drought, mixed forest, tree coexistence, competitiveness, species rank reversal, tree-ring analysis, forest growth models, LandClim, SILVA, *Fagus sylvatica*, *Quercus petraea.*

Introduction

As climatic extremes are increasing in intensity and frequency droughts and their effect on global forest biomes are of particular interest to forest sciences. Precursors of a future climate posing a drier growing season (Schär et al. 2004, Barriopedro et al. 2011, IPCC 2012) are seen already today as main causes of changes in tree growth, tree death and even die-backs in temperate forests (Gitlin et al. 2006, van Mantgem and Stephenson 2007, Worrall et al. 2008, Rehfeldt et al. 2009). Especially for mixed species silviculture – one of the epitomes of climate change risk mitigation – such alterations in the species' growth behaviour are most important from an ecological, silvicultural and economic perspective, and might precede the decline of less drought adapted species with severe ecological consequences (Carnicer et al. 2011).

European forests are usually dominated by few key tree species which drive ecosystem functions. A rank reversal in the dominance of these key species has to be expected when the interspecific competition changes. So far, the concept of rank reversal was used in the establishment phase of tree species in relation to light conditions (Baltzer and Thomas 2007, Beaudet et al. 2007, Osada 2012) or to compare ontogenetic growth patterns (Boyden et al. 2009, Pérez-Ramos et al. 2012) (Literature review S1). However, we argue that a changing climate can alter species performance and thereby induce rank reversals. Sánchez-Gómez et al. (2008) and Gómez-Aparicio et al. (2011) were the first to predict climate induced species rank reversals for mixed forests in Spain. This prompts the question at what point in the gradient of a possible future climate such rank reversals in mixed-species forests occur. We shall call this point the climatic turning point (hereafter short CTP).

Due to the complexity in tree species' climate-growth control and the interaction with ontogenetic growth behaviour the search for the CTP is not trivial. Particularly in long-lived ecosystems with long generation periods, the slow and gradual response of forest structure and species composition to changing precipitation regimes might remain unnoticed. Moreover, the species' regeneration success as the key determinant of the future forest's species composition takes only effect in the following generation (Sykes and Prentice 1996, Soja et al. 2007, Johnstone et al. 2010). Clearly, the response of the forest to changing climate conditions cannot simply be predicted by means of extrapolating regression functions or searching climate analogies (Fuhrer et al. 2006, Williams and Jackson 2007). We therefore employ a very cautious approach based on in-situ data on tree and stand growth under past and present climate in combination with climate-sensitive and structure-sensitive dynamic forest growth models.

Our study object are mixed stands of European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.), a forest type of considerable relevance which grows mainly on climatic and edaphic dry sites in Central Europe. A systematic literature search (ISI Web of Science ® Data base) on growth of beech and oak under drought resulted in 20 papers dealing with the coexistence of oak (*Quercus petraea* and/or *Q. robur*) and beech (*Fagus sylvatica*) (Tab. 1, Literature review S2). Among the two species, beech is predominant, and the light-demanding oak can only compete under less favourable abiotic conditions for beech, i.e. warm and relatively dry sites, or wet and clayey soils. Ellenberg (2009) suggest that oak becomes more competitive than beech at July-temperatures > 18 °C and precipitation < 600 mm/yr. The chosen stands lie in the region ‘Franconian plateau’ in south-eastern Germany, where the present climate is already close to above mentioned limits.

Strong climate change scenarios like the WETTREG 2010 A1B (Kreienkamp et al. 2009) predict an increase of summer aridity in that region. Under such conditions, both species can be expected to suffer a loss in productivity (Leuschner et al. 2001, Lebourgeois et al. 2005, Jump et al. 2006, Piovesan et al. 2008) and might be even prone to die-back (e.g. Bréda et al. 2006, Michelot et al. 2012). Yet, oak is considered to suffer less than beech due to a higher capability to resist advert climatic conditions or to recover better after climatic extreme events (Literature review S1). Under drought beech apparently down-regulates its photosynthesis earlier than sessile oak to avoid cavitation (Leuschner et al. 2001, Raftoyannis and Radoglou 2002, Bréda et al. 2006).

For the forest growth simulators we choose SILVA and LandClim. Both models operate on the individual tree level – a mandatory criterion if changes in structural competition are to be reproduced. Still, the two forest growth simulators were developed for different purposes and correspondingly differ in underlying assumptions and structure (Pretzsch et al. 2008). SILVA focuses on a precise prescription of the development of a particular stand with a focus on tree growth (i.e.

Tab. 1: A systematic literature search (ISI Web of Science ® Data base) on growth of beech and oak under drought resulted in 20 papers dealing with the coexistence of beech (*Fagus sylvatica*) and oak (*Quercus petraea* and/or *Q. robur*) (cf. Literature review S2). Notably, only two studies examine competition dynamics among the two species under future climates. Method: M=Modeling F=Field observation E=Experiment.

Reference	**Method**	**Target period**	**Target driver**	**Aim**
Bellassen et al. 2011	M	past	no	model validation
Bonn 2000	F	past	climate/weather	tree growth and competition
Bugmann and Cramer 1998	M	past	soil water balance	tree growth and competition
Czúcz et al. 2011	M	past	climate	tree growth and competition
Davi et al. 2009	M	past	carbon and water fluxes	tree growth and competition
Fabbio et al. 2006	F	past	forest management/extreme event	tree growth and competition
Friedrichs et al. 2009	F	past	climate	tree growth
García-Suárez et al. 2009	F	past	climate	tree growth and competition
Granier et al. 2007	M	past	climate/weather/extreme event	tree growth
Hlásny et al. 2011	M	future	climate	tree growth
Leuschner et al. 2001	F	past	soil water balance	tree growth and competition
Mérian & Lebourgeois 2011	F	past	climate	tree growth
Piedallu et al. 2011	F	past	soil water balance	tree growth, modelling, soil water holding capacity
Pollastrini et al. 2010	E	future	climate	tree growth
Scharnweber et al. 2011	M	past	climate	tree growth and competition
Scherrer et al. 2011	F	past	climate/extreme event	tree growth and competition
Solberg et al. 2009	F	past	climate/soil chemistry	tree growth
Szabados 2006	F	past	climate	tree growth
van der Werf et al. 2007	F	past	extreme event	tree growth
Zang et al. 2011	F	past	climate/extreme event	tree growth and competition

is strong in operational forest management planning), LandClim simulates long-term dynamics of forest at the landscape scale considering particularly demographic processes such as establishment, growth and mortality.

To determine the climatic turning point (CTP) for a mixed beech-oak forest of considerable relevance in Central Europe we combine empirical evidence and modelling. Data from repeated forest surveys and tree-ring analysis are used to assess current tree growth and to harmonize the forest models. These are then used to predict the forest development under climate change. This approach allows us to perform a straightforward analysis of the following two decisive hypotheses: 1) Projected future climate eventually crosses a climatic turning point with a drought-induced rank reversal in the species dominance and 2) the rank reversal is driven not only by climate, but also by the inherited stand structure.

Whilst literature is rich on climatic limits for species existence, we are concerned with the gradual response of ecosystem shifts in species composition within these limits and work out the CTP which serves as a landmark for investigating changing interspecific competition. A very cautious approach allows us to trace and discuss uncertainties in the determination of the CTP and their consequences for forest management practice.

Materials and Methods

Study site and data

The studied beech-oak forest stands are located in south-eastern Germany on the ‘Franconian plateau’ in an altitude of 300-400 m a.s.l.. Four sites are permanent investigation sites of different stand age which belong to the Bavarian long-term experimental plot network, the fifth site is a forest reserve of the Bavarian state forest institute LWF (Tab. 2). The experimental plots were installed in

Tab. 2: Stand parameters from surveys of the studied beech-oak stands near Schweinfurt. N = Stem number per hectare, H100 = Upper canopy/ top height, G = Basal area, V = Merchantable wood volume, dg = Root of mean diameter squared, B = Above-ground biomass (Schroeder et al. 1997)

Stand (initial age)	**Survey year**	**All tree species**					**Beech**		**Oak**		**Other**	
		N (ha^{-1})	H100 (m)	G (m^2/ha)	V (m^3/ha)	B (t/ha)	dg (cm)	G (m^2/ha)	dg (cm)	G (m^2/ha)	dg (cm)	G (m^2/ha)
27yrs	1995	3160	15.7	25.2	143.6	536	11.4	6.4	9.6	17.0	11.3	1.8
	2005	1751	19.9	28.4	233.2	824	15.1	9.1	14.3	18.0	11.4	1.3
54yrs	1995	1935	22.1	34.4	311.4	715	15.7	15.2	19.1	9.9	12.1	9.3
	2005	1384	25.2	40.7	449.3	778	20.4	19.3	22.5	12.1	15.6	9.3
86yrs	1995	1149	24.3	30.1	316.8	561	15.4	11.2	22.7	15.4	16.3	3.5
	2005	1037	26.8	36.9	443.2	636	18.5	14.2	25.7	18.8	18.6	3.9
106yrs	1995	676	27.8	25.7	323.3	422	18.8	14.4	30.9	10.4	24.9	0.9
	2005	615	30.4	30.5	425.7	485	21.4	16.6	34.9	12.8	27.1	1.1
Reserve	1978	723	25.8	30.4	355.1	472	27.2	12.9	35.6	6.4	18.0	11.1
(105 yrs)	1996	531	30.5	37.0	528.1	644	34.6	18.5	42.8	7.5	22.3	11.0
	2010	396	33.8	38.6	622.4	593	40.7	22.4	44.5	6.5	26.0	9.7

1995 and surveyed in 1995 and 2005. The stands are 2.25-6.8 ha large, even-aged and range from 27-106 years with merchantable wood volumes of 233-323 m^3/ha in 1995. The basal area ratios of oak:beech:other species range from 25:67:7 to 56:40:4, hornbeam (*Carpinus betulus* L.) shares up to 32%, lime (*Tilia cordata* P. Mill.) and maple (*Acer pseudoplatanus* L.) cover minor percentages. No thinning occurred between 1995 and 2005. The forest reserve with a core area of 0.99 ha was designated in 1978 and surveyed in 1978, 1996 and 2010. Since that time any forest management is forbidden. In 1978, tree age in the core area was 105 years, wood volume was 311 m^3/ha and basal area ratio of oak:beech:other species was 42:21:37 (Tab. 2).

For retrospective growth analyses, increment cores were extracted in the direct vicinity of the 86-year experimental plot in 2009. Two cores of each 15 dominant oak and beech trees were sampled at breast height. After wood surface preparation, ring width of each sample was measured using a LINTAB linear table (Rinn 2003) to a precision of 0.01 mm. The software TSAP-Win (Rinn 2003) was used to synchronize the ring width curves visually and statistically. The biological age trend in the original tree-ring series was eliminated using the dplR library v 1.5.5 (Bunn 2008) in R v 2.15.1 (R Development Core Team 2012) by applying a cubic smoothing spline of 2/3 of the series length. Autoregressive modelling was used to remove first order autocorrelation. Residual chronologies of beech and oak were obtained by averaging the ring width series using a biweight robust mean (Cook and Peters 1997).

Climate data

Climate data (daily values of temperature and precipitation for the period 01.05.1958 - 31.12.2003) were obtained from the weather station ‘Schweinfurt-Gartenstadt’ close to the study site (DWD station 4621, 50.06 °N; 10.22 °E; 240 m a.s.l.). These data were used for the retrospective growth analysis and calibration of SILVA and LandClim.

Basis for the projections of possible future forest development was the WETTREG 2010 A1B ‘normal’ scenario for the same climate station from 1961-2100 (Kreienkamp et al. 2009). For this scenario, ten realizations, with each of them covering two decades, are available. These climate time series provide a climatic gradient from moderate temperature and soil moisture conditions in the past and present to warmer and dryer conditions in the future, including a realistic temporal variability and autocorrelation (Tab. S1). Compared to 1971-2000 the WETTREG scenario projects for 2071-2100 a significant increase in the mean annual and May-Sep temperatures from 9.0 °C to 12.5 °C and 15.9 °C to 19.4 °C. The growing season with mean temperatures above 10 °C is thereby extended from 164 to 202 days (Fig. 1). Annual precipitation decreases from 558 mm to 523 mm and summer precipitation from 258 to 200 mm.

Current and future stand dynamics

In a first step, the empirical data were used to analyse tree growth and competition between beech and oak under past and present climatic conditions. In the present study a species' dominance was defined by its basal area (SILVA) or aboveground biomass (LandClim) being higher than any other species' basal area/biomass. A species' competitiveness was defined in terms of a gain or loss in its basal area share or biomass share. Competitiveness (and ultimately dominance) is determined by the conjoint effect of the demographic processes establishment, growth, and mortality. Basal area and biomass are standard measures in mixed species forest ecology (Pretzsch and Schütze 2009).

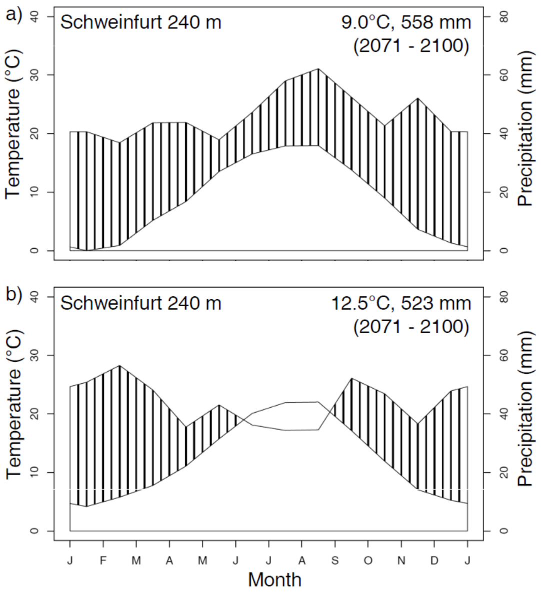

Fig. 1: Present and future climate of the study site Schweinfurt (south-eastern Germany). a) Present climate for the period 1971-2000 according to the DWD climate station Schweinfurt, b) future climate from 2071-2100 according to the WETTREG 2010 A1B scenario. As in Walter-Lieth climate diagrams hatched area indicate moist periods, dotted areas dry periods (Walter and Lieth 1967).

In a second step, the forest growth models SILVA and LandClim were employed to assess future forest dynamics, particularly the ‘climatic turning point’ (CTP). We define a climatic turning point as the climate where a rank reversal of the species’ dominance, i.e. basal area share (SILVA) and biomass share (LandClim) occurs. As postulated, the rank reversal and thereby the observed CTP might be affected by inherited stand structure. By ‘inherited stand structure’ we refer to the footprint of prior climate conditions and forest management causing a gradual response of forest structure and species composition in long-lived ecosystems with long generation periods. Therefore, a potential and actual CTP was distinguished. To determine the potential CTP forest succession was simulated for forests developing ex novo, i.e. establishing from seed rain, under different, but stationary climate conditions derived from the WETTREG data. The actual CTP was determined by the simulation of a forest succession in present forests along the projected gradient from moderate temperature and soil moisture to warmer and dryer conditions (WETTREG time series).

The models

SILVA is a site-condition sensitive, single-tree based, spatially explicit forest growth model (Pretzsch et al. 2002). The growth functions were statistically parameterized from data of long-term experimental plots across Central Europe. The parameterizations for beech and oak were based on 13,000 trees and 3,000 trees of altogether 89+37 plots, respectively. SILVA was developed as a growth simulator for operational forest management planning of the Bavarian state forest management, for educational and scientific purposes (Pretzsch et al. 2008). Due to its site-sensitivity, SILVA simulations have been included in the analysis of climate change effects on forest growth and the development of forest carbon stocks under different climate and management scenarios (Köhl et al. 2010, Rötzer et al. 2010).

LandClim is a spatially explicit forest landscape model that was developed to assess the importance of climatic effects, wildfire and management on forest dynamics (Schumacher et al. 2004, Schumacher and Bugmann 2006, Schumacher et al. 2006). It incorporates patch level processes of climate-dependent tree regeneration, growth and mortality, and landscape level processes such as forest disturbances and seed dispersal. Thereby several stand generations can be simulated and the influence of variables changing with time or space on forest dynamics can be assessed. LandClim operates on long time scales (hundreds to thousands of years) and large spatial extents (several hectares) at a relatively fine scale (grid cells of 25 by 25 m, monthly weather data), and has been tested and adapted to the European Alps, the North American Rocky Mountains, and Mediterranean forests (Schumacher and Bugmann 2006, Colombaroli et al. 2010, Henne et al. 2011, Briner et al. 2012, Elkin et al. 2012, Henne et al. 2012). Species parameters were taken from Schumacher et al. (2004) and Henne et al. (2011) except for an increase in the drought tolerance of *Quercus petraea* from 3.0 to 3.5 to reflect the slightly higher drought tolerance than *Fagus sylvatica* (drought tolerance = 3.0) reported in the literature (e.g. Leuschner et al. 2001, Raftoyannis and Radoglou 2002, Bréda et al. 2006, Scharnweber et al. 2011).

For model validation the SILVA simulations which were initialised with the experimental plot data could be compared directly with the true stand development. The simulation results for the 1981-2020 periods were validated against the data from the experimental plots and forest reserve. The simulated basal area growth matched the actual basal area well, except for 10-15% underestimation in the case of the 54 and 86-yrs old stands. The difference was due to an underestimation of the increment of the ‘other species’ which cluster several species with different growth characteristics. The growth ratio of oak to beech was generally estimated correctly; oak increment was slightly overestimated in the 27-yrs old stand. These results are acceptable for our purposes; a perfect match of reality is unrealistic since the stand interactions with the environment are much too complex for a stable model: E.g. late frost or other climate hazards, insect calamities, mast years all have a very unpredictable pattern and are essentially smoothed in the SILVA parameterization (Fig. S1).

LandClim was validated by translating the permanent plot data into biomass using the allometric function implemented in LandClim (Schroeder et al. 1997). Simulations were run with the current climate (DWD data) and results were compared to the real stands. As LandClim does not take into account the anterior oak fostering, stand biomass is dominated by beech which is more competitive under the current climate (Fig. S2).

Simulations

Mixed beech-oak forest growth under climate conditions from the WETTREG 2010 A1B scenario was simulated in order to determine the CTP between both species (Tab. 3). For the potential CTP, climate had to be stationary during the simulated succession so that forests developed in equilibrium with climate. To create such climate scenarios the WETTREG 2010 A1B time-series covering the period 1961-2100 was split into 20-year periods (for each of ten available realizations). Seven climate scenarios were generated by looping each 20-year time-

Tab. 3: Definition of simulation runs. Temperature and precipitation are given per annum (Temp.a, Prec.a) and per growing season (Temp.v, Prec.v), i.e. May-September of a respective year.

Simulation	Model	Initial age (yrs)	Sim. period (yrs)	Final age (yrs)	WETTREG A1B period (yrs)	Temp.a (Temp.v) (°C)	Prec.a (Prec.v) (mm)
Potential climatic turning point (simulation with quasi-constant climate conditions)	SILVA	27 (experimental stand)	120	147	1961-1980 (CLIM1)	8.9 (15.6)	546 (256)
					1981-2000 (CLIM2)	8.9 (15.9)	553 (251)
					2001-2020 (CLIM3)	9.3 (16.4)	561 (245)
	LandClim	0 (establishment from ‘global seed rain’)	150	150	2021-2040 (CLIM4)	10.3 (17.2)	534 (219)
					2041-2060 (CLIM5)	11.1 (18.2)	512 (227)
					2061-2080 (CLIM6)	11.9 (19.0)	500 (200)
					2081-2100 (CLIM7)	12.6 (19.4)	516 (195)
					Simulation span	**Data**	
Actual climatic turning point (continuous simulation acc. to WETTREG scenario)	SILVA	27 (experimental stand)	100	127	2001-2100	WETTREG A1B time series	
		54 (experimental stand)	100	154			
		86 (experimental stand)	100	186			
		106 (experimental stand)	100	206			
		105 (forest reserve)	120	205	1981-2100	WETTREG A1B time series	
	LandClim	0 (establishment from ‘global seed rain’)	180	180	1921-2100	From 1921 to 1960 WETTREG A1B time series ‘1961-1980’ was repeated twice, afterwards WETTREG A1B time series	

series as often as needed (for 150 years succession 7.5 times). Forest structure and species composition were evaluated at a stand age of 150 years. This is the upper limit for beech rotation and lower limit for oak rotation. Neither species should suffer from an age-dependent mortality. According to the different initialisation requirements of the growth models SILVA and LandClim, SILVA was initialised with the 27-year old experimental stand (Tab. 2) and LandClim with a beech-oak 'global seed rain' on bare ground.

For the actual CTP, beech-oak stand development was simulated according to the predicted climate development from the WETTREG 2010 A1B scenario until 2100 (for each of ten available realizations). Again, SILVA and LandClim had to be initialised differently. SILVA simulated stand dynamics of the four experimental plots and the forest reserve (Tab. 2). LandClim generated a hypothetical stand which was in 1961 already 40 years old. Following the initial beech-oak global seed rain, the first 40 years were assumed to grow under climate conditions similar to those from 1961 to 1980. In 2000, the LandClim stand was approximately as old as the 106-year-old experimental plot stand and the forest reserve (105 yrs).

Although climate data are identical, SILVA and LandClim use different data aggregations and time windows. For SILVA the temperature and precipitation data were translated into length of growing season, average temperature May-Sep, temperature amplitude Jan-Jul, precipitation May-Sep and the Martonne aridity index, each of the parameters averaged over 20 year periods (Pretzsch 2009). In contrast, LandClim worked with monthly mean temperatures and precipitation sums to calculate seasonal and annual indices for water availability (drought index; Bugmann and Cramer 1998, Bugmann and Solomon 2000) and energy availability (degree-day-sum; Bugmann 1994) as well as temperature of the coldest month. Beside differences in the representation of climate both models made specific assumptions on soil water and nutrient availability. Soil descriptions for the experimental plots were translated into the model requirements. Specifically, for the SILVA simulations a low soil water availability was assumed (0.3 on a scale between 0…1) and further dropped as the climate becomes warmer and drier. For LandClim, the maximum available soil water capacity, represented in the model as buckets size, was set to 80 mm.

Results

Current stand dynamics

In all but the 106 years old stands, beech expanded its basal area while oak remained unchanged or declined (Fig. 2). Beech expansion was particularly strong in the young 27 and 86 years old stands and in the forest reserve which had the longest time period between surveys. Here, from 1978 to 2010, the beech basal area share increased from 42% to 55%, partly at the expense of oak (decline from 21% to 17%), but mainly due to the decline of other species (37% to 25%).

A closer look at the 86-yrs old experimental site emphasised the dependence of basal area growth response on stand structure (DBH-distributions in Fig. S3). The tree-ring analysis showed an increase of mean DBH of dominant beech from 31.6 to 37.5 cm (+ 5.9 cm) and oak from 26.0 to 29.8 cm (+ 3.8 cm). So, in terms of diameter increase, beech trees exceeded oak trees by 40-60% in the upper canopy. However, the majority of the beech trees still grew in the subcanopy and was strongly suppressed so that, in total, the basal area share remained unchanged (Fig. S3).

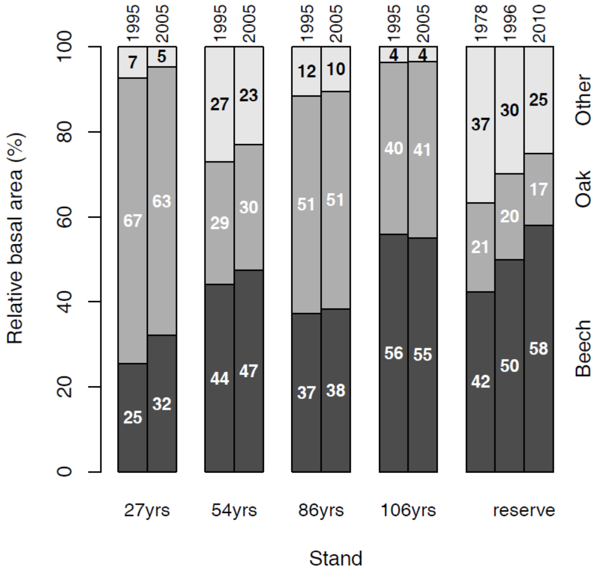

Fig. 2: Basal area share of beech, oak and other tree species of the four experimental plots (in 1995 and 2005) and the forest reserve (in 1978, 1996, and 2010) according to field surveys.

Correlations between tree-ring indices and climate data revealed that beech was much more sensitive to climate than oak. While oak only showed significant positive correlations with precipitation of the growing period, beech tree-ring indices were positively correlated with precipitation during spring and the growing season as well as to September during the year prior to growth. Correlations with temperature were negative for most months except for October of the previous year (Fig. S4). In the driest summer of 2003 (100 mm precipitation from May-Sep), beech ring-width index dropped to 0.5 while that for oak only decreased to 0.7 (Fig. 3a). However, the absolute ring-width values (Fig. 3b) showed that oak still did not grow stronger than beech in that summer (both species grew 1.2 mm). A 2nd degree polynomial (in approximation of an optimum-function) fitted to the tree-ring data had a stronger curvature for beech than for oak (Fig. 3). The hypothetical intersection between the two polynomials lied even below 100 mm precipitation (May-Sep). Thus, under current climate conditions, the tree-ring data confirmed a stronger competitiveness of beech than oak, even in years of extremely low precipitation.

Future stand dynamics

Potential climatic turning point

To search the potential CTP between beech and oak, the development of beech-oak stands under constant climate conditions calculated from seven consecutive 20 year time periods between 1961 and 2100 (WETTREG 2010 A1B) was simulated. The results of the SILVA simulations indicated that in all but the CLIM7 scenario (2081-2100) beech extended its initially low basal area share (Fig. 4a). However, the beech expansion decreased along the climatic gradient. In the last two scenarios CLIM6-7 (2061-2100) beech did not dominate anymore. While in CLIM6 (2061-2080) beech still slowly expanded and might eventually reach dominance in the long-term, in CLIM7 (2081-2100) beech basal area did not further expand. Notably, not only species composition changed, but also the final basal area value decreased from almost 38 m^2/ha in CLIM1 (1961-1980) to 26 m^2/ha in CLIM7 (2081-2100) – the latter with no net basal area increase compared to the initial 27 yr old stand.

The results of the LandClim simulations (Fig. 4b) were similar those of SILVA. From CLIM1-3 (1961-2020) beech dominated in all realisations with biomass shares of 75-89%. In CLIM4 (2021-2040) one out of ten climate realisations resulted in an oak dominance, in CLIM5 (2041-2060) already five out of ten. Finally, in CLIM6 (2061-2080) and CLIM7 (2081-2100) LandClim predicted mixed

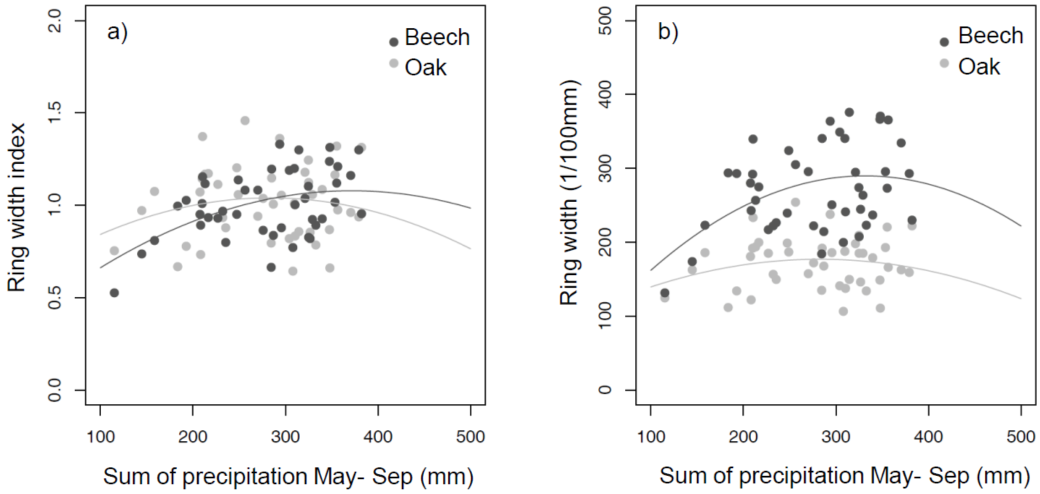

Fig. 3: a) Ring-width index and b) raw ring width series of beech and oak for the 86 yrs experimental plot in relation to precipitation sum during the growing season May-Sep.

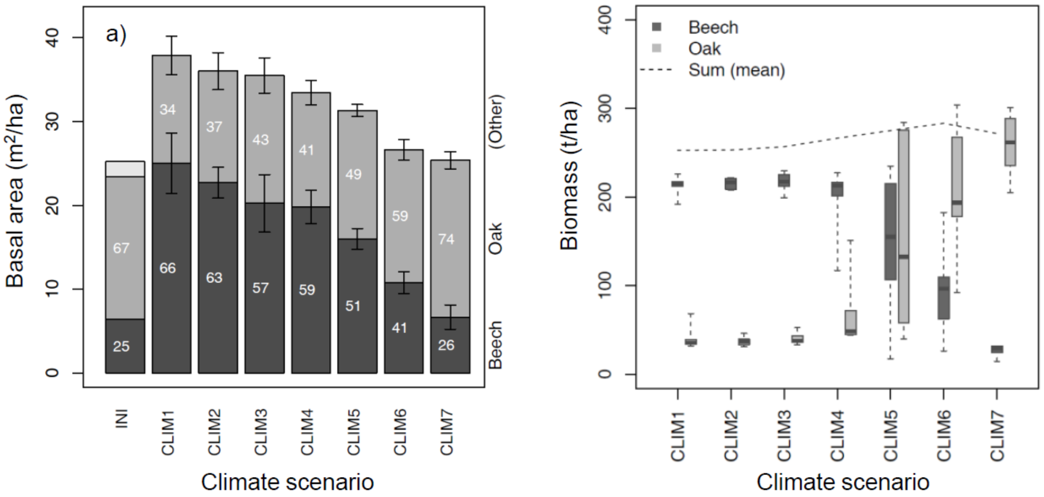

Fig. 4: Predicted species composition of ~150 yrs old beech-oak stands in a) SILVA and b) LandClim under seven climate conditions which correspond to periods of the WETTREG 2010 A1B scenario (CLIM1 = 1961-1980, CLIM2 = 1981-2000, ... CLIM7 = 2081-2100). a) Initial (INI) stand 27 yrs old experimental site, simulation span 120 years (final age: 147 yrs). b) Initial beech-oak seed rain (age 0) on bare ground, simulation span 150 years (cf. Tab. 3 for details).

stands with 64% respective 96% oak and 34% respective 11% beech (medians of ten realizations). Beech experienced higher mortality and adhered to the understorey owing to its shade tolerance. Oak dominated the upper canopy which led to a considerable increase in the biomass of large trees above 50 cm DBH: 168 t/ha in the CLIM1 (1961-1980) scenario vs. 225 t/ha in the CLIM7 (2081-2100) scenario. Thereby total stand biomass varied only little between the scenarios.

A more detailed analysis of the SILVA results regarding the economically most interesting target trees revealed that dominant beech trees grew higher than oak. Oak reached only larger diameters in the last three scenarios (2041-2100) (Fig. 5). Nevertheless, both diameter and height of the dominant trees decreased with increasing aridity. This negative effect became even more obvious when looking at the survival of the initially dominant beech and oak trees. From 1961-2060, more dominant beech than oak trees survived. In 2061-2100 significant upper canopy mortality caused death of almost all of the initially dominant beech trees.

Actual climatic turning point

In SILVA, the continuous development of five beech-oak stands under the WETTREG 2010 A1B climate scenario indicated for the four experimental sites a maximum in basal area around the year 2050 (Fig. 6a). From then on basal area fell until 2100. This pattern was mainly caused by the increase and decrease in beech basal area while oak basal area remained almost constant. The beech expansion in the first half of the 21st century was lowest in the 27 yrs old stand where oak competition was high due to its early growth climax. Beech expansion was highest in the 54 yrs old stand where beech has its growth climax. As a consequence, in 2050 beech occupied the upper canopy so effectively that in the second half of the 21st century oak still did not exceed its initial share (with exception of the 27 yrs old stand). In the forest reserve, only minor changes occurred in the absolute basal area and basal area shares.

In the LandClim simulations, which were best comparable to the SILVA simulations of the 27 yrs old stand, beech dominated the stand during the entire simulated succession (Fig. 6b). However, a decrease in beech biomass could be observed. This was mainly caused by decreased establishment success of beech with increasing drought stress. Notably, there was considerable variability among the ten climatic realizations.

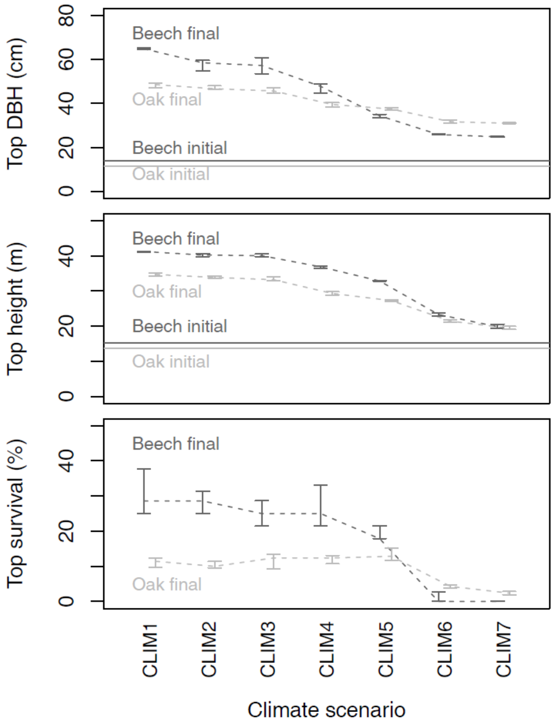

Fig. 5: DBH, height and survival of the dominant (‘top’) beech and oak trees after simulating growth of the 27 yrs old experimental plot for 120 years under seven climate conditions which correspond to periods of the WETTREG 2010 A1B scenario (CLIM1 = 1961-1980, CLIM2 = 1981-2000, … CLIM7 = 2081-2100). Top DBH and top height defined as the 90% percentile of the diameter and height distribution of each species; top survival: the survival of dominant 20% of each species in the initial stand (at age 27 yrs). Final age: 147 yrs.

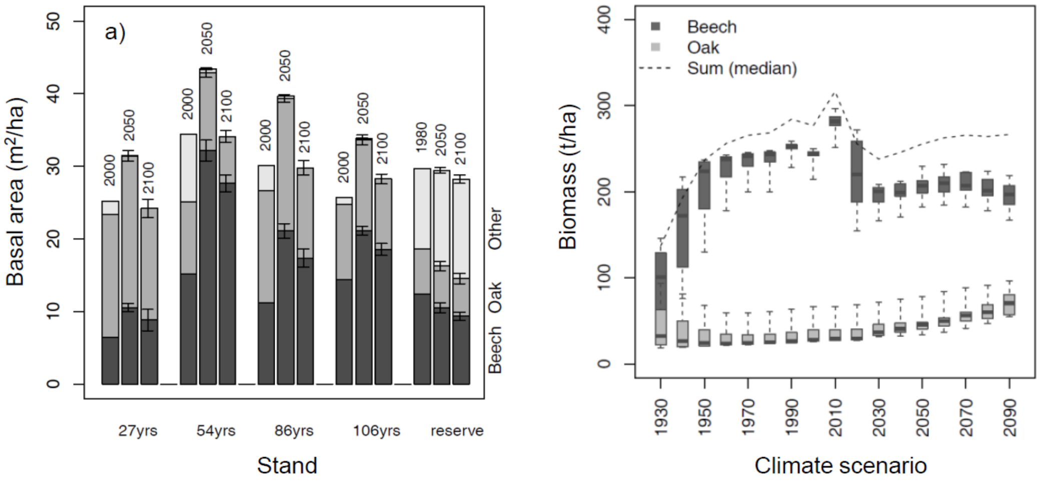

Fig. 6: Predicted development of beech-oak stands under the WETTREG 2010 A1B scenario until 2100 a) in SILVA for five stands evaluated in 2050 and 2100 and b) in LandClim for one stand, entire succession shown. a) SILVA was initialized with four experimental sites (age 27 to 106 yrs in 2000), and one forest reserve (~ age 105 in 1980); b) LandClim started with beech-oak seed rain on bare ground in 1921, thus stand age is comparable with SILVA simulations ‘106 yrs’ and ‘reserve’ (cf. Tab. 3 for details).

Discussion

Beech dominates oak under current climate

The rationale for the present modelling efforts to investigate a climatic turning point (CTP) between beech and oak was that under current conditions beech was more competitive than oak. Evidence from stand structural surveys and tree-ring data confirmed this. The analysis of tree-ring data resulted in a higher absolute diameter growth of beech than oak, even in the driest years with only 100 mm precipitation during the growing season May-September. Hence, beech dominance was not arguably. Nevertheless, the tree-ring data of the present study suggested that beech reacts more sensitive to dry summers than oak. This is in line with former studies on drought sensitivity of beech (Leuschner et al. 2001, Friedrichs et al. 2009, Scharnweber et al. 2011). It should be considered, though, that such drought years are embedded in an overall favourable climate and a single-year reaction can be buffered by tree internal resources from previous years. Predictions of ring width reactions responses to drought under other climate regimes are therefore naturally biased (Burkett et al. 2005, Fuhrer et al. 2006).

Notably, the study site was already under current conditions more arid than the climate suggested by Ellenberg (2009) to foster the dominance of oak compared to beech (July-temperatures > 18 °C and precipitation < 600 mm/yr). Also Scharnweber et al. (2011) found dominant beech trees to perform a superior diameter increment compared to oak under dryer conditions, i.e until annual precipitation falls below 540 mm in 100 yrs old mixed beech-oak forests of north-eastern Germany. An extensive summary by Bolte et al. (2007) lists sources of proves for beech dominance down to 550 mm and 18-19 °C July temperatures, but also highlights several other limiting factors such as winter temperatures and late frost.

The CTP regarding dominance does not necessarily reflect the species range of tolerated site conditions. Species usually tolerate a wider range of conditions and can remain as minor components in the community. According to Kölling´s (2007) climate envelopes, beech tolerates annual precipitation as low as 500 mm under 10 °C mean annual temperature (but requires 650 mm under temperatures of 12.5 °C). With 450 mm sessile oak needs less annual precipitation even under temperatures up to 12 °C. At the southern limits of beech distribution, the Spanish inventory records presence of beech even down to 587 mm and up to

13.7 °C and of sessile oak down to 540 mm and up to 16.2 °C (Gómez-Aparicio et al. 2011). Nevertheless, in the Mediterranean mountains, both Jump et al. (2006) and Piovesan et al. (2008) document declining beech populations as a consequence of increasing summer aridity.

Rank reversal between beech and oak under future climate

Based on this evidence the climate sensitive forest growth models SILVA and LandClim were employed to estimate the CTP, defined as the climate under which a rank reversal from beech to oak is to be expected. A potential CTP for constant climate conditions was distinguished from the actual CTP for changing climate conditions like projected by WETTREG. Rationale for this distinction was that in the latter case the inertia of the stand structure supposedly lead to a time delay of the rank reversal.

The simulation results confirmed both hypotheses stated in the introduction. 1) Simulations for the potential CTP predict both in SILVA and LandClim that the dominance of beech begins to deteriorate when mean annual temperature exceeds 11.1 °C and the annual precipitation drops below 510 mm (temperature May-Sep 18.2 °C, temperature July 20.9 °C, precipitation May-Sep 230 mm, cf. Tab. 3). The WETTREG 2010 A1B scenario projects such climate conditions for the second half of the 21st century. 2) Yet, in the continuous succession along the climatic gradient no such rank reversal occurred. In the projected forest succession, beech still remained dominant in 2100. The simulations for the actual CTP showed that the factors beyond the rank reversal are more complex. In the 'simplified world' of our models three main mechanisms interact to determine the balance of mixed beech-oak forests:

1. Climate sensitivity: Establishment, growth, maximum tree sizes and mortality of beech react stronger to climate than oak (cf. Fig. 5). In SILVA this led to a decline in the maximum site capacity in terms of basal area (SILVA -34%; Fig. 4 CLIM7 vs. CLIM1), while in LandClim total stand biomass was constant; the gain in oak biomass compensated the loss in beech biomass (Fig. 4). Apart from losses in the carbon sequestration potential, silviculturally, die-backs in the upper canopy as predicted by the SILVA simulations were the most severe consequence of climate change, and received high attention lately (Bigler et al. 2006, McDowell et al.

2008b, Allen et al. 2010). Hlásny et al. (2011) predicted a similar die-back of beech in lower altitudes of Hungary during the 21st century. However, the models only regarded climate effects on establishment, growth and mortality. In reality, major die-backs can only seldom be attributed directly to climate events (e.g. in McDowell et al. 2008a), mostly the factors are more complex (e.g. Bigler et al. 2006). Droughts are rather regarded as an inciting mortality factor (sensu Manion 1981), while secondary agents take advantage of the weakened immune response and kill the trees in the end.

2. The ‘inertia’ in the climate reaction due to the inherited stand structure was most obvious in the comparably short time spans of the surveys (cf. Fig. 2) and in the SILVA CLIM4 simulations close to the CTP. In both cases, beech could only slowly gain ground against the established oak from anthropogenic fostering. This effect could also be observed in the LandClim results for the projected forest succession (Fig. 6b). Species shares clearly switched from beech dominance in CLIM1 (1961-1980) to oak dominance in CLIM7 (2081-2100) whereas in the projected forest succession, beech still remained dominant in 2100. This can be explained by a higher sensitivity of beech seedlings to drought which favours oak in bare ground establishment scenarios (Fig. 4) while older beech trees which established under more beech favourable conditions can tolerate drought to some degree and additionally impede oak regeneration at the forest floor due to their strong shading (Fig. 6b).

3. Disturbances: The conjoint interpretation of the simulations points to the importance of disturbances as promoter of forest responses to climate change. Due to the inherited stand structure the forest response is time delayed. Disturbances initiate succession which can result in a completely different forest composition (Soja et al. 2007, Johnstone et al. 2010). Sykes and Prentice (1996) report similar findings for a study site in Sweden. Under climate warming, beech was expected to be the long-term replacement for spruce (in Pine-Spruce forests), but in simulations its dominance was delayed for centuries due to the persistence of old-growth spruce stands. Accordingly, Ellenberg (2009) state that beech out-shadows any other tree species in undisturbed stands within its physiological range.

Controversially discussed but not considered in the present study is the beech--oak suitability with respect to soil texture, fertility and water relations. Traditionally, oak is regarded as more competitive on extremely clayey, acidic-nutrient poor or water stagnant soils (Ellenberg 2009). The evaluation of natural beech invasion in unmanaged 50 years old seeded oak stands in south-western Germany showed that on limestone oak was pushed back to 5-25 %, while on sandstone beech only conquered 5-25 % (pers. comm. Abt 2012). Compared to our sites, we suggest that on more oak favourable soils, beech might – if at all – only slowly (perhaps after generations) become dominant. Examples of a re-conquering of oak-forests through beech even on extremely poor soils are known (Ellenberg 2009).

Implications for management

Arguably like no other life science, forest management is forced to think ahead of time due to its long production time spans. For more than 30 years, forest management in Central Europe has pursued a more sustainable and stable productivity through conversion of not site-suited coniferous forest to broadleaf forest and propagation of species mixtures (Spiecker et al. 2004, Pretzsch et al. 2013). As climate change moved into the focus of attention, species suitability decisions had to take into account possible future climate trends (Linder 2000, Bolte et al. 2009, Lindner et al. 2010). The important pending decision for already warmer and drier (edaphically not extreme) sites in Central Europe is beech and/or oak, and threshold values are sought for orientation. Temperature and precipitation are the most commonly applied factors and our study demonstrates that beech is currently not drought-limited in south-eastern Germany, even at the most dry sites. Simulations with SILVA and LandClim similarly predict limits of beech dominance for temperatures of 11.1 °C (annually), 18.2 °C (May-Sep), 20.9 °C (July), and precipitation of 510 mm (annually) and 230 mm (May-Sep). These values remain within the climate envelopes of Kölling (2007) for beech existence, but fall below the typical values given for beech dominance (cf. Bolte et al. 2007). Based on these values, there is still a buffer for beech forests also on the dryer sites in south-eastern Germany – at least until 2050 even under ‘worst-case’ assumptions like the WETTREG 2010 A1B scenario.

However, in view of the predicted beech decline in both SILVA and LandClim in the second half of the 21st century, the promotion of oak already today seems advisable due to the superior resistance and resilience of oak (pedunculate oak even more than sessile) to drought (Leuschner et al. 2001, Friedrichs et al. 2009, Scharnweber et al. 2011). Also the high value of oak wood might make oak more profitable than beech if stand productivity decreases as projected. Additionally, the facilitative behaviour of oak in mixed stands is a strong argument for a preferential choice of this species as stabilizing component of ecosystems under climate change. Only recently, independently of each other, Zapater et al. (2011) and Jonard et al. (2011) found evidence for hydraulic lift of oak in young mixed beech-oak stands. This could be the cause for a lower sensitivity of beech to water scarcity in mixed beech-oak stands than in pure stands. Furthermore, Pretzsch et al. (2012) found that growth of beech in mixture with oak decreases less than in monoculture and thereby improves its competitive strength. This stress release by mixing as an important emergent property implying that the realized climatic niche of beech in mixed stands might be wider than in pure stands (Pretzsch et al. 2013).

A further enrichment of mixed stands with typical ‘Quercetum’-species such as hornbeam (*Carpinus betulus* L.), lime (*Tilia spp.*) and *Sorbus spp.* or with drought tolerant species from present-day residual fragments of the postglacial northward migration (*Quercus pubescens* Willd., see Wellstein and Spada in press) or provenances (Thiel et al. 2012, Wellstein and Cianfaglione in review) can help to spread the risk further and reduce losses in production (Czajkowski and Bolte 2006, Bolte et al. 2009, Pretzsch and Schütze 2009).

Modelling challenges

Model comparisons are a powerful means to evaluate uncertainty in projections of ecosystem responses and are increasingly applied in global change studies (Pearson et al. 2006, Hlásny et al. 2011, Cheaib et al. 2012). SILVA and LandClim are two forest growth simulators developed for different purposes and correspondingly differ in underlying assumptions and structure (Pretzsch et al. 2008). SILVA was designed to project individual tree and stand development to assess growth and yield for practical management purposes. Major strength is its position-dependent competition calculation which allows for a precise reproduction of thinning and mixture practice alternatives. In contrast, LandClim was designed to simulate long-term forest dynamics under explicit consideration of competition, demographic processes, and disturbances (cf. Methods). The parametrization of

LandClim emphasized the reproduction of succession dynamics and landcape-scale species distribution patterns. The two models' respective strengths and weaknesses can be expected to highlight different aspects of uncertainty in estimates of future forest development and help to anticipate adverse consequences of climate change to facilitate reasonable adaptation measures (Littell et al. 2011). Despite their different structures both models gave very similar results and converged in their projection of the future development of beech-oak forests at the warm-dry distribution limit in Central Europe. Such agreement is rather atypical. Hlásny et al. (2011) for instance – after finding remarkable differences in the model output of BIOME-BGC and SYBILA for vegetation zones in Hungary – comment: 'This appears to be general problem of such modelling [...] The discrepancies [...] emphasize the need for multi-model assessment of future forest development in order to clarify and highlight differences in model assumptions and model sensitivities to environmental and human intervention'. A possible reason for the congruence in the results is the calibration against the empirical data (cf. Methods; Fig. S1/2) as suggested by Mäkelä et al. (2000).

Generally, process-based models incorporating tree physiology are given preference when addressing climate change issues (Mäkelä et al. 2000, Mäkelä 2003, Littell et al. 2011). They integrate physical site parameters (e.g. radiation, evapotranspiration, water availability) with basic physiological principles to calculate the photosynthetic potential (or more general carbon acquisition). Despite some freedom in species-specific parameter values, the physiological principles set reasonable limits to the possible growth even where parametrization data are scarce or contradictory. In contrast, models such as SILVA or LandClim employ empirical functions between growth parameter and growth reaction (cf. Bugmann 1994, Schumacher et al. 2004, Pretzsch 2009). Within their typical range, the direct relation between input (e.g. climate) and output variable (e.g. basal area growth) usually makes them much more precise than process-based models. Examples of approaches that promise to combine the strengths of either model type are hybrid models such as the BRIDGING model (Mäkelä 2003) or model coupling like the adjustment of SILVAs growth functions from BALANCE output (Moshammer et al. 2009).

Since the first yield tables of the 18th and 19th century, forest growth models have come a long way. Today, forest management relies strongly on complex computer-aided growth simulators and expects decision support in face of a large uncertainty due to the projected climate change. However, it is clear that no single model solution can possibly cover the entire complexity of any ecosystem. Therefore, one of the most urgent future challenge for the scientific modelling community lies in overcoming structural differences in model in- and output (as done here) and thereby to ease multi-model inferences in the context of global change research based on suites of dynamic simulation models.

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Zapater, M., Hossann, C., Bréda, N., Bréchet, C., Bonal, D. and Granier, A. 2011. Evidence of hydraulic lift in a young beech and oak mixed forest using ^{18}O soil water labelling. – Trees 25: 885-894.

Supplement

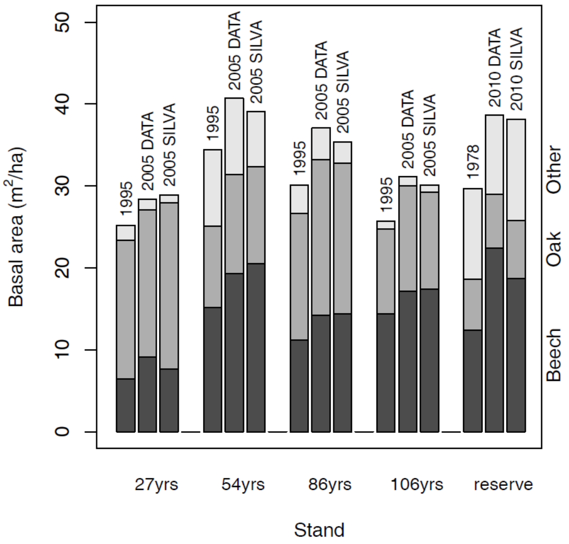

Fig. S1: Validation of SILVA vs. survey data. 10-years basal area development of the four experimental sites and the forest reserve. Comparison of the surveys 1995-2005 (1978-2010 in the case of the reserve) and SILVA simulation over 10 yrs (30 yrs in the case of the reserve) with the average climate from 1981-2000 (DWD station Schweinfurt).

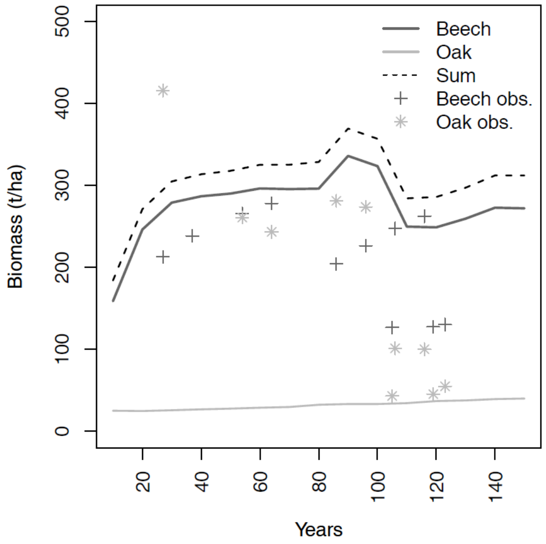

Fig. S2: Validation of LandClim vs. survey data. Simulations were run with the actual climate (DWD data) and results were compared to the real stands. Good reproduction of lower biomass shares of beech in young stands and a dominance of beech from c. 100 years on.

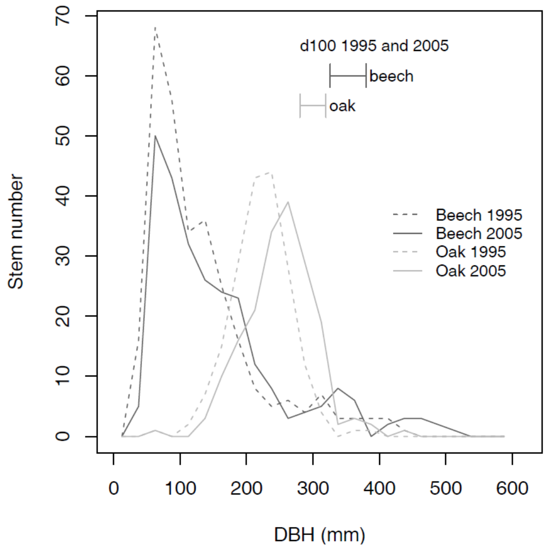

Fig. S3: Diameter at breast height (DBH) distribution of the 86-yrs old mixed beech-oak stand in 1995 and 2005. d100 = average diameter of the 100 dominant trees per hectare. The DBH distribution in the 86-year old stand displays that the stand structure consists of a dominant oak layer while beech mainly forms the subcanopy. However, the beech trees in the upper canopy layer expand stronger than oak: From 1995 to 2005, beech d100 increased from 32.58 cm to 37.98 cm (+ 5.40 cm) while oak d100 only increased from 28.02 cm to 31.96 cm (+ 3.94 cm).

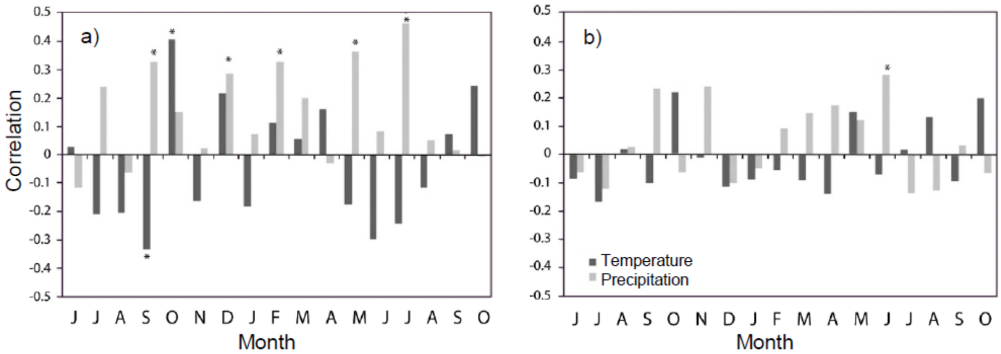

Fig. S4: Correlation coefficients for a 16-month period from June of the year prior to growth until October of the growth year between a) beech and b) oak tree-ring index curves and monthly climate data from Schweinfurt meteorological station for the period 1959-2003. Correlations significant at the $p < 0.05$ level are marked with an asterisk. Climate-growth relationships for both studied species were calculated as correlation functions between monthly climate data from Schweinfurt climate station and the dimensionless tree-ring indices as well as the raw ring-width data. The latter include the differences in the species' growth levels, so possible effects of tree age and size on the impact of climate on growth have to be regarded.

Tab. S1: Comparison of DWD and WETTREG 2010 A1B climate data for DWD weather station Schweinfurt from 1971 to 2000. T.a = mean annual temperature, T.v = mean temperature May-Sep (vegetation period), Prec.a = annual precipitation sum, Prec.v = precipitation sum May-Sep (vegetation period). Mean testing with Welch's t-test and standard deviation testing with an F-test on the ratio of the group variances (functions t.test and var.test in R statistics, cf. Dalgaard 2002: 86-89). DWD and WETTREG values different on a 0-0.001 error level (***), 0.001-0.01 error level (**), 0.01-0.05 error level (*), 0.05-0.1 error level (o).

	Mean			**Standard deviation**		
	DWD	**WETTREG**	**p-level**	**DWD**	**WETTREG**	**p-level**
T.a (°C)	9.04	9.06	0.8703	0.72	0.32	5.705e-14(***)
T.v (°C)	15.95	15.97	0.875	0.87	0.42	5.506e-11(***)
Prec.a (mm)	555	589	0.0886(o)	102	84	0.1276
Prec.v (mm)	261	279	0.1397	63	57	0.438

Dalgaard, P. 2002. Introductory statistics with R – Springer.

Literature review S1 'climatic turning point' and 'rank reversal'

Search items for searching the ISI Web of Science ® Data base for publications on 'climatic turning point' as well as rank reversal: Topic=('climatic turning point') OR Topic=('climatic turning points'). This resulted in only 3 papers on meteorology.

A search with the search term Topic=('rank reversal') OR Topic=('rank-reversal') AND Topic=(plants) AND Topic=(species) OR Topic=('rank reversals') OR Topic=('rank-reversals') refined by Subject Areas=('environmental sciences ecology' OR 'physiology' OR 'reproductive biology' OR 'biodiversity conservation' OR 'life sciences biomedicine other topics' OR 'developmental biology' OR 'evolutionary biology' OR 'forestry' OR 'plant sciences' OR 'agriculture' OR 'genetics heredity') resulted in 48 papers. After exclusion of zoology, neurophysiology and policy support, 14 papers remained with all of which but two deal with tree species. All of which but one are published currently, i.e. within these decade (the exception is from 1996).

Baltzer, J. L. and S. C. Thomas. 2007. Determinants of whole-plant light requirements in Bornean rain forest tree saplings. – Journal of Ecology 95:1208–1221.

Baraloto, C., Goldberg, D. E. and Bonal, D. 2005. Performance trade-offs among tropical tree seedlings in contrasting microhabitats. – Ecology 86:2461–2472.

Beaudet, M., Brisson, J., Gravel, D. and Messier, C. 2007. Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understorey of an old-growth forest. – Journal of Ecology 95:458–467.

Boyden, S.B., Reich, P. B., Puettmann, K. J. and Baker, T. R. 2009. Effects of density and ontogeny on size and growth ranks of three competing tree species. – Journal of Ecology 97:277–288.

Gomez-Aparicio, L., Garcia-Valdes, R., Ruiz-Benito, P. and Zavala, M. A.. 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. – Global Change Biology 17:2400–2414.

Gouvenain, R. C. de, Kobe, R. K. and Silander, J. A. 2007. Partitioning of understorey light and dry-season soil moisture gradients among seedlings of four rain-forest tree species in Madagascar. – Journal of Tropical Ecology 2007:569–579.

Kaelke, C. M., Kruger, E. L. and Reich, P. B. 2001. Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light-availability gradient. – Canadian Journal of Forest Research 31:1602–1616.

Osada, N. 2012. Crown exposure to light and tree allometry of 11 tree species in a snowy cool-temperate forest in Japan. – Plant Ecology 213:783–794.

Parker, W. H., Niejenhuis, A. van and Ward J. 1996. Genecological variation corresponding to forest ecosystem classification vegetation and soil types for jack pine and black spruce from northwestern Ontario. – Environmental Monitoring and Assessment 39:589–599.

Perez-Ramos, I. M., Urbieta, I. R., Zavala, M. A. and Maranon, T. 2012. Ontogenetic conflicts and rank reversals in two Mediterranean oak species: Implications for coexistence. – Journal of Ecology 100:467–477.

Sack, L. and Grubb, P. J. 2003. Testing performance rank reversals among coexisting species: Crossover point irradiance analysis by Sack & Grubb (2001) and alternatives. – Functional Ecology 17:276–287.

Sanchez-Gomez, D., Zavala, M. A., Schalkwijk, D. B. van, Urbieta, I. R. and Valladares, F. 2008. Rank reversals in tree growth along tree size, competition and climatic gradients for four forest canopy dominant species in Central Spain. – Annals of Forest Science 65:605-613.

Turnbull, L. A., Paul-Victor, C., Schmid, B. and Purves, D. W. 2008. Growth rates, seed size, and physiology: Do small-seeded species really grow faster? – Ecology 89:1352–1363.

Zavala M. A., Espelta, J. M., Caspersen, J. and Retana, J. 2011. Interspecific differences in sapling performance with respect to light and aridity gradients in Mediterranean pine-oak forests: Implications for species coexistence. – Canadian Journal of Forest Research 41:1432–1444.

Literature review S2 ‘Beech and oak coexistence’

Search items for searching the ISI Web of Science ® Data base for publications on growth of beech and oak under drought: Topic=(fagus OR beech OR ‘quercus robur’ OR ‘quercus petrea’ OR ‘sessile oak’ OR ‘Pedunculate Oak’ OR ‘English oak’) AND Topic=(drought OR ‘water shortage’ OR ‘water stress’) AND Topic=(‘height growth’ OR ‘forest growth’ OR increment OR ‘ring growth’ OR ‘tree growth’ OR dendrochronology OR ‘ring width’ OR ‘growth rate’ OR ring OR ‘physiological growth’ OR ‘stem growth’ OR ‘diameter growth’). In January 2012, this search produced 250 findings. Out of these results we aimed at proceedings that dealt with drought effects respectively water provision problems in the target species or in forest stands without publications concerning sap flow measurements under manipulated and natural conditions. Considering these specifications we found 141 target publications (Tab. S2). Within these target publications, 20 papers deal with coexistence of oak (*Quercus petraea* and/or *Q. robur*) and beech (*Fagus sylvatica*) (Tab. 1).

Tab. S2: Number of publications found in literature review S1 (ISI Web of Science ® Data base, January 2012) per item.

Term	**No of publications**
Fagus sylvatica	54
Quercus robur	27
Quercus petraea	12
Forest stands/ additional species	48
Different growth variables	38
Tree-rings or dendroecological tools	50
Total height (cm)	5
Relative change (%)	2
Stem diameter, volume and biomass	15
Increment	25
Breast-height radial growth	3

Manuscript 3: Symmetric and asymmetric competition

Symmetric and asymmetric competition in forests along the aridity gradient throughout the Iberian Peninsula

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Abstract

The relevance of competition and the ability of an organism to compete for a given resource might change along the abiotic stress gradient. The Spanish National Forest Inventories provide a solid basis to develop a statistical model for the influence of climate, competition and tree size on species growth. In order to formulate precise hypotheses it is important to distinguish between intensity and importance of competition. Competition intensity refers to the growth reduction due to the influence of neighbours. Competition importance refers to the negative effect of neighbours on growth relative to the effect of other factors. Furthermore, it is useful to distinguish between competition for water which is directly related to the climatic gradient, and competition for light which is largely independent. The first can be represented by the symmetric component, the latter by the asymmetric component of competition.

Three hypotheses were assessed applying a statistical model for tree growth: 1) The intensity of asymmetric competition increases with aridity, according to the shade-drought tolerance trade-off, 2) the intensity of symmetric competition, e.g. competition for water, increases with aridity, according to the supply and demand theory, and 3) the importance of symmetric and asymmetric competition falls with increasing aridity, according to Grime´s C-S-R framework.

The results were in agreement with former studies and ecological knowledge regarding general species response to climate and competition. However, the three hypotheses were not entirely supported. The within-species shade-drought tolerance trade-off was only found for broadleaved oaks and beech but not for coniferous pines. The effect of supply and demand was indeed found for all species. Contrary to the third hypothesis, importance of symmetric and asymmetric competition increased with aridity for most species. Only for light demanding pines asymmetric competition importance fell. Hence, in Mediterranean forests the importance of symmetric competition increased relative to asymmetric competition along the aridity gradient. This might cause an additional disadvantage for less drought tolerant oaks compared to pines under climate change.

Keywords: Shade-drought tolerance trade-off, Grime´s C-S-R framework, supply and demand, *Pinus spp.*, *Quercus spp.*, National Forest Inventory, Iberian Peninsula

Introduction

The joint effect of climate, light, nutrients and biotic interactions determines forest growth at a particular site. Out of the large amount of biotic interactions competition is supposed to be among the most important factors (Sánchez-Gómez et al. 2008, Kunstler et al. 2011). Until now it is not conclusively resolved how site conditions and competition among trees act together (individuals or species level; cf. Freckleton and Watkinson 2001). To investigate the interaction of competition with environmental stress, communities in Mediterranean regions are particularly interesting because they cover a long aridity gradient reaching close to the abiotic limits of the studied species.

Competition is an interaction between organisms or species that determines the share of resource allocation and in which the fitness of one organism is lowered by the presence of another. It can be split into a symmetric, size-relative and asymmetric component (Weiner 1990). Symmetric competition means that individuals share resources whereas asymmetric competition implies that one species is able to dominate the resource. Size-relative competition can be considered as a special case of asymmetric competition (or symmetric, depending on the point of view) where resource allocation is proportional to the size of the individual. Symmetric competition is assumed mainly for belowground resources such as water and nutrients (Weiner et al. 1997, Cahill and Casper 2000 but see also Leuschner et al. 2001). Asymmetric competition is assumed mainly for the resource light (Coomes and Grubb 2000). Both, symmetric and asymmetric competition decrease resource availability for an organism and subsequently increase stress.

The tolerance of an organism to one stress, e.g. drought stress, is typically reduced by other co-occurring stress agents such as shading due to asymmetric competition (Hereford 2009). The shade-drought tolerance trade-off implies that there are morphological and physiological reasons that species or individuals are either shade or drought tolerant. Shade and drought tolerance can be defined as the ability to maintain growth in deeper shade or under fewer water supply. Under low light conditions, plants invest proportionally more biomass in leaves and aboveground parts. This increases the transpiration surface relative to the amount of roots and, consequently, the susceptibility to dry conditions (Smith and Huston 1989). Conflicting requirements for shade and drought tolerances have been supported by several empirical studies (Kubiske et al. 1996, Valladares and Niinemets 2008, Hallik et al. 2009, Montgomery et al. 2010). Niinemets and Valladares (2006) observed significant negative correlations between shade and drought tolerance rankings, except for evergreen angiosperms. However, this research topic is apparently not conclusively resolved as also contrary patterns were found (Sack 2004, Martínez-Tillería et al. 2012). A reason for conflicting results might be a negative correlation between shading and drought stress due to lower temperatures and evapotranspiration under closed canopies (Sack and Grubb 2002). This negative correlation is considered the reason for a positive effect of shading resulting in facilitation, mainly during establishment. The shade-drought tolerance trade-off can be assessed at the intraspecific and interspecific level. At the interspecific level it can be ask if shade tolerant species are less drought tolerant than shade intolerant species (cf. Niinemets and Valladares 2006). At the intraspecific level it can be ask if trees grown under dry conditions and subsequently adapted to drought, are more sensitive to shading (Kubiske and Abrams 1994, Ruiz-Benito et al. 2013). The change of the effect of asymmetric competition on growth under increased aridity relates to the individual level.

Another theory related to competition and changes of its effect along environmental gradients is known as the ‘supply and demand’ theory. In economy, the law of supply and demand is considered as one of the fundamental principles (cf. Thweatt 1983). It states that as supply increases the value of the resource (its price) will tend to drop or vice versa, and as demand increases the value will tend to increase or vice versa. This theory is widely used in economics and can be transferred into ecology. In an ecological context it states that resource availability of an individual is determined by absolute resource availability and the abundance of competitors at the same time (supply minus demand; Davis et al. 1998, Taylor et al. 1990). Unlike in economics in ecological systems supply is usually an external variable (e.g. amount of water) which does not feedback on demand (cf. Muth 1961). Equilibrium is therefore reached exclusively by changes in demand. If demand is less than supply the difference can be consumed by upcoming individuals, i.e. forest density can increase. If demand is higher than supply, individuals starve and subsequently die. Which individual will die in particular could be determined by chance, yet, it is more likely mediated by its ability to persist/avoid stress and to aggregate resources relative to its competitors. Along a resource gradient such as the aridity gradient, supply decreases. Thereby, the equilibrium stand density falls and competition intensity increases (Briones et al. 1998, Davis et al. 1998, Bennett et al. 2012).

In the context of Grime´s C-S-R framework it has been stated that the importance of competition increases as disturbance and stress decline (cf. Grime 1977, Huston and Smith 1987), or comparably formulated that growth reductions due to competition relative to other factors falls with increasing abiotic stress (Brooker and Kikvidze 2008; be also aware of the 'Tilman debate' summed up in e.g. Goldberg et al. 1999, Brooker et al. 2005, Craine 2005). There are two possible mechanism behind this: The first one follows Liebig's law of the minimum, which states that only the most limiting resource is relevant, at least at the organism level (Odum and Barrett 2005). Under abiotic stress (such as drought) the organism is limited mainly by this stress and not by competitors. The second mechanism is a lower carrying capacity of high-stress environments (Tomé et al. 1996, Boisvenue and Running 2006) and thereby reduced stand basal area and subsequently less competitors. Variable climates like the Mediterranean produce fluctuating resource levels, which in turn might cause the size of populations (or stand density when referring to forests) to decrease below the level at which competition for resources occurs. Accordingly, it has been argued that competition might be less frequent in high-stress communities, though not less important (Fowler 1986, Vilà and Sardans 1999).

The stress-gradient hypothesis agrees generally with Grime´s C-S-R framework but adds another aspect (Maestre et al. 2005, Lortie and Callaway 2006, Maestre et al. 2009, Pretzsch et al. 2013). It predicts that the frequency of facilitative and competitive interactions will vary inversely with increasing abiotic stress, with facilitation being more common when abiotic stress is high (Bertness and Callaway 1994, Holmgren et al. 1997, Maestre et al. 2006, Danger et al. 2008). It has been stated that under some conditions neighbours have positive effects that outbalance negative effects. Whereas neighbours lower soil water (belowground resource, symmetric competition) and reduce available light (aboveground resource, asymmetric competition) they might also have positive influences. Among the most important are modified micro-climate and soil conditions (Gómez-Aparicio et al. 2005, Aponte et al. 2011, Granda et al. 2012).

A number of studies show that the nature of competition actually changes along ecological gradients. For grasslands Bennett et al. (2012) assessed the validity of

Grime´s predictions and the patterns expected by the supply and demand theory. A decline in competition with productivity was found. For forests the mode of competition has been found to change from asymmetric to symmetric along a nutritional gradient from fertile to poor sites (Hara 1993, Pretzsch and Biber 2010). This indicates that under low nutrient supply the effect of competition for the target resource increases relative to the effect of competition for light. A similar pattern was observed by Zang et al. (2012) for Norway spruce. There was evidence for a change in competition mode from asymmetric competition under conditions with sufficient soil water supply to a more symmetric competition under dry conditions. An analysis of Kunstler et al. (2011) found that the importance of competition varied along the climatic gradient (degree-day sum and water availability) in a mountain forest of France. According to their analysis actual competition importance fell with increasing abiotic stress while intensity remains the same. Such changes in mode and effect of competition particularly along climatic gradients can even cause rank reversals in species performance (Sánchez-Gómez et al. 2008, Gómez-Aparicio et al. 2011, Scharnweber et al. 2011).

Within this study we ask if the influence of symmetric and asymmetric competition on tree growth changes along the Mediterranean climatic gradient throughout the Iberian Peninsula. A statistical model for tree growth based on the National Forest Inventories of Spain was developed. The model considered the influence of climate, competition and tree size on individual tree growth. In order to formulate precise hypotheses it was necessary to distinguish between intensity and importance of competition (Brooker et al. 2005, Brooker and Kikvidze 2008, Freckleton et al. 2009, Kikvidze and Brooker 2010, Freckleton and Rees 2011). We defined competition intensity as growth reduction due to competition relative to growth in the absence of neighbours (but the same abiotic conditions). Given that competition has a negative effect on performance, intensity can be interpreted as the percentage of decrease in performance due to the presence of neighbours for given abiotic conditions, i.e. the absolute effect of competition is scaled to the local growth potential (Eq. 4). To competition importance we refer to as the negative effect of neighbours on growth relative to the impact of other (abiotic) factors (Eq. 5), i.e. the absolute effect of competition is scaled to the overall growth reduction.

Using these indices we investigated the validity of three hypotheses motivated by the theories described above:

1. Intensity of asymmetric competition increases with aridity, according to the shade-drought tolerance trade-off.
2. Intensity of symmetric competition, e.g. competition for water, increases with aridity, according to the supply and demand theory.
3. Importance of symmetric and asymmetric competition compared to other factors falls with increasing aridity, according to Grime´s C-S-R framework.

To address the first hypothesis the sensitivity to asymmetric competition under different abiotic conditions was compared. This could be done by comparison of the absolute effect of competition on growth (as difference between growth without neighbours and with neighbours). However, the change of this absolute difference along the gradient lacks its quantitative context and can therefore hardly be evaluated and compared among species. Intensity as percentage of growth reduction due to competition is scaled to the local growth potential.

Similarly, the supply and demand theory was assessed by the change in intensity of symmetric competition. The intensity of competition as the percentage of growth reduction due to neighbours represents the local value of the target resource. The resource value is hypothesized to fall with supply, i.e. the intensity of competition falls. In contrast, the effect of competition on growth compared to other factors was assessed by the share of growth reduction by competition relative to the overall growth reduction (here only climate was considered).

Methods

Spanish National Forest Inventories

Mediterranean regions occur in middle latitudes between parallels 30° to 40° North and South in five regions of the world: The Mediterranean Basin, California, central Chile, the Cape region in South-Africa and southwestern and southern Australia. Summer drought is the defining factor of the Mediterranean climate and particularly throughout the Iberian Peninsula, Spain (Köppen 1923).

Annual rainfall ranges from about 1500 mm in montane forest to below 90 mm in the most arid sites. Annual mean temperatures range from about 11 °C to 17 °C.

In the present study the Second and Third Spanish National Forest Inventories conducted between 1986-1996 and 1997–2007 were used (Villaescusa and Diaz 1998, Villanueva 2004). Survey plots were arranged in a regular 1 km raster. They consist of four concentric radii (i.e. the minimum tree diameter measured varied with the radius of the plot): All trees with diameter at breast height (*DBH*) of 7.5 cm were measured within a 5 m radius plot, trees with *DBH* = 12.5 cm within a 10 m radius plot, trees with *DBH* = 22.5 cm within a 15 m radius plot, and trees with *DBH* 42.5 cm within a 25 m radius plot. The 12 most frequent species were modelled (*Pinus spp.*, *Quercus spp.* and *Fagus sylvatica*; refer to Tab. 2). Non-native species were not modelled. Climatic data such as annual mean temperature (°C) and annual precipitation sum (mm) were provided by the Spanish Institute of Meteorology, as an interpolation of the information recorded in meteorological stations from 1971 to 2000 with 1 km spatial resolution (Gonzalo 2008).

Bayesian non-linear model

For this study we chose the annual ‘relative basal area increment’ (*relBAI*) as response variable (Eq. 1). Explaining variables were climate (temperature and precipitation), competition and tree size (Eq. 3). Relative basal area increment times hundred is the percentage of annual basal area increment for a given tree basal area. Thereby the pure geometric effect *DBH* on growth increment was eliminated.

$$\begin{aligned} BA &= \pi \cdot \left(\frac{DBH}{2}\right)^2 \\ relBAI &= \frac{BA_{III} - BA_{II}}{BA_{II}} \cdot \frac{1}{yrs} \end{aligned} \qquad \text{Eq. 1}$$

BA: Basal area (cm^2). Index denotes second and third NFI.
DBH: Diameter at breast height (cm)

Numerous approaches exist to calculate measures for competition (Dale et al. 1985, von Oheimb et al. 2011). Two different competition measures were used within this study (non-spatially explicit, no differentiation of inter- and intraspecific competition): Stand basal area for symmetric competition *SC* and basal area of larger trees for asymmetric competition *AC*. To account for the inventory method, *SC* (for each plot) and *AS* (for each tree) were calculated under consideration of the reference area for each *DBH* class (Eq. 2). Within each survey plot the trees are ordered according to their *DBH*.

$$SC_p = 100 \cdot \sum_{i=1}^{4} \sum_{j=1}^{n} \frac{\pi}{4} \cdot \frac{DBH^2}{A_i} \qquad \text{Eq. 2}$$
$$AC_k = 100 \cdot \sum_{i=1}^{4} \sum_{j=k+1}^{n} \frac{\pi}{4} \cdot \frac{DBH^2}{A_i}$$

SC_p: Symmetric competition in plot p as stand basal area in % of plot area.

AC_k: Asymmetric competition for target tree k as stand basal area of langer trees in % of plot area.

DBH_{ij}: Diameter at breast height (cm)

A_i: Plot area within DBH class of tree ij was measured (cm^2)

Iterator 4: Number of sub-plots with different radii in the Spanish National Forest Inventory.

Symmetric competition was the same for all trees within a plot whereas asymmetric competition differed among individual trees. The stand basal area minus the basal area of the target tree is an alternative measure for symmetric competition. This measure differs among trees within the same plot (considered as neighbours) by their own size difference. The larger the target tree the smaller is the index compared to other trees within the same plot. Thereby an asymmetric component is included in this measure. Since we aimed at separating symmetric and asymmetric competition such an index would have been contra-productive.

Mediterranean species distributions and tree growth show good correlations with annual mean temperature and annual precipitation sum (Thuiller et al. 2003, Sánchez-Gómez et al. 2008, Rodríguez-Sánchez et al. 2010, Gómez-Aparicio et al. 2011, Kunstler et al. 2011). Precipitation served as proxy for water availability and thereby aridity and drought stress. An interaction between temperature and precipitation was considered in the model. The relative basal area increment *relBAI* (Eq. 1) of individual trees was modelled as a non-linear function of climatic variables (temperature and precipitation), local interactions with neighbouring trees (symmetric and asymmetric competition) and tree diameter (*DBH*). All independent variables were normalized. Separate models were fitted for 12 selected species.

We decided for the following model structure with a gamma error distribution as basis for backward model selection:

$$\begin{aligned} relBAI = \exp(\alpha + \beta_T \cdot T + \beta_{T2} \cdot T^2 + \beta_P \cdot P + \beta_{P2} \cdot P^2 + \beta_{TP} \cdot T \cdot P + \beta_{DBH} \cdot DBH + \beta_{DBH2} \cdot DBH^2) \\ + \beta_C \cdot (\gamma \cdot SC + (1-\gamma) \cdot AS) + \beta_{CT} \cdot T \cdot (\gamma_T \cdot SC + (1-\gamma_T) \cdot AS) + \beta_{CP} \cdot P \cdot (\gamma_P \cdot SC + (1-\gamma_P) \cdot AS) \\ + \beta_{CT2} \cdot T^2 \cdot (\gamma_{T2} \cdot SC + (1-\gamma_T) \cdot AS) + \beta_{CP2} \cdot P^2 \cdot (\gamma_{P2} \cdot SC + (1-\gamma_P) \cdot AS) + \epsilon \end{aligned} \quad \text{Eq. 3}$$

T: Annual mean temperature (°C)
P: Annual precipitation sum (mm)
DBH: Diameter at breast height (cm)
SC: Symmetric competition (% of basal area of neighbouring trees)
AC: Asymmetric competition (% of basal area of taller trees)
γ constrained to $0 \leq \gamma \leq 1$; for specification of other priors and JAGS code see Supplement 1.

For precipitation *P*, temperature *T* and *DBH* linear and quadratic terms were tested whereas for competition a linear relation was assumed. Additionally, an interaction for precipitation and temperature was included. Linear interaction terms for competition with climate allow for a change in absolute growth reduction due to competition along the gradient. Competition was divided into its symmetric and asymmetric component. Since they are naturally correlated (e.g. for the smallest tree in stand *SC* = *AS*; for the tallest *AS* = 0) they could not be used as two independent variables. Therefore, competition was included as a joint regression term. Within this term the effect (β_C) of competition on *relBAI* was shared between *SC* and *AS* by parameters γ. Quadratic interaction terms for climate and competition allowed for a change of positive and negative interaction along the gradient (important when the species growth optimum is at intermediate values; Gómez-Aparicio et al. 2011).

We used R.2.15.2 (R Development Core Team 2008) for data manipulations and JAGS 1.0.3 (Plummer 2003) for the Bayesian modelling (the R2jags package was used to interface between R and JAGS). We checked for convergence with two Monte Carlo Markov Chains using the potential scale reduction factor Rhat, setting our convergence threshold at Rhat < 1.01 and the Gelman and Gewke test for convergence (confidence = 0.95). We decided for a flexible burn-in period by resuming the mcmc after each 5,000 iterations if convergence was not reached, and a thinning of 2. After convergence was reached the two Monte Carlo Markov Chains were run another 10,000 iterations and the chains inspected visually. Model quality was evaluated additionally by calculation and visual inspection of the bias of prediction (0.9 < bias < 1.1) and residual diagnostics (QQ-plot inspection). Due to high computation costs not the entire data was used to fit the model but a random selection of 10,000 trees (for each species). The final models were selected from the candidate models (Tab. 1) by the evaluation of DIC and R^2. The null-model for the calculation of R^2 constituted a model containing only intercept α. Furthermore, the principles of backward selection were applied, i.e. start with the full model (Eq. 3) and drop parameters on by one. Further decision rules to drop parameters: Quadratic terms before linear terms and interactions terms before non-interaction terms.

Response curves for climate and competition were calculated for each species. Precipitation, temperature and symmetric and asymmetric competition were set to the dataset means, *DBH* to the species mean.

Intensity and importance of competition

Competition intensity measures growth reduction due to competition compared to abiotic factors. Changes in the intensity of competition along the precipitation and temperature gradient were analysed using the index

$$C_{\text{int}} = \frac{G_{-N} - G_{+N}}{max\left(G_{+N}; G_{-N}\right)} \quad \text{Eq. 4,}$$

where G_{+N} and G_{-N} denote growth of the target species in the presence (+N) and absence (-N) of neighbours (Kikvidze and Brooker 2010, Brooker and Kikvidze 2008, Gaucherand et al. 2006). An intensity of 0.1 denotes a reduction of relative basal area increment by 10% due to interactions with neighbours. Competition importance is the proportional impact of competition relative to the overall impact

Tab. 1: Regression terms of the candidate models (cf. Eq. 3).

Model	β_P	β_{P2}	β_T	β_{T2}	β_{PT}	β_{DBH}	β_{DBH2}	β_C	β_{CP}	β_{CT}	β_{CP2}	β_{CT2}
2	x	x	x	x	x	x	x	x	x	x	x	
3	x	x	x	x	x	x	x	x	x		x	
4	x	x	x	x	x	x	x	x	x	x		
5	x	x	x	x	x	x	x	x	x			
6	x	x	x		x	x	x	x	x	x		
7	x		x	x	x	x	x	x	x	x		
8	x		x		x	x	x	x	x	x		
9	x	x	x	x	x	x	x	x				

of the environment. Index C_{imp} can be used to express changes in competition importance along productivity gradients (Eq. 5).

$$C_{imp}=\frac{G_{-N}-G_{+N}}{G_{max}-min\left(G_{+N};G_{-N}\right)} \quad \text{Eq. 5}$$

Again, G_{+N} and G_{-N} denote growth of the target species in the presence (+N) and absence (-N) of neighbours, G_{max} is the growth without neighbours at the climatic optimum regarding precipitation and temperature. Since this index for competition importance depends on the abiotic growth optimum of each species it is highly sensitive to the abiotic range considered and has to be interpreted carefully.

Competition intensity and importance were calculated along the precipitation and temperature gradient (but only shown for precipitation because temperature had almost no effect). For symmetric competition *AC* was set to zero and *SC* to the dataset mean, and vice versa. *T* was set to the 11 °C (data set mean was 11.5° C but *P. uncinata* did not occur at this temperature), *DBH* was set to the species means.

The absolute increase or decrease of these two competition indices (C_{int} and C_{imp}) over the gradient depends on the definition of 'with neighbours'. The more neighbours the stronger is the change of the indices along the climatic gradient (given that an interaction exists). If the interaction between the abiotic variable and competition is weak (and given that $G_{+N} < G_{-N}$) the indices could even increase for low competition values (low stand density or tall trees) and decrease for high values (high stand density or small trees).

Stand basal area and thereby symmetric and asymmetric competition presumably change along the stress gradient, i.e. productivity decreases with increasing aridity (Tomé et al. 1996, Boisvenue and Running 2006). Under dry conditions individuals are subjected to lower absolute values of symmetric and asymmetric competition. Thereby, relevant levels of competition (values of *SC* and *AC*) decrease along the aridity gradient. 'Actual' *SC* and *AC* were calculated along the gradient using a linear regression. Competition intensity and importance were than calculated using these actual occurring values. These values were used to calculate the 'actual' competition intensity and importance (cf. Kunstler et al. 2011).

Results

Final models

Model selection was based on DIC, R^2 and the posterior distributions of the parameters. Best models according to the DIC were the models with less parameters with posteriors close to zero (Tab. 2). R^2 ranged between c. 0.07 (*Q. suber*) and 0.25 (*P. sylvestris*) (Tab. 3). For all but *F. sylvatica* the final models contained

Tab. 2: DIC for candidate models calculated by JAGS. Bold: Final models.

Species	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9
P. halepensis	-46334	-46063	-46134	-46258	-46029	-**46362**	-46195	-46088	-46138
P. nigra	-47432	**-49262**	-48516	-49001	-48477	-48674	-48463	-48697	-48933
P. pinaster	**-48945**	-43350	-43013	-43298	-43433	-42824	-43022	-42976	-42902
P. pinea	-43057	-47311	-47057	-47178	**-47432**	-46831	-46750	-46893	-47138
P. sylvestris	-47821	-48238	-48058	-47842	**-48397**	-48253	-47962	-48357	-48249
P. uncinata	**-55857**	-55738	-55728	-55771	-55699	-55711	-55612	-55735	-55698
Q. faginea	-54498	**-54831**	-54612	-54776	-54666	-54688	-54714	-54609	-54673
Q. ilex	**-56683**	-56416	-56279	-55878	-55921	-56296	-56457	-56306	-55988
Q. pyrenaica	-51888	-52217	-52123	-51957	**-52790**	-52375	-52457	-52284	-52342
Q. robur	-38915	-38915	-38917	-38918	-38916	-38920	-38920	**-38922**	-38908
Q. suber	-56031	-56240	-55818	-56180	-56048	-55997	**-56309**	-56197	-56203
F. sylvatica	-55467	-55052	-55255	-55483	-54799	-55422	-55127	-55162	**-55505**

Tab. 3: R^2 for candidate models. R^2 was calculated as the explained variance relative to a Null-model only containing the intercept (= mean relBAI). Bold: Final models.

Species	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9
P. halepensis	0.192	0.182	0.194	0.184	0.181	**0.194**	0.175	0.173	0.183
P. nigra	0.234	**0.252**	0.270	0.270	0.263	0.268	0.265	0.261	0.276
P. pinaster	**0.258**	0.261	0.267	0.261	0.269	0.234	0.239	0.246	0.261
P. pinea	0.281	0.231	0.242	0.235	**0.240**	0.230	0.233	0.234	0.235
P. sylvestris	0.247	0.258	0.241	0.258	**0.263**	0.259	0.238	0.253	0.258
P. uncinata	**0.235**	0.232	0.229	0.231	0.232	0.228	0.224	0.228	0.225
Q. faginea	0.149	**0.151**	0.149	0.149	0.149	0.149	0.148	0.147	0.149
Q. ilex	**0.154**	0.151	0.152	0.150	0.146	0.147	0.152	0.143	0.147
Q. pyrenaica	0.135	0.137	0.139	0.136	**0.140**	0.137	0.133	0.131	0.138
Q. robur	0.149	0.150	0.149	0.148	0.148	0.148	0.148	**0.149**	0.147
Q. suber	0.060	0.058	0.058	0.057	0.062	0.055	**0.068**	0.062	0.060
F. sylvatica	0.107	0.107	0.102	0.102	0.102	0.106	0.104	0.104	**0.104**

an interaction for climate and competition (Tab. 4). The interaction with temperature was weaker in average and even dropped out for some species (*P. halepensis, Q. robur, Q. suber, F. sylvatica*).

Species response to climate and competition

Relative basal area increment was higher for pines than for oaks and beech (Fig. 1). Also plasticity regarding growth was higher for pines, i.e. absolute changes in growth along both the shade and precipitation/aridity gradient were larger for pines. We found that higher temperatures generally had a positive or neutral effect on growth of broadleaved species, but negative effects on conifers.

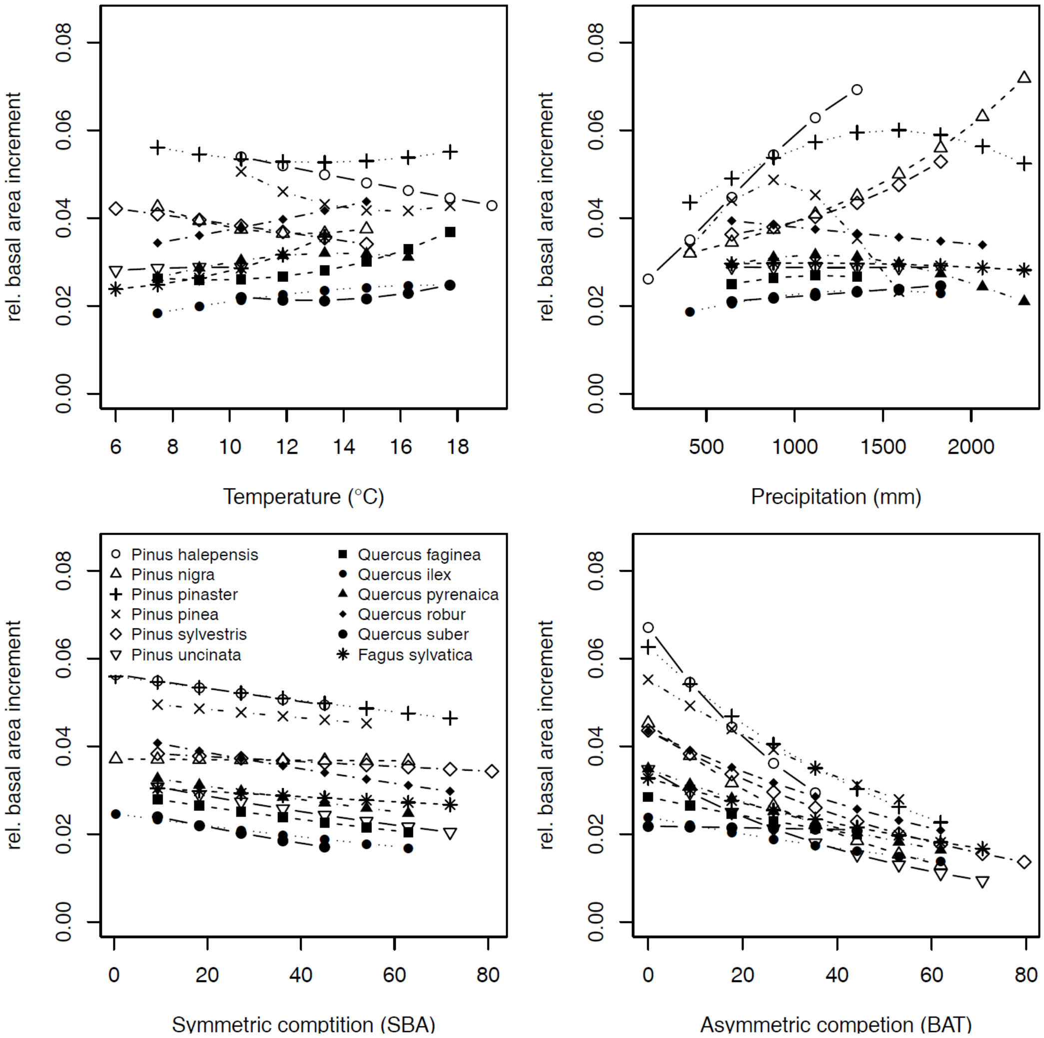

Fig. 1: Species response curves for temperature, precipitation and competition. Precipitation serves as proxy of aridity. All variables were set to their means, DBH was set to species specific means. (SBA: stand basal area in %; BAT: Basal area in %)

Precipitation had a positive effect on all species, despite on *Q. robur,* and a pronounced unimodal effect on *P. pinea*. Symmetric as well as asymmetric competition had a negative influence on tree growth for all species (the model structure did not allow for complementary absolute effects). The effect (β_C) was larger for pines than for oaks and beech. Furthermore, parameter γ indicated a stronger effect of asymmetric competition ($\gamma < 0.5$) for all species despite *Q. faginea*, *Q. ilex* and *Q. suber* (Tab. 4). In general, for pines γ tended to be smaller than for oaks and beech. For increasing asymmetric competition species performances became more similar, e.g. differences among species became less under high shading (note that here were only adult trees assessed). A rank reversal of pines and oaks in absolute growth occurred at higher levels of asymmetric competition ($AC > 40$).

Interaction of aridity and competition

The interaction between competition and precipitation was stronger than between competition and temperature. Change of overall competition effect along the aridity gradient was therefore mainly mediated by parameter β_{CP} which was mostly positive (Tab. 4). This led to an additional increase of growth with precipitation under the presence of neighbours, i.e. an additional decrease with aridity. A parameter value of $\gamma_{CP} > 0.5$ means that the absolute effect of symmetric competition changed stronger than the effect of asymmetric competition (the only exception was *P. pinea*).

Asymmetric competition intensity increased with aridity for broadleaved species like hypothesized (H1) but fell for conifers (Fig. 2). For *F. sylvatica* asymmetric competition intensity did not change. *Symmetric competition intensity* increased with aridity for all species like hypothesized (H2), or remained unchanged (Fig. 2). Contrary to hypothesis 3, competition importance did not fall with aridity but even increased for some species. Differentiation of symmetric and asymmetric competition importance revealed that particularly the *importance of symmetric competition* increased for oaks while for pines it remained unchanged. *Asymmetric competition importance* also increased for oaks, *P. pinea* and *P. uncinata*. Only for *P. halepensis, P. nigra, P. pinaster* and *P. sylvestris* asymmetric competition importance fell like hypothesized (H3). These patterns did not change for both intensity and importance, when not median competition levels were used but the quantiles 0.1 and 0.9.

Pearson correlation of stand basal area with precipitation was r = 0.35 (Tab. S1). Linear regressions resulted in a decrease of $SC = 7.98 + 0.014 \cdot P$ and $AC = 3.56 + 0.0076 \cdot P$ (no significances are given because the regressions were used for interpolation). Thereafter, actual occurring competition levels decreased with aridity. Calculation of competition importance using these SC and AC gradi-

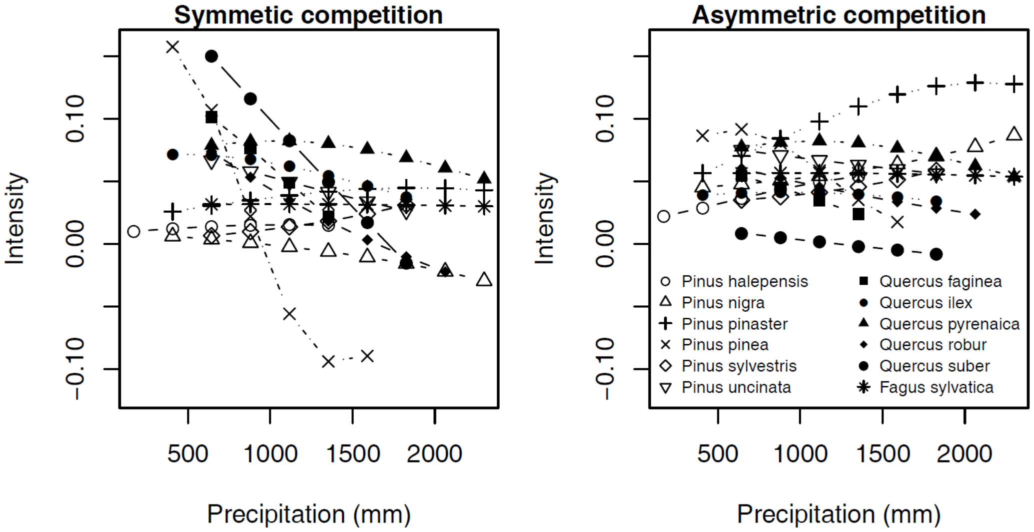

Fig. 2: Intensity of symmetric competition increases for for oaks while is remains rather the same for more drought tolerant pines. Asymmetric competition intensity also increases for oaks but decreases for some pines.

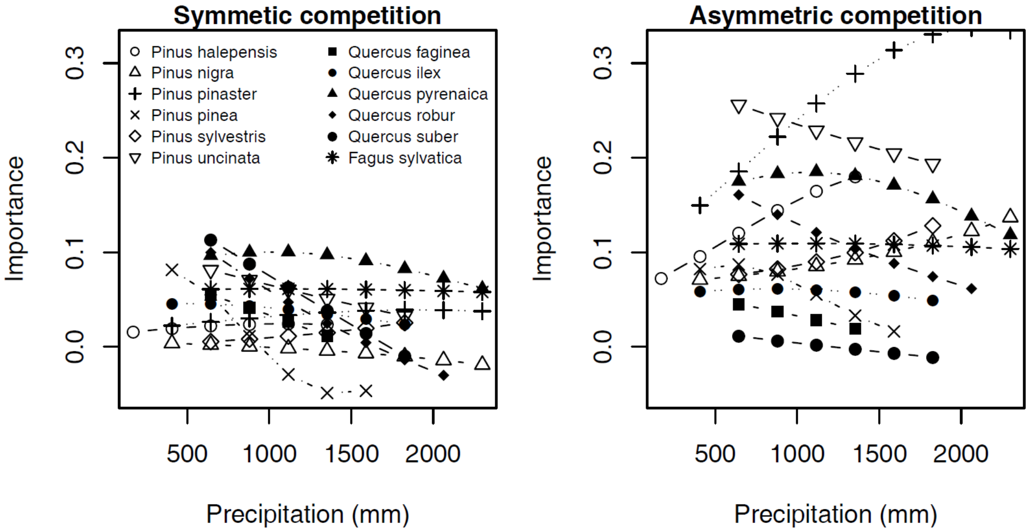

Fig. 3: Importance of competition increases with aridity, particularly symmetric competition importance for rather drought intolerant oaks. Only asymmetric competition importance decreases for most pines (Exceptions: *P. nigra*, *P. sylvestris*).

Tab. 4: Model parameters (means) and R^2 of the final models.

	α	β_P	β_{P2}	β_T	β_{T2}	β_{PT}	β_{DBH}	β_{DBH2}	β_C	β_{CP}	β_{CP2}	β_{CT}	β_{CT2}	γ	γ_P	γ_T	R^2
P. halepensis	-3.140	0.145	-0.010	-0.033		0.025	-0.226	0.020	-0.152	0.002				0.163	0.536		0.194
P. nigra	-3.320	0.072	0.003	-0.023	0.009	0.002	-0.313	0.029	-0.183	0.005	0.002	-0.011		0.020	0.697	0.262	0.252
P. pinaster	-2.971	0.114	-0.030	-0.007	0.003	-0.009	-0.296	0.038	-0.205	-0.023	0.000	-0.006	0.000	0.075	0.069	0.387	0.258
P. pinea	-3.209	0.112	-0.037	-0.031	0.028	0.067	-0.254	0.027	-0.175	0.040		-0.006		0.406	0.835	0.473	0.241
P. sylvestris	-3.257	0.048	0.006	-0.036	-0.001	0.013	-0.300	0.031	-0.177	-0.008		-0.006		0.127	0.626	0.396	0.263
P. uncita	-3.663	0.008	0.000	0.005	-0.003	0.005	-0.286	0.030	-0.168	0.009	0.006	-0.009	-0.016	0.160	0.604	0.422	0.235
Q. faginea	-3.587	0.031	-0.013	0.022	0.011	0.000	-0.257	0.024	-0.118	0.024	0.003	0.014		0.504	0.608	0.532	0.151
Q. ilex	-3.712	0.056	-0.009	0.035	-0.016	-0.006	-0.291	0.047	-0.083	0.010	-0.003	0.013	0.014	0.472	0.599	0.497	0.154
Q. pyreica	-3.453	0.028	-0.017	0.051	-0.013	-0.022	-0.237	0.023	-0.155	0.001		-0.008		0.343	0.509	0.602	0.140
Q. robur	-3.295	-0.021		0.040		0.001	-0.222	0.033	-0.110	0.025				0.169	0.638		0.148
Q. suber	-3.771	0.017		0.044	0.012	-0.001	-0.170	0.027	-0.084	0.022				0.928	0.827		0.068
F. sylvatica	-3.685	-0.003	-0.003	0.076	0.011	0.025	-0.154	0.007	-0.122					0.182			0.103

ents resulted in the expected pattern of lower importance under arid conditions and higher values under moist conditions compared to the calculations with constant competition levels (Fig. S2). Actual symmetric competition importance fell for pines which showed a neutral pattern for the other calculation (Fig. 3). For oaks actual symmetric competition importance did not change considerably with aridity. The same pattern was also true for intensity (Fig. S1).

Discussion

This study deals with the question whether the effect of competition on tree growth changes along the Mediterranean aridity gradient. This question is closely related to three basic theories: The shade-drought tolerance trade-off, the supply and demand theory and Grime´s C-S-R framework (see introduction). By separating competition into its symmetric and asymmetric component it was possible to address these theories, carefully choosing the competition index, i.e. intensity and importance of competition (Brooker et al. 2005). The hypotheses specified in the introduction were not entirely supported by the model results, which allows for an interesting discussion and opens further research opportunities.

Species response to climate and competition

The final models for tree growth showed the well known reaction of species to temperature and precipitation (cf. Gómez-Aparicio et al. 2011). Conifers distribution ranges reached the dry edge of the Mediterranean climate whereas the optima of broadleaved oaks and beech occurred at intermediate precipitation. While precipitation representing aridity had a positive effect on tree growth for most species the effect of temperature was not that univocal. Remarkably, temperature had a negative effect on conifers while for broadleaved a positive effect was found (see also Gómez-Aparicio et al. 2011). A possible reason for the negative effect of temperature on growth for conifers might be that they cannot react to higher evapotranspiration following higher temperatures due to their leaf architecture and further morphological and physiological differences between gymnosperms and angiosperms (Bond 1989). However, a recent study by Ruiz-Benito et al. (2013) using the same data (Spanish NFI) showed a general negative effect of temperature on both, conifers and broadleaved by an increase in mortality (exceptions are *P. uncinata*, *Q. suber*, *P. pinea*).

Besides the modelled effect of climate on growth, a stronger effect of asymmetric competition on conifers than on broadleaved is in agreement with ecological knowledge, i.e. shade tolerances of species (Zavala et al. 2000, Niinemets and Valladares 2006; Tab. S3). Furthermore, the common pattern of lower plasticity in growth (Chambel et al. 2005, Valladares et al. 2007) of rather shade-tolerant species (beech, oaks) than that of shade-intolerant species also appeared in our growth model (Sánchez-Gómez et al. 2006, Richter et al. 2012). However, it has to be considered that this plasticity was observed within a large spatial extent and might also be caused by genetic diversity due to local adaptation of provenances (for example for *Pinus nigra;* Jagielska et al. 2007, Lucic et al. 2010). Together with the response of species to climate induced aridity the studied species can be arranged in Grime´s C-S-R triangle: Broadleaved oaks and beech are more at the competitors side whereas coniferous pines are more at the stress-tolerator side (Grime 1977).

Besides direct effects of the independent variables on growth also interactions among them were included in the model structure. The interaction term for temperature and precipitation mostly had a positive sign. This supports the negative effect of aridity on growth (increased temperatures increase evapotranspiration which was attenuated by coinciding increase in precipitation). The interaction of competition and climate ranged in the same amplitude. Whereas the direct effect of competition was stronger for the asymmetric component the interaction with climate was stronger for the symmetric component (see also below ‘competition importance’). This is plausible because the resource water strongly changes with precipitation whereas the resource light changes only slightly due to the correlation of canopy density and aridity (or site capacity and aridity).

Despite the present model gave reasonable results which are in agreement with former studies and ecological expectations, it had a relatively low fraction of explained variance R^2. A hierarchical model accounting for variability among survey plots caused by other factors than climate and competition, insect infestations, soil fertility etc. could increase R^2 for such a large dataset. However, we decided to only use measured variables since the aim of this study was not to make predictions on future tree growth at the same sites but to assess ecological principles. As long as non of the unknown variables which could be represented by the variable ‘survey site’ is correlated with the used ones general results will not differ.

Shade-drought tolerance trade-off – intensity of asymmetric competition

At the interspecific level the shade-drought tolerance trade-off was observed for broadleaved angiosperms and coniferous gymnosperms (Niinemets and Valladares 2006). Conifers do not tolerate so well shading but are less vulnerable to drought due to strong stomata regulation to avoid hydraulic failures under water scarcity (‘stress avoiders’), whereas broadleaved suffer more from drought stress but are considered to be more shade tolerant (Bond 1989, Zavala et al. 2000, Hallik et al. 2009). The first hypothesis in the present study refers to an intraspecific shade-drought tolerance trade-off. We presumed that a shade-drought tolerance trade-off should lead to an increase in intensity of asymmetric competition with aridity. Interestingly, this pattern was only found for oaks. Relative to other tree species within the Mediterranean forest communities oaks are rather shade tolerant and drought sensitive angiosperms (Tab. S2). An explanation therefore might be the ability of oaks as broadleaved angiosperms to adjust leaf structure and photosynthesis related properties in response to shading and increased aridity (e.g. Niinemets 2010, Wyka et al. 2012 for shade; Abrams 1990 for drought). Coniferous pines have lower abilities to adjust their leave structure and therefore no such trade-off could be observed (Bond 1989). This finding leads to the expectation that broadleaved oaks and beech might loose their advantage of higher shade tolerance to some degree under increased aridity (as expected due to climate change).

Supply and demand – intensity of symmetric competition

We hypothesized that the intensity of symmetric competition, e.g. competition for water, increases with aridity, according to the supply and demand theory. This proved to be true for all species. Assuming constant stand basal area a movement along the aridity gradient led to falling supply while demand remained unchanged. If demand remains unchanged and supply decreases, a shortage occurs, leading to a higher resource ‘price’, i.e. higher competition intensity. The relationship of symmetric competition intensity and stand basal area was similar to the relation of price and demand and can be interpreted as a movement on the demand curve in terms of microeconomics. In contrast, the relationship of symmetric competition intensity and supply is not similar to the relation of price and supply. This is due to the essential difference between most economic and ecological systems that there is no feedback of supply on changes in demand (mediated by price) (Rapport 1991). The economic principle of supply and demand (Thweatt 1983) can thus be found in Mediterranean forest communities, with the mentioned modification. Under more arid conditions like expected due to climate change this might lead to a more competitive environment regarding symmetric competition for water.

Competition importance and aridity

Changes of competition importance along the stress gradient are closely related to Grime´s C-S-R framework and the stress gradient hypothesis as well as to the Tillman debate. To address this topic it was essential to separate symmetric and asymmetric competition because they represent competition for different resources, here water and light. While water supply changes along the aridity gradient, light availability is not directly influenced. Contrary to expectations according to Grime´s C-S-R framework, the importance of competition rather increased with aridity (but refer to discussion on actual competition importance below). The strong effect of supply and demand in the studied communities provides a reason for the increase of symmetric competition importance. The effect of supply and demand was stronger than the general growth reduction due to aridity. This is in agreement with Tilman's idea that competition moves from canopies to roots with increasing aridity (e.g Brooker et al. 2005). Also the shade-drought tolerance trade-off for oaks is in accordance with an increase of symmetric and asymmetric competition importance under aridity. However, for most pines at least asymmetric competition importance fell, i.e. growth reduction due to aridity actually gained importance (refer to Liebig's law of the minimum; Odum and Barrett 2005). This is in accordance with lack of a shade-drought tolerance trade-off for pines.

According to the present findings in more arid environments competition might gain importance (Gómez-Aparicio et al. 2011). A more differentiated evaluation results in a shift of relative importance of symmetric and asymmetric competition in favour of the first (Zang et al. 2012). This is advantageous for pines and could outbalance negative effects of increased importance of overall competition in a probably more arid future.

Actual competition intensity and importance

Under dry conditions individuals actually are subjected to lower absolute values of symmetric and asymmetric competition. Accounting for changed stand basal area ‘actual’ competition intensity and importance were calculated. According to Kunstler et al. (2011) the actual importance of competition falls with increasing abiotic stress which is largely in accordance with the present study. However, the patterns for intensity differ among the studies. Contrary to Kunstler et al. (2011), particularly actual intensity of asymmetric competition changed with aridity. Differences in findings could not only be attributed to differences in the representation of competition and model structure but also to the climatic gradients. Whereas Kunstler et al. (2011) assessed a spatially smaller and generally moisture site in France the aridity gradient of the Spanish peninsula is longer as well as more extreme.

Moreover, when actual competition intensity and importance are used it has to be considered that there is a reason for lower stand basal area: Carrying capacity of the site is lower due to lower resource supply. The regulation of stand basal area is at least partly mediated by competition and not only by abiotic growth reductions and increased mortality (Ruiz-Benito et al. 2013). Symmetric competition intensity as local value of the resource water was found to increase with aridity whereas the effect was smaller under consideration of actual occurring competition levels. This supports the presumption that symmetric competition is a candidate for regulation of stand basal area with decreasing resource supply, particularly for oaks. In contrast, actual asymmetric competition intensity strongly fell and is therefore not good a candidate.

In the present study a consideration of actual levels of competition along the aridity gradient did result in a decrease of actual competition importance. This is in accordance with Grime´s C-S-R framework that is perhaps better addressed using actual occurring conditions (e.g. a consideration of actual occurring levels of competition). Particularly, the decrease in actual occurring asymmetric competition results in a strong loss of competitiveness of shade tolerant oaks with increasing aridity. Thereby, an underestimation of changes in competitiveness with aridity is likely when only the mere interplay of shade and drought tolerance with aridity is evaluated but changes in stand basal area are not considered.

Conclusions

For the Iberian Peninsula under climate change a temperature rise is expected while precipitation is projected to decrease. According to the IPCC 'there is medium confidence that droughts will intensify in the 21st century in some seasons and areas, due to reduced precipitation and/or increased evapotranspiration' (IPCC 2012, p. 14). Although Mediterranean species are adapted to summer drought, an impact on forests is expected because already today the conditions in drier regions are near their limit.

In Mediterranean forests competition for both light and water strongly influences tree growth along the entire aridity gradient. The importance of competition even increases with aridity, with some exceptions. This indicates more competitive environments with proceeding climate change. The model indicated that particularly the effect of symmetric competition for water changes along the aridity gradient. Thereby growth reductions due to symmetric competition for water increase stronger than growth reductions due to asymmetric competition for light. This leads to the expectation that symmetric competition might gain importance in shaping Mediterranean forest communities under increased aridity. Shade tolerant and drought sensitive species such as broadleaved oaks and beech might thereby have a relative disadvantage under future climate, additionally to mere abiotic causes. This disadvantage might even be larger when changes of basal area due to site productivity and falling levels of actual asymmetric competition are considered. In any case, expected increase in aridity due to climate change has negative effects on all studied species.

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Supplement

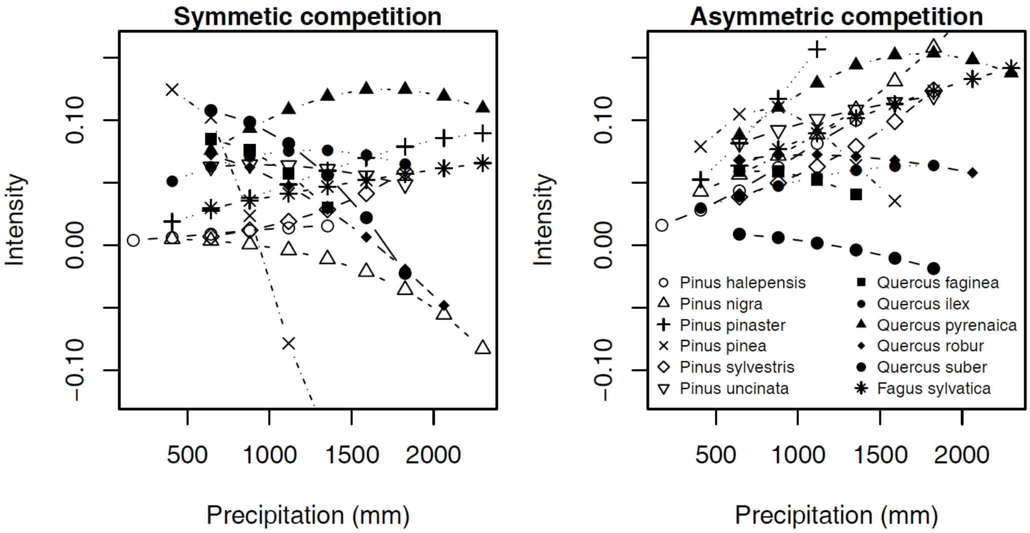

Fig. S1: ‚Actual‘ competition intensity: Intensity of symmetric competition increased for most species or remained more or less unchanged. Asymmetric competition intensity fell for pines and some oaks.

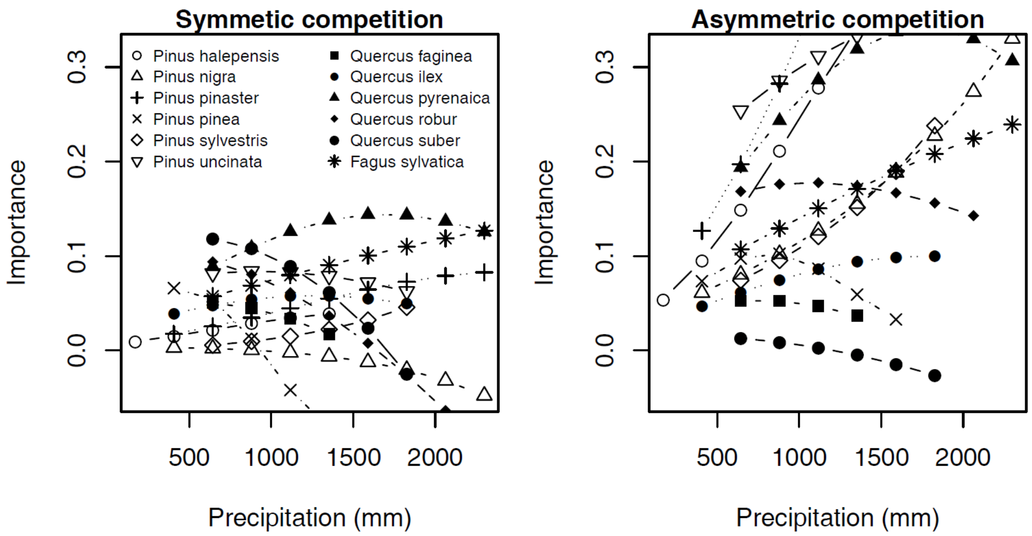

Fig. S2: ‚Actual' competition importance: Actual symmetric competition importance fell for pines. For oaks actual symmetric competition importance did not change considerably with aridity.

Tab. S1: Correlation between variables in the Spanish NFI. relBAI: Relative basal area increment; T: Temperature; P: Precipitation; SC: Symmetric competition; AC: Asymmetric competition.

	relBAI (mm)	**T (°C)**	**P (mm)**	**SC**	**AC**
T	0.05				
P	0.09	-0.31			
SC	-0.17	-0.36	0.35		
AC	-0.06	-0.26	0.25	0.70	
DBH	-0.29	0.03	0.13	0.15	-0.20

Tab. S2: Species ranges in the Spanish NFI for the variables considered in the model. relBAI: Relative basal area increment; T: Temperature; P: Precipitation; SC: Symmetric competition; AC: Asymmetric competition; DBH: Diameter at breast hight. Mean (Minimum-Maximum).

Species	relBAI (mm)	T (°C)	P (mm)	SC	AC	DBH (cm)
P. halepensis	0.043 (0-0.84)	14 (9.9-19)	550 (170-1500)	12 0.39-53)	5.8 (0-43)	200 (75-990)
P. pinaster	0.037 (0-0.55)	11 (6.2-16)	780 (360-2300)	20 (0.39-67)	9.9 (0-63)	210 (75-960)
P. pinea	0.049 (0-1.4)	12 (6.7-18)	850 (320-3100)	24 (0.39-74)	12 (0-67)	260 (62-1100)
P. nigra	0.041 (0-0.81)	14 (9.6-19)	630 (300-1700)	16 (0.4-57)	7.3 (0-56)	260 (75-1300)
P. sylvestris	0.038 (0-1.2)	9 (3.4-15)	960 (430-2000)	26 (0.42-81)	13 (0-80)	230 (54-1100)
P. uncinata	0.025 (0-0.43)	5.8 (1.8-11)	1200 (520-2000)	29 (0.62-76)	15 (0-72)	240 (75-1300)
Q. faginea	0.028 (0-0.41)	11 (6.3-19)	780 (410-1500)	14 (0.39-68)	7.2 (0-49)	200 (75-1600)
Q. ilex	0.025 (0-0.59)	13 (6.6-19)	740 (270-2000)	11 (0.39-70)	6 (0-70)	230 (75-1500)
Q. pyrenaica	0.031 (0-1.1)	11 (6.4-16)	930 (440-2300)	18 (0.4-67)	9.1 (0-66)	210 (75-1500)
Q. robur	0.036 (0-0.77)	12 (6.3-15)	1400 (630-2300)	22 (0.45-80)	11 (0-70)	310 (74-1300)
Q. suber	0.024 (0-1.6)	15 (10-19)	870 (430-1900)	16 (0.43-53)	8.1 (0-50)	300 (75-1500)
F. sylvatica	0.025 (0-0.91)	9.1 (4.2-14)	1200 (590-2500)	27 (0.53-80)	15 (0-80)	290 (72-1600)

Tab. S3: Shade and drought tolerances according to Niinemets and Valladares (2006).

Species	Shade tolerance	Drought tolerance
P. halepensis	1.35	4.97
P. pinaster	2.46	2.2
P. pinea	-	-
P. nigra	-	-
P. sylvestris	1.67	4.34
P. uncinata	1.2	3.88
Q. faginea	-	-
Q. ilex	3.02	1.04
Q. pyrenaica	-	-
Q. robur	2.45	2.95
Q. suber	-	-
F. sylvatica	4.56	2.4

Supplement 1: JAGS-Code for the full model including priors and the error distribution.

```
model{
   for (i in 1:n) { # Distribution of response variable relBAI[i] ~
dgamma(pow(mu[i],2)/pow(sigma,2), mu[i]/pow(sigma,2)) # Model formula
log(mu[i]) <- alpha + beta.P * P[i] + beta.P2 * pow(P[i], 2) + beta.T *
T[i] + beta.T2 * pow(T[i], 2)+ beta.TP * P[i]* T[i] + beta.DBH * DBH[i] +
beta.DBH2 * pow(DBH[i],2) + beta.C * (gamma * SC[i] + (1-gamma)*AC[i]) +
beta.PC * P[i] * (gamma.P * SC[i] + (1-gamma.P)*AC[i]) + beta.TC * T[i] *
(gamma.T * SC[i] + (1-gamma.T)*AC[i]) + beta.PC2 * pow(P[i],2) * (gamma.P
* SC[i] + (1-gamma.P)*AC[i]) + beta.TC2 * T[i] * (gamma.T * SC[i] + (1-
gamma.T)*AC[i]) }

    # Priors for parameters; uninformative
    alpha ~ dnorm(0, 0.001)
    beta.P ~ dnorm(0, 0.001)
    beta.P2 ~ dnorm(0, 0.001)
    beta.T ~ dnorm(0, 0.001)
    beta.T2 ~ dnorm(0, 0.001)
    beta.TP ~ dnorm(0, 0.001)
    beta.DBH ~ dnorm(0, 0.001)
    beta.DBH2 ~ dnorm(0, 0.001)
    beta.C ~ dnorm(0, 0.001)
    beta.PC ~ dnorm(0, 0.001)
    beta.PC2 ~ dnorm(0, 0.001)
    beta.TC_S ~ dnorm(0, 0.001)
    beta.TC2_S ~ dnorm(0, 0.001)
    gamma ~ dunif(0, 1)
    gamma.P ~ dunif(0, 1)
    gamma.T ~ dunif(0, 1)
    sigma ~ dgamma(0.001, 0.001)
    beta.TC <- beta.TC_S / 1000
    beta.TC2 <- beta.TC2_S /1000
}
```

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Manuscript 4: Ecotype mixing as climate change adaptation

Ecotype mixing as climate change adaptation in forests: The interplay of self-thinning and the portfolio effect

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Abstract

Growing conditions for trees are expected to change drastically with climate change. The introduction of presumably better-adapted populations (i.e. ecotypes) from other locations is therefore currently in discussion. One strategy is to grow the ecotype which is best adapted to a future climate. This ecotype will provide optimal yields. However, this strategy ignores uncertainties in climate projections and the long-term performance of particular ecotypes. One way to deal with uncertainty frequently applied in economics is 'conservative bet-hedging' aiming at benefiting from the portfolio effect. The portfolio effect stabilizes yield, however, it also decreases chances for high yields. Competition between tree individuals is likely to be based on the same measure as yield, i.e. performance. Thereby the portfolio effect might be exempted from its drawback of lower chances for high yields by natural self-thinning. In order to evaluate the combined effects of statistical averaging underlying the portfolio effect and self-thinning on yield, a simulation model based on data from common garden experiments was applied. The results show that the portfolio effect is actually largely exempted from its drawbacks via natural self-thinning. Thus, ecotype mixing is a valid opportunity to adapt forest stands to on-going climate change.

Keywords: Provenance, *Pinus nigra*, *Fagus sylvatica*, insurance, simulation model, artificial data, risk management

Introduction

Present climate change is expected to affect forests considerably (Allen et al. 2010, Hanewinkel et al. 2012). Aside from the expected alterations in mean climate conditions, increasing variability and more frequent occurrences of extreme events (IPCC 2012) pose challenges for ecosystem management. Particularly, the management of long-lived ecosystems such as forests faces uncertain future growing conditions, where long-term decisions are essential and need to be made now. One possible way to deal with expected changes is the introduction of individuals of the same tree species but from another ecotype (‘provenance’), which are better adapted to expected future environments (Jentsch and Beierkuhnlein 2010, Beierkuhnlein et al. 2011, Kreyling et al. 2011). With the term ecotype we refer to distinct genotypes (or populations) within a species, resulting from adaptation to local environmental conditions (Hufford and Mazer 2003). Local adaptations to climate, i.e. a higher fitness of local individuals at their home site compared with that of non-local individuals of the same species (Biere and Verhoeven 2008) are commonly found for trees species (e.g. O’Neill et al. 2008, Reich and Oleksyn 2008, Bennie et al. 2010). Therefore, it is hypothesized that best-adapted ecotypes could be selected based on the similarity between current climate at the origin of donor ecotypes and future climate projections for the target area (Kreyling et al. 2011). Growing the best-adapted ecotype would provide optimal yields in the future. However, local adaptations might have evolved in lieu of specific stressors, e.g. frost and drought occurrence eventually controversially for the same set of ecotypes (Kreyling et al. 2012b, C. Wellstein and C. Cianfaglione unpublished manuscript). In addition, climate projections cannot yet be made with sufficient precision, in particular with regard to weather extremes. These two drawbacks hamper the selection of a single best-adapted ecotype for the management of a given stand. Alternatively, mixing of several ecotypes from different regions (presumably containing various adaptations) within the distribution range of a species, has been suggested recently by several authors as a promising silvicultural measure to dampen the adverse effects of climate change (and its uncertainty) and to enhance the adaptive potential of the species (Sgrò et al. 2011, Frascaria-Lacoste and Fernández-Manjarrés 2012, Thiel et al. 2012).

Unlike economics, ecosystem management has hardly introduced systematic risk management accounting for uncertainty into decision making processes

(Knoke et al. 2005, Hanewinkel et al. 2011; but compare to Linder 2000, Hildebrandt and Knoke 2011). One possible way to deal with uncertainty that is frequently applied in economics is conservative bet-hedging aiming at benefiting from the portfolio effect (cf. Childs et al. 2010, Starrfelt and Kokko 2012). The portfolio effect (described by Markowitz 1952) states that a diversification of investments, thus betting on several assets and not only on the apparently best asset, reduces the risk of a complete loss of yield while also limiting the achievement of high yields (Hopper 1999, Boyce et al. 2002, Childs et al. 2010). Several assets not entirely positively correlated together result in lower variability of yield than each single asset due to the effect of statistical averaging. In forests, the portfolio effect can be related to reduced variability of a population property such as biomass, due to complementary dynamics in different components such as species, ecotypes, and individuals of the ecosystem (Cottingham et al. 2001). Ecosystem stability regarding the target property thereby increases due to unsynchronized responses of the components.

Although perception and application of the principle underlying the portfolio effect is gaining attention in ecology, the closely related insurance hypothesis is still more familiar (Yachi and Loreau 1999, Bodin and Wiman 2007). According to the insurance hypothesis ecosystem stability in face of changing environments increases with increasing species diversity due to their individualistic behaviour. In addition to statistical averaging, the insurance hypothesis considers compensatory responses of species. It is assumed that the decline of one species might not only affect the aggregated system property directly (such as total biomass) but also other species due to biotic interactions such as competition (Pretzsch et al. 2013). If species functions in ecosystems are redundant, the decline in one species population can be compensated by the increase of another (Ehrlich and Ehrlich 1981, Walker 1992). Both the portfolio effect and the insurance hypothesis cannot only be applied to different species but also to intraspecific variability, e.g. different ecotypes of the same species.

Proper ecosystem management should maximize the expected net present value of stands and at the same time minimize risk (Yousefpour and Hanewinkel 2009). In forests, growth determines stand biomass and yield. Conservative bet-hedging as opposed to dependence upon the ‘right choice’ of a specific species or ecotype could help adapt forest stands to climate change uncertainties as well as the uncertainty of the (long-term) performance of species or specific ecotypes (Donaldson-Matasci et al. 2008). The complexity of effects and possible advantages of mixed stands is currently intensively studied (Pretzsch et al. 2010, Pretzsch et al. 2012). However, there is an important difference between forest management and other fields of product management. In forests, self-thinning takes place due to competition among individuals. Forest management modifies this selection process further (Huuskonen and Hynynen 2006, Bradford and Palik 2009, Tikkanen et al. 2012). This natural process reduces the number of individuals considerably over time (Pickard 1983, Lonsdale 1990). Thereby, in forests, not all assets (i.e. individual trees) of the portfolio (the stand) remain until the date of harvest (i.e. they die due to competition). While in economic product management a drop out of single assets of the portfolio usually comes along with profit losses, in forests the drop out of tree individuals is necessary to provide space for the surviving trees to grow well. In the present study, two different plantation strategies appear apart from betting on the apparently best ecotype. The first strategy is to grow ecotypes in several single-ecotype stands, the second is to mix ecotypes within one stand (termed 'ecotype mixing'). The type of planting strategy determines whether only individuals of the same or of several ecotypes compete. It can be expected that considering self-thinning together with ecotype mixing gives different results regarding yield depending on the planting strategy.

We consider the competitive ability among tree individuals to be correlated with growth and general performance as yield (Bigler and Bugmann 2003, Shifley et al. 2006, Wunder et al. 2008, Luo and Chen 2011). In order to evaluate the combined effect of statistical averaging and self-thinning with ecotype mixing, we apply a simulation model which we term 'maximum selection'. Compensatory effects, such as increased growth of tree individuals due to a release from competition as suggested in the insurance hypothesis, are not considered in this study. Two alternative models in addition to maximum selection are tested. Hereby lottery sampling is applied as a null-model, including only the effect of ecotype mixing but without a selection mechanism. Ecologically, this means that performance and survival during self-thinning and yield are uncorrelated. By means of this selection method the simulation model can further be related to the mere portfolio effect. Minimum selection is applied as the inversed scenario compared to maximum selection. Ecologically, this means that performance and survival during self-thinning and yield are negatively correlated.

In this study we utilize experimental data from common garden experiments (Kreyling et al. 2012A, Thiel et al. 2012) with important European tree species (*Fagus sylvatica* L. and *Pinus nigra* Arn.) as well as artificial data. Due to experimental constraints, the present study is based on sapling growth. Sapling growth during competition in the self-thinning phase might not adequately reflect the performance of adult trees. Nevertheless, we do not expect a negative correlation between growth at different ontogenetic stages if environmental conditions remain similar during the overall tree life span (or rotation period). By means of artificial data, constituting a known 'truth', mathematical artefacts in methodology can be detected (Austin 1976, Steinbauer et al. 2012). Furthermore, such analysis enables ecologists to test hypotheses in the lack of data. Thus, the simulations were scaled by the experimental data, whereby the artificial data aided in the understanding of the influence of the data structure. Expected yield was simulated for each dataset under different mixing strategies (no mixing and mixing of two to n ecotypes) and selection mechanisms (maximum selection, lottery sampling, minimum selection). This simulation model explores the effect of ecotype mixing, self-thinning, and statistical averaging on expected yield; the risk of low and the chance for high yield. The consequences of an increase of within-stand variability in biomass production by ecotype mixing on expected yields and their uncertainty are assessed. We hypothesize that the reduced risk of low yields due to the portfolio effect are not accompanied by lower chances for high yields in forest stands as a result of self-thinning. If this is the case, ecotype mixing constitutes an opportunity for the adaptation of forest stands to current climate change.

Methods

Experimental data

Here, we focus on two species: *Pinus nigra* (European black pine), a generally drought-resistant species with a patchy (sub-) Mediterranean distribution range (Isajev 2003), which is a potential candidate to replace climate change-threatened conifer species such as *Picea abies* (Norway spruce) in Central Europe. We also consider *Fagus sylvatica* (European beech), which is the dominant native forest species in Central Europe yet considered threatened in the face of climate change (Geßler et al. 2006, Ohlemuller et al. 2006). The data used in this study stemmed from a common garden experiment (EVENT 3) in the Ecological-Botanical gardens of the University of Bayreuth, Germany (Jentsch and Beierkuhnlein 2010, Beierkuhnlein et al. 2011) where the differences in performance among various ecotypes of key European forest species were studied. Seedlings of eight ecotypes of *P. nigra* (Thiel et al. 2012) and seven ecotypes of *F. sylvatica* (Kreyling et al. 2012a) were planted in pots and through 2009/2010 (*P. nigra*) and 2010 (*F. sylvatica*). The *P. nigra* dataset included 42 replicates per ecotype, whereas the *F. sylvatica* dataset comprised of 18 replicates per ecotype. The individuals of both species were irrigated according to the local daily 30-year average precipitation. Application occurred twice a week, using collected rain water. The height of the plants was recorded before and at the end of the growing season. The relative increment rate was determined as the difference between these two measurements in percent (Fig. 1 and 2).

Artificial data

In addition to the experimental data, artificial datasets with the same structure were created using R 2.15.2 (R Development Core Team 2012, R-Code provided in online Supplement 1). The artificial datasets consisted of seven ecotypes characterized by mean growth and variation (normal distributed data represented by 100 individuals). Means of the ecotypes were randomly selected from a normal distribution. Variation within each ecotype was held constant (Fig. 1A). This basic dataset A was modified to assess the influence of data structure on expected yields. Firstly, the means of the ecotypes were multiplied with a constant in order to increase differences between them (Fig. 1B, constant is 10). Next, the basic dataset was modified by creating an over-performing ecotype with significantly higher increment rates than others (Fig. 3C, adding 10 to ecotype g). The following data-scenario was the same as in Fig. 1C, i.e. one over-performer, but also contained an under-performing ecotype (Fig. 1D). The same was done with two over-performers (Fig. 1E), where one data scenario again contained an under-performer (Fig. 1F). The three different selection procedures described below were applied to these datasets in the same way as for the experimental data.

Maximum selection

Maximum selection mimicked an experiment where several individuals were hypothetically planted together. The best performing individual (i.e. best growing) of each plantation was assumed to survive and its growth was measured. The underlying assumption was that performance/growth is closely linked to competitiveness and survival and thereby controls the result of self-thinning (Bigler and Bugmann 2003, Wunder et al. 2008). In the sampling procedure carried out in R 2.15.2 (R Development Core Team 2012, R-Code provided in online Supplement 2) the first step was to create a data subset for each possible combination of ecotypes. The resulting number of subsets corresponded to the binomial coefficient. Then, five individuals were selected randomly from a subset and the value of the best performing individual was saved. The number of five individuals determined the difference between mean performance of the ecotype and the increase due to maximum selection. As the same value for that parameter was used in all simulations, a change only resulted in absolute differences but not relative differences between resulting patterns. Ecologically, this parameter represents the number of individuals which compete in a stand in first order neighbourhood, for which five seems to be a reasonable estimate. This selection rule was repeated 5000 times for each subset. For each subset, the minimum, median, maximum and the quantiles 0.05, 0.25, 0.75, and 0.95 were calculated from the repetitions. Quantile data was then grouped according to the number of ecotypes of the originating subset, i.e. to their degree of ecotype mixing, and the median for each quantile and number of ecotypes was given. From this point onward ‘quantiles’ refers to the median of these quantiles from the sampling procedure. The 0.50 quantile, i.e. the median, means that yield is higher than the quantile value with a probability of 0.5 (thus in 50% of cases). The 0.05 quantile means that yield is higher than the quantile value with a probability of 0.95.

For *P. nigra* with eight ecotypes this resulted in 255 subsets belonging to eight ecotype richness groups and for *F. sylvatica* and the artificial data 127 subsets occurred which belonged to seven ecotype richness groups. The number of data points within the groups differed according to the number of possible combinations. The effect of this was attenuated by the method of calculation of the quantiles.

Lottery sampling

For lottery sampling one random individual was selected out of five randomly chosen individuals instead of the best performing. This simulation procedure was considered as an ecological and methodological ‘null-model’, although we did not test the model for significance but only for the effect that the process maximum selection had (Gotelli 2001). Ecologically, lottery sampling means that survival of self-thinning and yield are uncorrelated. This can occur due to a lack of correlation between performance and self-thinning or due to a lack of correlation between performance and yield. Methodologically, simulations with lottery sampling give the same results as simply mixing the distributions (individuals representing the distributions) of the subsets for each group and calculating quantile values. In case subsets consist of only one ecotype, i.e. no ecotype mixing, the resulting quantiles are the same as the quantiles of a mixed distribution consisting of the single-ecotype distributions. This relates directly to the portfolio effect.

Minimum selection

In order to develop an ecologically ‘worst-case’ model, or a methodologically inversed model, we selected not for the best performing individual (maximum selection), but for the worst, i.e. we selected for the minimum (minimum selection). This represents a negative correlation between performance and self-thinning or a negative correlation between performance and yield (which is considered unlikely). A negative correlation between performance and self-thinning might occur if other factors than competition (mediated by performance) are the main causes of mortality such as herbivory or other disturbances (Franklin et al. 1987, White and Jentsch 2001, Dietze and Moorcroft 2011).

Results

Maximum selection resulted in increasing medians for yield with an increasing number of ecotypes, particularly for datasets with high variability among ecotypes and presence of over-performers. Inter-quantile distances increased along the gradient of ecotype richness, resulting in asymmetrically higher chances for high yield in more diverse stands (Fig. 1). The artificial dataset A, with normally distributed median performances and low variance between the ecotypes, resulted in almost no changes of median yield with increasing number of mixed ecotypes. A higher variance between ecotypes, like in dataset B, led to a stronger increase of the median yield with increasing ecotype richness in one stand. Inter-quantile distances were asymmetric to the benefit of higher yield the more ecotypes were combined. Adding one over-performer to the low variance dataset (dataset C) caused a steep increase of the upper quantiles (0.5, 0.75, 0.95 and maximum) of expected growth response from subsets with three ecotypes to subsets with four ecotypes, with a slight decrease of the median with five or more ecotypes included in the subset. Adding one under-performer did not change these patterns considerably (dataset D). Dataset E, with two over-performers, exhibited a steep increase of expected growth from the single-ecotype subset to subsets with two ecotypes and a stable performance from that point on. Again, adding one under-performer did not change the pattern (dataset F).

Maximum selection of the experimental data for *F. sylvatica* showed an increase of yield from subsets with one ecotype to subsets with two ecotypes for the quantiles 0.05 to 0.75. The expected maximum growth (0.95 and maximum) increased with increasing number of ecotypes. Subsets with more than four ecotypes did not yield additional positive effects on expected growth maxima. For *P. nigra,* with an increasing number of ecotypes, only the upper quantiles (0.95, maximum) increased. However, the increase in expected growth maxima (maximum, 0.95) culminated when 5-6 ecotypes were included. More ecotypes did not have additional positive effects. All other quantiles (minimum, 0.05, 0.25, 0.5, 0.75) remained remarkably stable, independent of the number of ecotypes included. Experimental data for *P. nigra* and *F. sylvatica* thus showed patterns similar to the artificial datasets C ‘one over-performer’ and E ‘two over-performers’. This indicated that the variability among ecotypes was large enough to show an effect for ecotype mixing and that it was not as small as in the artificial dataset A where the effect was not detectable (within versus between ecotype variability). However, *P. nigra* was a rather low variability dataset with only one or two weak over-performers (ecotypes c and e; boxplots in Fig. 2). Under maximum selection, the increase in median profit was therefore low, but still detectable. The dataset of *F. sylvatica* contained over-performers (ecotype a and e) and showed a clear increase of yields with increasing ecotype mixing.

For the lottery sampling, the medians for yield remained unchanged with an increasing number of ecotypes. Inter-quantile distances increased, implying stronger effects with increasing ecotype richness. The influence of under- and over-performers was directly reflected in the quantile lines. Over-performers led to asymmetric patterns in the direction of high yield, under-performers in the direction of low yield (because the mixed distributions were skewed). The effect of statistical averaging causing the portfolio effect appeared in Fig. 1 and 2 by the comparison of the median of the lottery sampling for growing ecotypes separately,

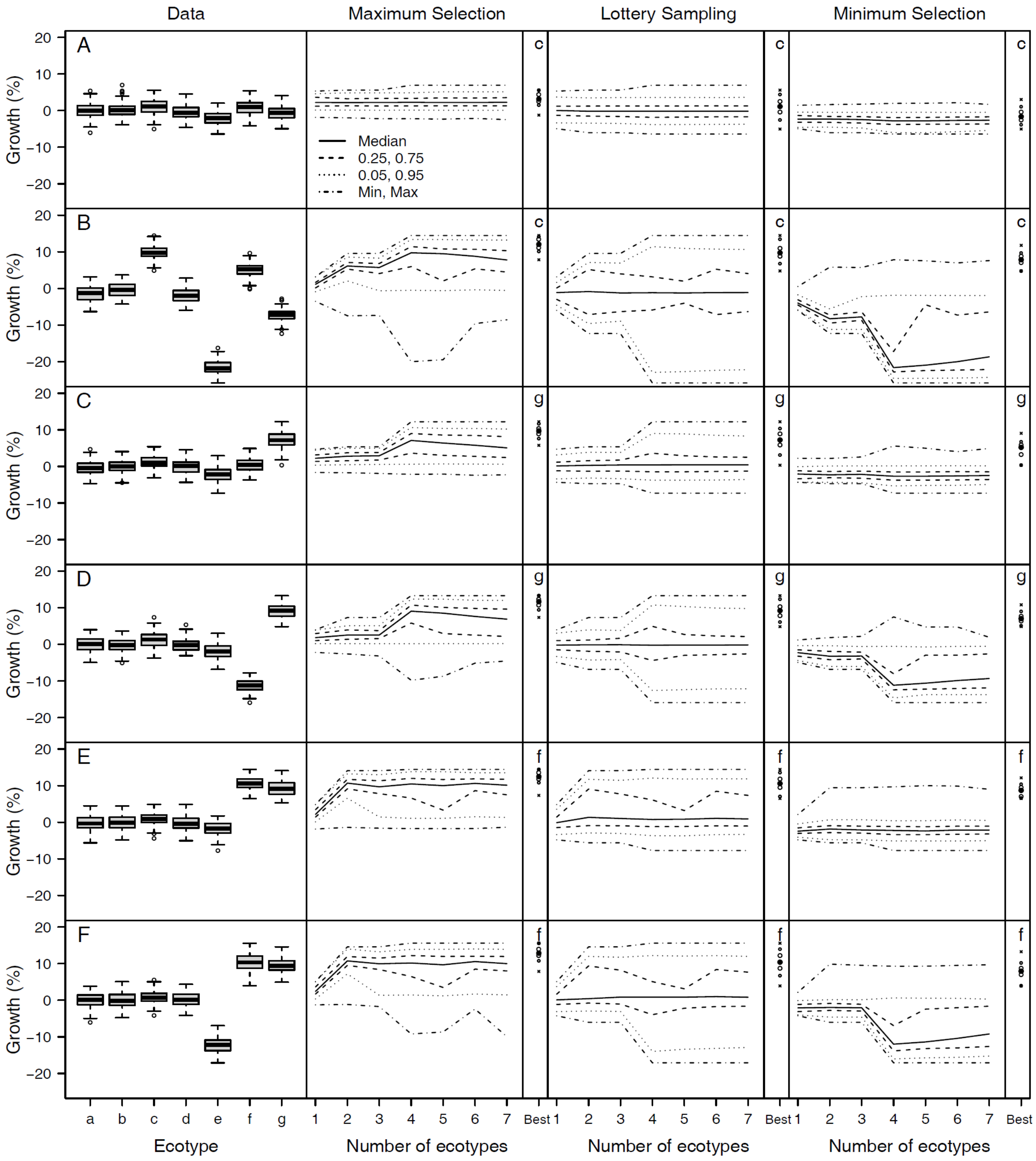

Fig. 1: Artificial data sets. A) Low variance, B) variance increased by factor ten, C) low variance data set with one over-performer, D) with one over-performer and one under-performer, E) with two over-performers and F) with two over-performers and one under performer on the right side, and on the left side the corresponding results of the simulations. Lines represent the medians of the quantiles (0, 0.05, 0.25, 0.5, 0.75, 0.95, 1) of 5000 replicates grouped according to number of ecotypes included.

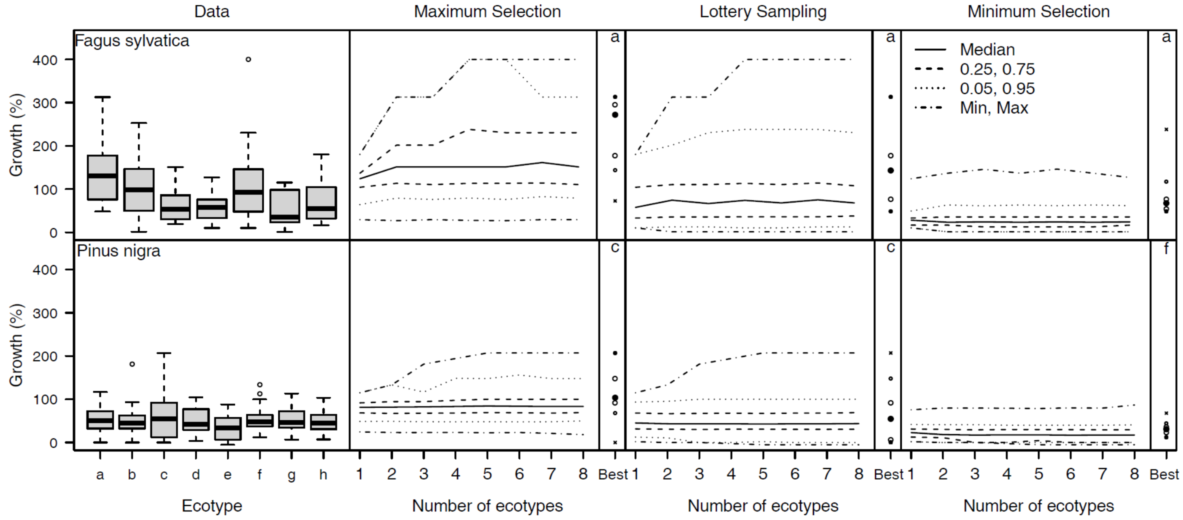

Fig. 2: Data and results of the three selection methods for *P. nigra* and *F. sylvatica*. Lines represent the medians of the quantiles (0, 0.05, 0.25, 0.5, 0.75, 0.95, 1) of 5000 replicates grouped according to number of ecotypes included. Additionally the same quantiles for the best performing ecotype are given.

i.e. single-ecotype stands, with the medians of the data boxplots. A change in the median performance of ecotype g between the datasets A and C only had a weak influence on the median of the simulated performance (Fig. 1). The results for the experimental data for *F. sylvatica* and *P. sylvestris* differed from the artificial data regarding the lower quantiles because they were truncated at zero. Contrary to the artificial data, lower quantiles were therefore close to zero and did not change with ecotype mixing.

For minimum selection, inverse patterns regarding under- and over-performers compared to the maximum selection were observed, i.e. medians for yield decrease with increasing ecotype richness. In the artificial datasets B and D (containing under-performers), minimum selection resulted in a strong reduction of median yields (Fig. 1). Over-performers had almost no effect, only in dataset E with two strong over-performers. For the results of the experimental data the same was true as under lottery sampling, i.e. lower quantiles were close to zero and did not change.

In the introduction it was argued that optimal yield could be reached when the ‘best’ ecotype is chosen (and grown without mixing). Therefore, the simulation results for single-ecotype stands with the highest median yield are also shown for each simulation (Fig. 1; ‘Best’). It appears that for maximum selection the optimal choice actually led to higher yield than mixed stands. Also for the experimental data choosing the best ecotype resulted in higher yield (Fig. 2; ‘Best’). This was also true for lottery sampling and minimum selection, where the difference was even larger.

Discussion

The present simulation study aids to understand the effects of self-thinning and statistical averaging (i.e. the portfolio effect) on expected yields applying ecotype mixing. We hypothesized that the interplay of these two processes linked by performance might exempt the portfolio effect from its drawback of lower chance for high profits (Hopper 1999, Boyce et al. 2002, Childs et al. 2010) while the advantage of stabilization remains (Markowitz 1952). If this is the case, ecotype mixing constitutes an opportunity for the adaptation of forest stands to present climate change, above all to prevent possibly high yield losses. Although we only explore intra-species diversity in terms of ecotypes, these results also apply to the species level (i.e. mixing species instead of ecotypes).

In the present study, two different plantation strategies are addressed as opposed to betting on the apparently best ecotype. The first strategy of growing ecotypes in separate stands is directly related to the classical portfolio effect with its advantage of stabilization of products compared to betting on the assumed best ecotype under high uncertainty. In this strategy, single-ecotype stands can be considered as assets of a portfolio of stands. For the portfolio effect the expected yield of each single asset is compared to the expected yield of the bundle of assets. The expected yield of the portfolio has a lower variability than the expected yield when only one asset with unknown performance was chosen. However, the opportunity provided by the process of self-thinning does not apply for this planting strategy as self-thinning would only take away individuals of the same ecotype.

The second planting strategy is ecotype mixing. Only when ecotypes are actually mixed in the same stand do they compete, and the beneficial effect of self-thinning can occur (individuals as assets, stand as portfolio). However, mixing of ecotypes results in mixed distributions. Assuming lottery sampling, expected yield in such stands is the same as the expected yield for the portfolio of single-ecotype stands. However, the variance of a mixed distribution is larger than the variances of the single distributions in case their means differ (Boes 1966).This is the reason for the divergence of the quantile lines representing the probabilities to obtain a yield equal or lower than that value, with increasing ecotype richness (Fig. 1 and 2). The uncertainty of the median yield is therefore higher for the strategy of ecotype mixing than for a portfolio of single-ecotype stands. Thus, in case the reaction of ecotypes is not known, and under the assumption of lottery sampling, the median yield is not stabilized by ecotype mixing as compared to single-ecotype stands (finding 1).

However, under the assumption that both, selection and yield are determined by performance, ecotype mixing leads to higher median yield than a portfolio of single-ecotype stands (maximum selection). This is due to self-thinning removing low performance individuals from the stands. By this, especially low quantiles are increased considerably as compared to lottery sampling and minimum selection. The more over-performers are among the ecotypes, the earlier the median increases (probability larger than 0.5 that over-performer is in the mixture). If maximum selection is an appropriate model for the interplay of performance, self-thinning and yield, ecotype mixing increases the chance for high yield but does not increase the risk of low yield despite an increase of within-stand variability. However, yield is not as high as it could be under the optimal choice of the best performing ecotype. The portfolio effect is thereby not entirely but largely exempted from its drawback of lower chances for high yields (finding 2).

Patterns for the experimental data are similar to the artificial datasets with one and two over-performers and show an increase of expected yields under ecotype mixing. This points to the opportunity that the intra-species variability for *F. sylvatica* and *P. nigra* have a structure, which results in a positive effect of ecotype mixing (for low variability datasets ecotype mixing has no effect). The results for the experimental data differ from the artificial data because they have a lower boundary of growth (zero). Under-performers are therefore limited and the lower quantiles change less with ecotype mixing. The other patterns described above are found for the experimental data, especially for *F. sylvatica* while the effects are rather small for *P. nigra*. This is caused by the lack of strong over-performers in the *P. nigra* dataset. Contrary to the data used in the present study, former studies have found high intra-specific differences on a genetic level not only for *F. sylvatica* (Konnert 1995, Vornam et al. 2004) but also for *P. nigra* (Aguinagalde et al. 1997, Varelides et al. 2001, Jagielska et al. 2007, Lucic et al.

2010). These findings imply that, particularly for species with large intra-specific differences within their distribution range, ecotype mixing might ensure productivity of stands under variable/unknown climatic conditions.

Opportunities and drawbacks

Our simulations suggest that increasing the number of ecotypes (or species) can stabilize yield for a given forest stand in accordance with the portfolio effect. In addition, self-thinning based on performance increases the chance for high yield beyond the expectations from the portfolio effect (under the assumption of maximum selection), making forests a special case. Highest yield, however, can still be expected by the use of the best adapted ecotype. Even for maximum selection, the expected median yield is still lower than the one of the best single-ecotype stand but much higher than in the classical case, i.e. a portfolio of single-ecotype stands. One could argue that the local ecotype in combination with silvicultural experience comes closest to this optimal choice under stable environmental conditions. This view is supported by the multitude of studies showing superior performance of ecotypes at their home sites (e.g. O'Neill et al. 2008, Reich and Oleksyn 2008, Bennie et al. 2010). With regard to climate change and the uncertainty of future growing conditions, however, our data suggests that increasing ecotype richness of forest stands is reasonable in order to stabilize yield.

All of these considerations depend on the assumption that maximum selection is a realistic model for the interplay between performances, self-thinning and yield. Seedling growth during competition in the self-thinning phase might not adequately reflect the performance as adult trees. Nevertheless, we would at least not expect a negative correlation between growth at these different ontogenetic stages if environmental conditions remain similar for a tree life span (or rotation period).

Under temporally varying growing conditions, no or even negative correlations between growth during self-thinning and growth later on are hypothetically possible. If selection and self-thinning occur under well-watered conditions, highly drought-tolerant ecotypes cannot profit as strongly as less-drought tolerant ecotypes, they will be outcompeted and disappear from the stand. If conditions then become very dry, these lost ecotypes might, however, be the ones which would grow best or, in the worst case, be the only ones which would survive. Such scenarios would tend towards minimum selection where ecotype mixing could even result in a loss of yield. Under the influence of climate change, self-thinning occurs along a climatic gradient and could possibly comprise of such effects. Nevertheless, ecotype mixing allows for the postponement of the decision on which ecotype to plant to a latter and possible better informed point in time. Examples of such trade-offs between adaptations to different environmental stressors have been found (Hereford 2009), e.g. soft, broad leafs being beneficial against shading but disadvantageous against drought (cf. Niinemets and Valladares 2006, Hallik et al. 2009).

Extreme climatic events represent another case where mortality can occur independently of performance. Selection towards tolerant ecotypes will not occur prior to these events. Drought and heat-waves emerge as the main reasons for tree mortality (Allen et al. 2010) and it remains unclear whether this mortality is related to performance. Other factors that can influence survival during self-thinning include, e.g., herbivory, diseases and sensitivity to pollution (Franklin et al. 1987, Dietze and Moorcroft 2011).

Until now, the introduction of species or ecotypes from warmer or drier regions is proposed to counter the negative impacts of rapid climate change in Europe (Bolte et al. 2009, Rose et al. 2009, Beierkuhnlein et al. 2011, Kreyling et al. 2011, Pedlar et al. 2011, Wortemann et al. 2011). General plasticity in terms of growth is assumed to be smaller for stress tolerant species and ecotypes (Grime 1977, Valladares et al. 2005, Sánchez-Gómez et al. 2006, Aranda et al. 2010, but see also Gimeno et al. 2008). Particularly for *P. nigra,* growth differentiation among ecotypes is found to be more likely on productive sites, which will lower yield when good conditions exist (Varelides et al. 2001). For *F. sylvatica,* general differences in growth among ecotypes are reported as well (Jazbec et al. 2007). A concentration on a particular drought adapted species or ecotype might therefore lead to yield reductions and thereby limit the effectiveness of the introduction of new ecotypes for climate change mitigation (Richter et al. 2012). These considerations emphasize the necessity to better understand the interplay between self-thinning and performance, both early on and later in the ontogenetic development of single trees in order to make optimal use of ecotype mixing. With a better understanding, management measures regarding thinning such as low or crown thinning, ecological thinning and commercial thinning (Huuskonen and Hynynen 2006, Bradford and Palik 2009, Tikkanen et al. 2012) could further improve the benefits of ecotype mixing.

The introduction of non-local ecotypes might further have important genetic consequences which are likely irreversible (Frascaria-Lacoste and Fernández-Manjarrés 2012). The introduction of non-local genes (Savolainen and Kärkkäinen 1992) might lead to hybridization which might lead to a disruption of co-adapted gene complexes through recombination and might result in outbreeding depression (Hufford and Mazer 2003, Lefèvre 2004). The introduction of non-local genotypes might additionally result in the demographic or genetic swamping of local genotypes and consequently the loss of local adaptations (Lesica and Allendorf 1999). Hybridization, genetic swamping or loss of local adaptations might have negative consequences for performance and intraspecific biodiversity, which are not only unwanted from the foresters viewpoint, but also where nature conservation is concerned (Hooper et al. 2005).

Model reconsideration & further research

The present simulation study constitutes a highly simplified representation of the processes which actually occur in forest stands. Particularly the representation of self-thinning appears to be critical for final conclusions about ecotype mixing. In the present study, we assume that yield is positively correlated with performance and that the correlation of self-thinning and performance can change from a positive one to a negative one. Maximum selection assumes a positive correlation between performance (determining competitiveness) and the survival of the self-thinning phase, which relates to regular mortality (Keane et al. 2001, Bigler and Bugmann 2003), while lottery sampling assumes no correlation between performance during self-thinning and yield. Survival of self-thinning can even be negatively correlated with performance when adaptation trade-offs are considered, represented by minimum selection. Aside from the model for self-thinning mechanisms, also the data contain some constraints. In the present study, the simulation of ecotype mixing is based on experimental data of one growing season, in which one-year old saplings were grown under long term mean conditions. This experimental design provides a basis for the assessment of the opportunities provided by the classical portfolio effect together with ecotype mixing for climate change adaptation. It lacks, however, the option to test self-thinning and long-term performance under variable climatic conditions. In order to paint a more realistic picture, experimental data are required in which individuals are exposed to ‘normal’ conditions for several years in order to select towards these conditions before being subjected to extreme climatic conditions (Jentsch and Beierkuhnlein 2010). Hereby, possible trade-offs for stability and plasticity as well as adaptation trade-offs could appear.

These considerations show that the conclusions based on our abstract simulation model cannot directly answer whether ecotype mixing will be successful at a particular site. Which of the described cases actually applies to a particular site, i.e. the impact of climate time series (occurrence of climatic extremes such as drought) and disturbance regimes together with adaptation trade-offs could be further assessed by the application of more complex models together with site-specific expert knowledge and empirical data. Data from experimental studies are particularly useful because experiments can be designed specifically (Luo et al. 2011). Existing gap models and landscape models can be adapted to such specific research questions by the implementation of the following involved processes (Pretzsch et al. 2007): Climate in sufficiently high spatio-temporal resolution (Lasch et al. 1998), disturbance regimes (Schumacher et al. 2006, Colombaroli et al. 2010) and mortality (Manusch et al. 2012).

Conclusions

The trade-off between stabilizing yield and low chances for high yield due to the portfolio effect does not apply for forestry. If selection during self-thinning is based on tree performance, increasing the number of assets (ecotype richness, species richness) leads to better chances for high yields without impeding the well-known reduced risk of strong losses. Increasing ecotype (or species) richness is therefore a promising management option for uncertain future environmental conditions for which best-adapted ecotypes or species cannot be determined. If, however, growth during self-thinning and growth afterwards are not positively correlated, e.g. if mortality is uncorrelated with growth due to single extreme events, this positive effect of mixing can be lost. A negative effect of increasing within-species richness appears unlikely, although genetic consequences such as outbreeding depressions, genetic swamping or loss of local adaptations need to be explored. A better understanding of the self-thinning process under increasingly variable climate conditions is required to make optimal use of ecotype (or species) mixing in forest management.

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Supplement

Supplement 1: R-Code to create the artificial datasets.

```
### Create data
data<- vector("list", 9)
np <- 7   # Number of ecotypes
means <- rnorm(np, mean=0, sd=1)  # Mean performance of ecotypes
data[[1]] <- createData(means=means, sds=rep(2, np))
data[[2]] <- createData(means=means*10, sds=rep(2, np))
data[[3]] <- createData(means=means+c(0,0,0,0,0,0,+10), sds=rep(2, np),
ni=100)
data[[4]] <- createData(means=means+c(0,0,0,0,0,-10,+10), sds=rep(2, np),
ni=100)
data[[5]] <- createData(means=means+c(0,0,0,0,0,+10,+10), sds=rep(2, np),
ni=100)
data[[6]] <- createData(means=means+c(0,0,0,0,-10,+10,+10), sds=rep(2,
np), ni=100)
save(data, file="…/artifDat.RData")

### Plot data
abc<- paste(letters[1:9], ")", sep="")
windows(width=7, height=7)
par(mfrow=c(3,3))
for(i in 1:length(data)) boxplot(response~ prov, data=data[[i]], ylab="",
xlab="Provenance", col="lightgrey", main=abc[i], ylim=c(-15, 17))
```

Supplement 2: R-Code used for maximum and minimum selection and lottery sampling applied on the artificial data.

```
### Load data: provenances differ in their means, not in standard
deviations
load(".../artifDat.RData")
##################################################################
### Variable values for SIMULATIONS
response <- "response" # Name of response column in dataset.
ns <- 5      # Number of individuals of same provenance which "compete"
by func.
funcs <- c(max = function(x) max(x), lottery=function(x) sample(x, 1),
min=function(x) min(x))
reps <- 5000
resultnames <- paste("Daten/", c("maximumSelection.RData",
"lotterySampling.RData", "minimumSelection.RData"), sep="")

### SIMULATIONS: max, lottery and minimum.
for(j in 1:length(funcs)){
  result<- vector("list", length(data))
  print(paste(Sys.time(), " Start Simulation with function ",
names(funcs)[j],
  ".",sep=""))
  for(i in 1:length(data)){ print(i) result[[i]] <- simulate(data[[i]],
response=response, n=ns, func=funcs[[j]], replicates=reps) result[[i]]
$data <- i }

  Sys.time()
  result<- do.call(rbind, result)
  save.image(resultnames[j])
}
```

Manuscript 5: Disturbance interactions

Towards a better understanding of forest disturbance interactions: Lessons from a strategic model

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Abstract

Forests are subjected to multiple disturbances shaping their structure and species composition. These disturbances, e.g. fire, bark beetles, windthrow and drought, interact with each other, rendering estimations of shifts in disturbance regimes due to environmental changes difficult. Assessing the character of interactions, i.e. whether interactions are positive or negative, is generally challenging and a common framework for their quantification remains missing. However, empirical studies often find that positive interactions predominate and even form closed feedback loops. Since systems containing such interactions are considered to be mostly unstable, the question arises why and under which conditions forest persist.

Based on a concept of disturbance interactions derived from empirical studies a mathematical model is developed. It suggests the most parsimonious way to quantify interaction strength and shows that although there were exclusively positive interactions and self-feedbacks among disturbances, a stable equilibrium might exist. At the same time the interaction model reveals that at least in this highly simplified model a threshold for interaction strengths can be specified that characterizes the stability or instability of a given forest. Furthermore, disturbance interactions might cause only a minor part of overall disturbances regimes and alterations in climate are of much higher importance. The model clearly names the system components involved in disturbance interactions, i.e. disturbance history, physical features, direct interactions, and the indirect effect of amount of susceptible forest. It enables quantitative study comparisons and a discussion about the overall importance of disturbance interactions.

Keywords: Climate change, system analysis, regime shift, tipping point, temperate forest

Introduction

Disturbances are one key factor influencing forest structure and dynamics. Dale et al. (2000) identify 'fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, wind storms and ice storms' as the key forest disturbance agents. These disturbance regimes are influenced by physical and vegetational features such as climate and tree species composition. Forests are exposed to multiple interacting disturbances, and synergistic effects as well as mutual reinforcement of disturbance regimes are important but difficult to predict (Turner 1989). Interactions between disturbances might be positive or negative and can contain one or more feedback loops. While the direct influence of climate on disturbances has been frequently assessed (Seidl et al. 2009, Lorz et al. 2010) the contribution of interactions to the total abundance of disturbances has not been conclusively quantified to date (Veblen et al. 1994, Bebi et al. 2003, Jactel et al. 2012). Nevertheless, recently an increasing number of studies on disturbances and also their interactions are conducted (Seidl et al. 2011). With the future climate expected to systematically alter disturbance regimes (Dale et al. 2001) an improved understanding of disturbance interactions is called for in order to evaluate and manage future risks (Ayres and Lombardero 2000).

To take a step forward in the understanding how disturbance interactions affect in particular temperate forests we suggest a concept of disturbance interactions that we believe is implicitly used in the planning and statistical analysis of empirical studies but has not yet been explicitly outlined and studied. Based on this concept of disturbance interactions we develop a mathematical model. This model helps to assess theoretical consequences, particularly for forest persistence under multiple positive feedback loops, and facilitates quantitative comparisons between results of empirical studies.

Disturbance interactions

We first like to introduce into the topic of disturbance interactions and show that mostly positive interactions between disturbances have been found. A review of each disturbance and of their interactions within this article could not nearly satisfy the complexity and diversity of forests. We therefore relegate to already existing, comprehensive reviews on each interaction for elaborated descriptions (references are given below) and give only a simplified overview.

With disturbance interaction we refer to a change of occurrence probability for one disturbance due to another. This has a different implication than the compounde effect of several disturbances on an ecosystem. The compound effect of disturbances occurring in a short time span has in some cases been found to be stronger than just the sum of the effects of each single disturbance (Paine et al. 1998). For example Kulakowski et al. (2013) found that the compound effect of fire and windthrow on a Sub-alpine forest in north-western Colorado could change the species dominance from conifers to *Populus tremuloides* while each single disturbance does not have such high impact. The probability of conjoint occurrences of several disturbances increases when the probability for each single disturbance becomes higher, either due to climatic changes, land use changes, or also due to positive interactions. Thus changes of occurrence probability of disturbances due to interactions and compound effects of co-occurring disturbances on an ecosystem are closely linked research topics and have to be considered together in evaluations of impacts of changed disturbance regimes on ecosystems.

The focus of this study lies on interactions including bark beetles. This biotic disturbance is particularly interesting in the face of climate change because their life history is highly sensitive to temperature (Logan et al. 2003, Wermelinger 2004, Jonsson et al. 2007), and because bark beetle outbreaks interact with fire, drought and windthrow. The multiple ways in which bark beetles interact with fire, drought, and windthrow, particularly in temperate coniferous forests, are integrated by our conceptual framework that highlights two main feedback loops (Fig. 1). This framework constitutes the basis on which the mathematical model of disturbance interactions is developed.

Fire

Recent review papers on the basis of numerous empirical studies show that the interaction between bark beetles and fire is complex and two-sided (Parker et al. 2006, Jenkins et al. 2008, Negron et al. 2008). Firstly, on small scale, fire creates suitable habitats by partial burned and therefore weakened trees. This results in a relaxation from intraspecific competition within bark beetle populations. In addition, Geiszler et al. (1980) and others observed special attraction mechanisms of bark beetles to partially burned trees in some cases. Thereby, populations can proliferate and potentially become strong enough to attack healthy trees within the burned area and in the surrounding. In contrast, it has also been found that in some cases fire advances defence of surviving trees by increasing resin flow (Knebel and Wentworth 2007). Secondly, on larger time scales like several years, fire influences stand age structure in a way that inhibits population dynamics of bark beetles (pine: Dordel et al. 2008, Kulakowski et al. 2012; spruce: Veblen et al. 1994, Bebi et al. 2003). Higher fire frequency decreases stand age and thereby decreases bark beetle risk because trees have to exceed a certain age before they can serve as suitable hosts for many bark beetles species (e.g. about 70 years for *Ips typographus*; Veblen et al. 1994). Thus the observed influence of fire on bark beetle infestations depends on the considered time scale. Assessing short term interactions resulted mostly in a positive effect, while studies addressing long term interactions found a negative effect. It is thus of particular interest to distinguish between these mechanisms and to ask which effect outbalances.

Generalizations about the effects of bark beetle on fire characteristics are still unresolved (Hicke et al. 2012) but found (Geiszler et al. 1980, Bigler et al. 2005, Lynch et al. 2006, Parker et al. 2006). During and after bark beetle outbreaks dead and alive fuel accumulates due to injured or killed trees and falling branches. This potentially increases fire severity. However, the amount of fuel accumulation and fuel types depend on the time since bark beetle outbreak and can even change the interaction from positive to negative (Page and Jenkins 2007, Jenkins et al. 2008). Additionally it has to be taken into account that fire risk and severity not only depend on fuel availability but also on weather conditions, ignition frequency and further factors (Berg and Anderson 2006). This can diminish the importance of the positive feedback of bark beetles on the fire regime especially in regions with frequent ‘fire weather’, such as intense drought, high winds and lightning (Bessie and Johnson 1995).

Drought

Recent articles show that the influence of drought on bark beetles is mediated through defence mechanisms of trees (Rouault et al. 2006, Fettig et al. 2007, Jactel et al. 2012). Low intensity drought stress can actually increase tree defence by lowering growth rates and shifting the use of photosynthates to the synthesis of defensive chemicals thus resulting in a negative feedback between mild drought and bark beetle infestation success. In contrast, extended drought or severe drought stress (which usually refers to drought as a disturbance) reduces tree defence and increases the probability of bark beetle outbreaks due to depleted carbon reserves (Christiansen et al. 1987, Berg et al. 2006, Jactel et al. 2012). Therefore, a positive feedback with bark beetle infestations can be assumed for drought stressed trees (Powers et al. 1999, Dobbertin et al. 2007, Hebertson and Jenkins 2008).

Windthrow

The third main forest disturbance interacting with bark beetles is windthrow (Kulakowski and Veblen 2003, Bouget and Duelli 2004, Gandhi et al. 2007). This interaction is mediated through habitat availability. Windthrown injured and killed trees provide suitable habitats for bark beetles because of low or lacking defence mechanisms (Okland and Bjornstad 2003, Hebertson and Jenkins 2007, Schroeder 2007). Killed trees are suitable for bark beetles for about two years until decay has progressed too much (Schmid and Frye 1977). Injured or partially broken trees still have roots connected to the soil and might thus provide easily accessible habitats for several years. Schroeder (2007) found that besides a release from intraspecific competition, an escape from enemies on windthrow areas facilitates a proliferation of bark beetles. Other disturbances producing downed host material (such as avalanches, snow and ice damage) can contribute to the rapid increase of bark beetle populations in the same way (Hebertson and Jenkins 2007). Eriksson et al. (2005) additionally suggest that the effectiveness of colonizations of windthrown trees depends on the population level before the storm. Particularly in years with favourable climatic conditions which might differ across systems, such as winters with low hibernation mortality followed by warm spring temperatures, bark beetles can proliferate (e.g. for genus *Dendroctonus* in forests of North America; Coulson 1979). Healthy trees in the neighbourhood of a windthrow area can be infested due to high bark beetle attack intensity. This increases the probability of an outbreak.

Feedbacks

Since windthrow, drought and fire interact with bark beetles and additionally reinforce each other, a complex interaction system results and it is challenging to estimate how this system will respond to changes in environmental conditions. Within this disturbance interaction framework we identified two closed feedback loops (Fig. 1).

The first possible feedback loop within temperate forests contains bark beetles, fire and drought. Drought does influence both, bark beetle outbreak risk and the probability of wildfires. Fuel properties and amount depend on the drought regime and as a generalization it can be assumed that more frequent and longer lasting phases of drought enhance the probability of wildfires (Cumming 2001, Reineking et al. 2010). However, the interaction between fire and drought is much more specific than indicated. In particular the influence of different drought regimes (respective frequency, time of occurrence and severity) on types of fire, like crown and ground fires, is mediated by the kind of fuel created and differs among forest types. Concurrently to the effect on fire, drought affects bark beetle infestation success by lowering tree defence. Bark beetle outbreaks can at least temporarily alter fuel load of forests and by this influence fire severity. Wildfires reduce bark beetle infestations in the long term indirectly by influencing stand age structure and increase bark beetle infestations directly in the short term by weakening tree defence. The observed character of feedback – positive or negative – hence, depends on the focal time scale. This first feedback loop emphasizes the importance of the considered time scale and thereby of the medium of interaction.

The second feedback loop contains bark beetles, fire and windthrow. It acts similar to the first loop concerning the interactions of bark beetles and fire. Additionally, windthrow enhances fire through fuel creation and concurrently creates

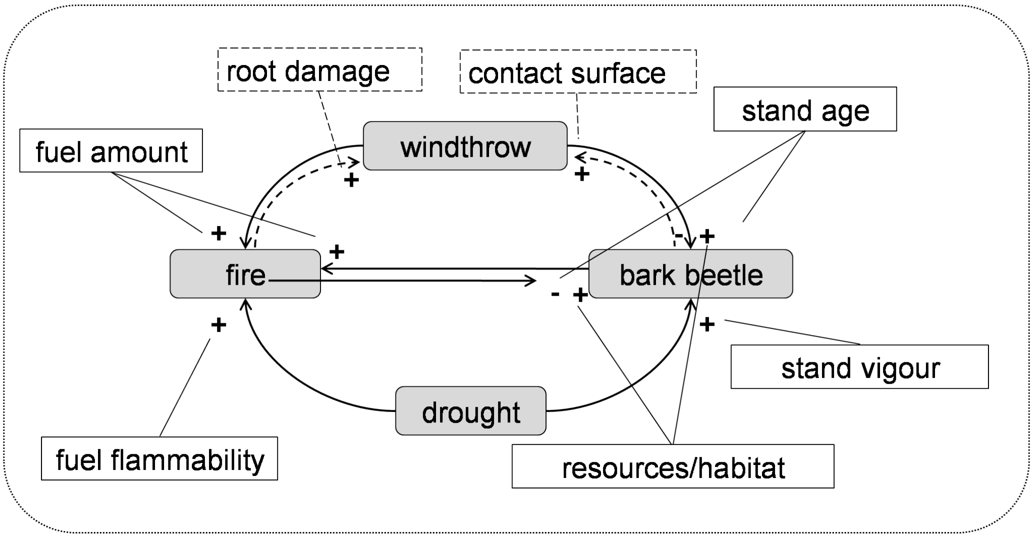

Fig. 1. Conceptual framework of the main disturbance agents and their interactions with a focus on bark beetles. Findings of empirical studies suggest that positive interactions predominate.

suitable habitat for bark beetles. A further interaction between fire and windthrow might be possible, especially for spruce forests. Fire-weakened spruces have been observed to fall in wind storms after wildfires because their shallow roots are damaged (Ryan and Amman 1994, Gibson et al. 1999). On the opposite, fire reduces stand age and thereby reduces susceptibility to windthrow (Kulakowski and Veblen 2002). Additionally, the susceptibility to windthrow is known to be increased at stand edges (Mitchell 1995). Severe bark beetle outbreaks and fire occasional create clearings which could function as contact surface for wind storms. The relative, quantitative importance of these effects is not well studied yet and thus largely unknown. Therefore, these interactions are not considered further within this study.

Concept of disturbance interactions

The basic concept underlying empirical studies is found to be that the current disturbance state of the forest is influenced by past conditions, by physical and vegetational features (e.g. climate, tree species) and additionally by interactions between disturbances. Few empirical studies actually quantify interactions, many only find significant correlations. Additionally, even the character of interaction, i.e. whether it is positive or negative, could not be established unambiguously, especially for bark beetles and fire (Knebel and Wentworth 2007, Hicke et al. 2012). Three main sources hindering an integration of results could be identified. Firstly, different measures for the disturbance impact (e.g. affected area, beetle number, number of killed trees; Bebi et al. 2003, Okland and Berryman 2004, Fettig et al. 2007) and also for the interaction strength (a parameter which characterizes the change of a disturbance due to another one) were used (e.g. effect sizes, regression parameters: Bradley and Tueller 2001, Schroeder and Lindelow 2002, Okland and Berryman 2004, Lynch et al. 2006; importance of a variable in a classification tree: Kulakowski and Veblen 2007, Hebertson and Jenkins 2008; fraction of affected area: Kulakowski and Veblen 2006). Secondly, different time scales ranging from years to decades were considered (Schroeder and Lindelow 2002, Bigler et al. 2005). Direct interactions such as impact of drought or fire on tree defence were thereby conceptually not distinguished from the indirect effect of changes in susceptible forest (e.g. bark beetles infest only older stands) on the amount of newly disturbed forest. Thirdly, data scarcity and shortness of time series limit parameter estimation of statistical models as much as process-based models (Okland and Berryman 2004). This diversity in methodological approaches, naturally emerging due to diverging research interests, funding constrains and possibly a missing common framework, prevented a quantitative comparison of results of disturbance interaction studies as well as the practicability of predictions. However, both, comparison of results among studies and the practicability of predictions are basic principles of science. Furthermore, it prevented to identify important interactions regarding management decisions.

Nevertheless, findings of positive interactions clearly predominate (Fig. 1). Mutual positive feedback is a self-enhancing process in comparison to the self-controlling property of negative feedback. In systems dominated by positive feedbacks we should expect very large effects building up from very small initial causes. When positive feedback loops dominate we will usually observe unstable behaviour (cf. Berryman and Kindlmann 2008 p.11ff). On the other hand, negative feedback loops will tend to control. On a conceptual level this raises the question whether and why forests persist with all interactions being positive. Furthermore, there might exist a tipping point (parameter threshold) for disturbance abundance and/or interaction strength for which being passed the ecosystem will change dramatically in taxonomic composition, structure, ecological functions, and process rates (cf. Folke et al. 2004 on regime shifts in ecosystems). Paine et al. (1998) show a schematic representation of the possible effects of co-occurring disturbances on ecosystems which will happen more often when their individual frequency increases, partly caused by positive interactions: Recovery after multiple disturbances or a long-term alteration of the system. As one example they describe possible changes of boreal forests subjected to the compound effect of wildfires, fragmentation, and logging. Especially for tropical rain forests a tipping point due to disturbances and their interactions is suggested and assessed in numerous studies (Laurance and Williamson 2001, Nobre and de Borma 2009).

Study aims

To improve our understanding of forest disturbance interactions we develop a mathematical model that represents the concept of disturbance interactions found in literature. Contrary to earlier studies profoundly examining the functioning of disturbance interactions, one strength of this mathematical approach is to allow for a general perspective (cf. Grimm 1994). Reduced complexity indeed reduces precision of predictions (Levins 1966) but can help to understand which processes produce at least some of the empirically observed patterns. Application of different approaches on the same topic (profound research together with a bird´s eye view) and their consolidated interpretation strengthens the reliability of conclusions.

In this study we aim at clearly naming the components of the system ‘disturbance regime’ to enable a discussion about their definition and importance. Furthermore, the model illustrates one possible way to define and quantify ‘interaction strength’ facilitating a quantitative consolidation of results of different studies. By means of this model we assess the theoretical consequences of the concept of disturbance interactions for forest persistence under increased disturbance rates and interaction strength (Fig. 1). We ask why and under which conditions forests might persist like they are despite all interactions being positive. We show that even assuming that there are exclusively positive interactions and self-feedbacks a stable equilibrium exists following a condition of stability. At the same time the interaction model reveals that a threshold of the cumulative interaction strengths can be specified characterizing the stability or instability of a given ecosystem (e.g. persistence or collapse) regarding the disturbance regime.

The established interaction model is a non-linear discrete-time model containing parameters for the basic susceptibility of the forest to each disturbance (physical and vegetational features) and one parameter for each direct interaction. Thereby the abundance of a disturbance without considering interactions and the emerging disturbance regime including interactions are conceptually separated. Susceptible area which captures the indirect negative interaction between disturbances due to stand age (or hight in the case of windthrow) is integrated. We do not decide for more complexity because we believe that already in this very simplified model plenty phenomena require understanding. We consider our approach as a point of departure for further model development and discussion on such theoretical approach to assess disturbance interactions.

Methods

Disturbance interaction model

The interaction model is based on an assumption of many empirical studies, namely that the current disturbance state of the forest is influenced by past conditions, by physical and vegetational features (e.g. climate, tree species) and additionally by interactions between disturbances. Within the model only disturbance interactions are explicitly taken into account while physical and vegetational features are represented only generally by a constant. Thus, only the abundance of a disturbance 'without' considering one-way and two-way (mutual) interactions is integrated. The model outcome is the emerging disturbance regime including the effect of interactions. For an exemplary ecosystem with the four disturbances fire (*F*), bark beetles (*B*), windthrow (*W*) and drought (*D*) and the assumption of discrete time the concept can be generally formulated as follows:

$$\begin{aligned} F_{t+1} &= f_1(F_t, B_t, W_t, D_t, S_t) \\ B_{t+1} &= f_2(F_t, B_t, W_t, D_t, S_t) \\ W_{t+1} &= f_3(F_t, B_t, W_t, D_t, S_t) \\ D_{t+1} &= f_4(F_t, B_t, W_t, D_t, S_t) \end{aligned} \quad \text{Eq. 1,}$$

where f_1, f_2, f_3 and f_4 are linear functions relating the past disturbances to the current state and include the physical features (Eq. 1). F_t , B_t , W_t and D_t are the affected fractions of the total area in m^2/m^2 at time *t*. S_t denotes the fraction of the total area which can be affected by a disturbance in a particular time step, i.e. the fraction of insusceptible forest G_t , e.g regrowing forest (Eq. 2).

$$S_t = 1 - G_t \quad \text{Eq. 2}$$

By including susceptible area it is possible to separate direct interactions between disturbances (such as host material for bark beetles, alive/dead fuel load for wildfires) from the indirect effect of stand structure influencing the amount of susceptible forest (the less susceptible forest the less disturbances occur). Insusceptible area G_t is updated in each time step as it depends on the disturbance history. It increases by newly disturbed area and is diminished by regrown forest area (Eq. 3).

$$G_t = G_{t-1} \cdot \left(1 - \frac{1}{\tau}\right) + \Sigma R_{t-1} \quad \text{Eq. 3}$$

G_t: Insusceptible forest.
τ: Recovery time. Time during which a regenerating forest is insusceptible for disturbances.
R_t: Newly disturbed area. Area size for each time step.

As time step we select 'one year', because disturbances in temperate ecosystems often occur preferentially in particular seasons. In temperate regions bark beetles (e.g. *Ips typographus*) proliferate from spring to autumn, windthrow typically occurs in autumn, wildfires and drought usually in the hot and dry summer period. In order to simulate and analyse this model, functions relating past disturbances to the current state are specified. We follow Schroeder and (Lindelow 2002), who employed linear functions of type $y = a + b \cdot x$ in a regression. The intercept *a* can be interpreted as an ecosystem's inherent susceptibility to the disturbance caused by unobserved factors while slope *b* of the regression line represents the incidence of the disturbance due to another, e.g. the interaction strength. Using this parsimonious approach the model for four interacting disturbance regimes can be formulated, in matrix notation, as follows (Eq. 4):

$$R_{t+1} = (c + M \cdot R_t) \cdot S_t$$

$$\begin{pmatrix} F_{t+1} \\ B_{t+1} \\ W_{t+1} \\ D_{t+1} \end{pmatrix} = \left(\begin{pmatrix} c_F \\ c_B \\ c_W \\ c_D \end{pmatrix} + \begin{pmatrix} m_{FF} & m_{BF} & m_{WF} & m_{DF} \\ m_{FB} & m_{BB} & m_{WB} & m_{DB} \\ m_{FW} & m_{BW} & m_{WW} & m_{DW} \\ m_{FD} & m_{BD} & m_{WD} & m_{DD} \end{pmatrix} \cdot \begin{pmatrix} F_t \\ B_t \\ W_t \\ D_t \end{pmatrix} \right) \cdot S_t \qquad \text{Eq. 4.}$$

R_t: Disturbance regime at time t
S_t: Susceptible area at time t
c: Base value. Disturbance regime due to physical features before accounting for interactions.
M: Interaction matrix
For definition of the other parameters refer to Tab. 1.

R_t is the affected proportion of the total susceptible area at time *t*, and *c* (c_F, c_B, c_W, c_D) are the ecosystem inherent susceptibilities to each disturbance due to physical features before accounting for interactions (Tab. 1). The parameters in matrix *M* (m_{FF}, m_{BF}, m_{BB} etc.) quantify the interaction, i.e. the increase or decrease of the incidence of one disturbance due to another. To give an example, a value $m_{BF} = 1$ means that for each bark beetle disturbed forest unit in the previous time step the same amount would be added to the base value of fire c_F.

Variables and parameter values are constrained by their definitions:

$$\begin{gathered} 0 \leq F, B, W, D, G, S, c, c_F, c_B, c_W, c_D \leq 1 \\ F + B + W + D + G + S \leq 1 \end{gathered} .$$

As a special case of the model recovery time is set to one, resulting in S_t being constantly 1. This assumption yields a linear, affine, discrete time model. In matrix notation, a model with the four main forest disturbances (fire *F*, bark beetles *B*, windthrow *W*, drought *D*, Tab. 1) is presented in Eq. 5

$$R_{t+1}=(c+M\cdot R_t)$$

$$\begin{pmatrix} F_{t+1} \\ B_{t+1} \\ W_{t+1} \\ D_{t+1} \end{pmatrix} = \begin{pmatrix} c_F \\ c_B \\ c_W \\ c_D \end{pmatrix} + \begin{pmatrix} m_{FF} & m_{BF} & m_{WF} & m_{DF} \\ m_{FB} & m_{BB} & m_{WB} & m_{DB} \\ m_{FW} & m_{BW} & m_{WW} & m_{DW} \\ m_{FD} & m_{BD} & m_{WD} & m_{DD} \end{pmatrix} \cdot \begin{pmatrix} F_t \\ B_t \\ W_t \\ D_t \end{pmatrix} \quad \text{Eq. 5,}$$

where all symbols retain the meaning as in Eq. 4 and with the following parameter constrains:

$$\begin{array}{c} 0\leq F, B, W, D, c, c_F, c_B, c_W, c_D \leq 1 \\ F+B+W+D\leq 1 \end{array} .$$

Model analysis

An important advantage of the model formulation as a linear, affine, discrete-time model is that standard techniques for its analysis are available (Otto and Day 2007, Maxima 2011). The equilibria are calculated by solving the linear equation system for $R_{t+1} = R_t$ (Eq. 5). Stability of the equilibrium is analysed by means of eigenvalues and eigenvectors of matrix M. For the real part of the leading eigenvalue ranging between -1 and 1 an equilibrium is stable. From this condition parameter ranges for a tipping point can be calculated for which being passed the forest collapses. If an equilibrium exists the system can approach its equilibrium smoothly or it can spiral towards it. When the leading eigenvalue has a complex part, the system will spiral towards its equilibrium (or to infinity for the unstable case).

The generality of the results derived with the linear model are supported using the augmented interaction model considering susceptible area depending on regeneration time (Eq. 2-4; Supplement 2).

Case studies

The interaction model is applied in four case studies with increasing degree of complexity. They constitute special cases of the general model (Eq. 5). Technically the most simple case study contains only one disturbance regime and no self-feedback: $W_{t+1}=c_W$. This trivial case can be augmented by a term for self-feedback: $W_{t+1}=c_W+m_{WW}\cdot W_t$. However, our study addresses disturbance interactions. Therefore, as first case study the most simple model for a disturbance regime including a one-way interaction but no self-feedback is formulated. It describes the influence of windthrow on bark beetles like in the study of Schroeder and Lindelow (2002). This case study is valid for all systems consisting of two disturbances with a one-way interaction, thus one disturbance influencing the other but not the other way around (drought/fire, drought/bark beetle, windthrow/fire, windthrow/bark beetle).

$$\text{Case study 1:} \quad \begin{pmatrix} B_{t+1} \\ W_{t+1} \end{pmatrix} = \begin{pmatrix} c_B \\ c_W \end{pmatrix} + \begin{pmatrix} 0 & m_{WB} \\ 0 & 0 \end{pmatrix} \cdot \begin{pmatrix} B_t \\ W_t \end{pmatrix} \quad \text{Eq. 6}$$

For the second case study the most simple model formula for the disturbance regime of fire and bark beetles is used. This model contains a mutual interaction and thereby a closed feedback loop. The self-feedback terms are again set to zero.

$$\text{Case study 2:} \quad \begin{pmatrix} F_{t+1} \\ B_{t+1} \end{pmatrix} = \begin{pmatrix} c_F \\ c_B \end{pmatrix} + \begin{pmatrix} 0 & m_{BF} \\ m_{FB} & 0 \end{pmatrix} \cdot \begin{pmatrix} F_t \\ B_t \end{pmatrix} \quad \text{Eq. 7}$$

Study 3 assesses the influence of additionally considering self-feedbacks. This results in the following model:

$$\text{Case study 3:} \quad \begin{pmatrix} F_{t+1} \\ B_{t+1} \end{pmatrix} = \begin{pmatrix} c_F \\ c_B \end{pmatrix} + \begin{pmatrix} m_{FF} & m_{BF} \\ m_{FB} & m_{BB} \end{pmatrix} \cdot \begin{pmatrix} F_t \\ B_t \end{pmatrix} \quad \text{Eq. 8.}$$

The fourth study aims to model the concept of disturbance interactions derived from literature including the disturbances bark beetles, fire, windthrow and drought (Fig. 1, Eq. 9).

$$\text{Case study 4:} \quad \begin{pmatrix} F_{t+1} \\ B_{t+1} \\ W_{t+1} \\ D_{t+1} \end{pmatrix} = \begin{pmatrix} c_F \\ c_B \\ c_W \\ c_D \end{pmatrix} + \begin{pmatrix} m_{FF} & m_{BF} & m_{WF} & m_{DF} \\ m_{FB} & m_{BB} & m_{WB} & m_{DB} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \cdot \begin{pmatrix} F_t \\ B_t \\ W_t \\ D_t \end{pmatrix} \quad \text{Eq. 9}$$

Estimates for the parameters, aiming at representing a mixed temperate forest (e.g. spruce or pine forests) are used to investigate the influence of different parameter values. In practice parameter values certainly differ among forests. Beyond that, the main disturbances could not only involve fire, bark beetles, windthrow or drought but others such as avalanches or inundations. There is no study quantifying all parameter values for one specific forest, thus we obtain parameter values

M and c for an exemplary, hypothetical temperate forest from several empirical studies (for references see Tab. 1). For interaction parameter values the linear relation between disturbances based on given data are calculated or values directly given are taken (e.g. Lynch et al. 2006 for an increase in fire risk due to repeated mountain pine beetle infestations). A recent meta-analysis of Jactel et al. (2012) is the most comprehensive study we find. While they report a mean interaction strength of 0.23 for drought and bark beetles, we choose the more extreme value 1.2 as reported by Dobbertin et al. (2007). This value still lies within the confidence limits calculated by Jactel et al. (2012). In order to identify critical values of interaction strength which determine stability we do a sensitivity analysis for m_{FB} and m_{BF}.

Base values c of disturbances (disturbance regime without interactions) cannot be observed and measured directly. They can only be calculated for example as the intercept, i.e. an extrapolation of a linear regression (assuming constant interaction strength). In any case, the analytical analysis of our model reveals that base values do not influence the general model behaviour but only the sum of disturbed area. We therefore decide for example values which are similar to those in empirical studies (cf. Splechtna and Gratzer 2005) and seem suitable to describe a temperate forest. Additionally the base values are increased systemically in ten equidistant steps to a maximum value in order to test for sensitivity (Tab. 1). Thereby, we aim at exemplary assessing possible changes in disturbance regimes due to climate change and further show the possibility of contra-intuitive system behaviour.

Case studies 1-4 are supplemented by simulations with the model accounting for forest regeneration, thus with $\tau > 1$ (R-Code in Supplement 2; results shown only for case study 4). Thereby, the indirect negative effect of stand structure on disturbance abundance is represented. Simulations are conducted in 2.15.2 (R Development Core Team 2012) for both the linear and non-linear model (R-Code in Supplements 1 and 2).

Tab. 1. Parameter descriptions and estimates used in case study 4.

Symbol	Description	Value current/max	References
Fire F			
c_F	Fire importance before interaction	0.005/0.01	In temperate forests fires have low impact in comparison to windthrow and bark beetles.
m_{FF}	Self-feedback of fire.	-0.10	Consumption of fuels within the stand.
m_{BF}	Influence of bark beetles on fire	0.10	Lynch et al. (2006): 0.11
m_{WF}	Influence of windthrow on fire	0.05	Since windthrow acts similar to bark beetles (e.g. creation of fuels) we chose a value in the same range as for bark beetles.
m_{DF}	Influence of drought on fire	0.50	We assume that drought stronger influences fire than bark beetles. Main problem is the definition of drought.
Bark beetle B			
c_B	Bark beetle importance before interaction	0.01/0.02	Fettig et al. (2006): 0.00 to 0.03 Dobbertin et al. (2007): 0.10 Bradley and Tueller (2001): 0.01
m_{FB}	Influence of fire on bark beetles	0.25	Bradley and Tueller (2001): 0.25
m_{BB}	Self-feedback of bark beetles	0.10	High population density leads to higher attack densities in the following year.
m_{WB}	Influence of windthrow on bark beetles	0.10	Schroeder and Lindelow (2002): 0.40 Eriksson et al. (2006): 'low' Kulakowski and Veblen (2003): 0.00
m_{DB}	Influence of drought on bark beetles	1.20	Dobbertin et al. (2007): 1.2 Jactel et al. (2012): 0.29
Windthrow W			
c_W	Windthrow importance before interaction	0.05/0.07	Splechtna and Gratzer (2005)
m_{FW}	Influence of fire on windthrow	0.00	Windthrow is mainly driven by climate, e.g. storms
m_{BW}	Influence of bark beetles on windthrow	0.00	
m_{WW}	Self-feedback of windthrow	0.00	
mt	Influence of drought on windthrow	0.00	
Drought D			
c_D	Drought importance before interaction	0.02/0.04	Drought is mainly driven by climate and soil properties.
m_{FD}	Influence of fire on drought	0.00	
m_{BD}	Influence of bark beetles on drought	0.00	
m_{WD}	Influence of windthrow on drought	0.00	
m_{DD}	Self-feedback of drought	0.00	

Results

Case study 1: One-way interaction

The equilibrium of the simplest model comprising the one-sided interaction for bark beetles and windthrow (Eq. 6) is reached when $W_{t+1} = W_t$ and $B_{t+1} = B_t$. The values of the disturbance fractions at equilibrium $R*$ are given by:

$$B^* = c_B + m_{WB} \cdot c_W \quad \text{Eq. 10.}$$
$$W^* = c_W$$

As long as these values are within the range of definition a stable equilibrium exists (eigenvalue of matrix $M = 0$).

Case study 2: Two-way interaction

The equilibrium of the simplest model comprising the mutual interactions for bark beetles and fire (Eq. 7) can also be calculated by solving $F_{t+1} = F_t$ and $B_{t+1} = B_t$. The values of the disturbance fractions at equilibrium $R*$ are given by:

$$F^* = \frac{c_F + m_{BF} \cdot c_B}{1 - m_{BF} \cdot m_{FB}}$$
$$\text{Eq. 11.}$$
$$B^* = \frac{c_B + m_{FB} \cdot c_F}{1 - m_{FB} \cdot m_{BF}}$$

To analyse stability of the equilibrium eigenvalues and eigenvectors of the interaction matrix M (Eq. 7) are calculated. Local stability analysis shows that an equilibrium exists for $-1 < m_{BF} \cdot m_{FB} < 1$. The system spirals for $m_{BF} \cdot m_{FB} < 0$ towards the equilibrium in case an equilibrium exists, or to infinity, when the equilibrium condition is not fulfilled.

A time series with different starting conditions is calculated to illustrate the model behaviour (Fig. S1 and S2). Depending on the system state, the importance of each disturbance increased or decreased approaching the equilibrium.

Case study 3: Two-way interaction considering self-feedbacks

More complexity was added to the model by considering self-feedbacks of disturbances (Eq. 8). The equilibrium state $R*$ of fire and bark beetles is given by

$$\begin{aligned} F^* &= \frac{c_F \cdot (1 - m_{BB}) + m_{BF} \cdot c_B}{m_{BB} \cdot m_{FF} - m_{FF} - m_{FB} \cdot m_{FB} - m_{BB} + 1} \\ B^* &= \frac{c_B \cdot (1 - m_{FF}) + m_{FB} \cdot c_F}{m_{BB} \cdot m_{FF} - m_{FF} - m_{FB} \cdot m_{BF} - m_{BB} + 1} \end{aligned} \quad \text{Eq. 12.}$$

Changes in the base values (c_F, c_B) are directly reflected in the equilibrium of each disturbance. In addition, the equilibrium changes due to the self-feedback of the other disturbance, respectively. Adding more disturbances with self-feedbacks results in a further product of the base value for each self-feedback combination.

For this system an equilibrium exists when the following condition, similar to the model of case study 2 but modified by the self-feedbacks, is fulfilled:

$$m_{FF} + m_{BB} + m_{FF} \cdot m_{BB} - 1 < m_{BF} \cdot m_{FB} < m_{FF} + m_{BB} + m_{FF} \cdot m_{BB} + 1 \quad \text{Eq. 13}$$

The system spirals for $m_{BF} \cdot m_{FB} < \frac{-(m_{FF} - m_{BB})^2}{4}$ (Eq. 14), thus for positive interactions we generally do not expect spiralling. Spiralling exclusively occurs when the interaction parameters have different signs (Fig. S3).

Case study 4: Conceptual framework

Finally, the conceptual framework derived from literature can be formulated (Eq. 9, Fig. 1). The equilibrium $R*$ of the interaction system is calculated as

$$\begin{aligned} F^* &= \frac{(1 - m_{BB}) \cdot c_F - m_{BF} \cdot (-m_{WB} \cdot c_W - m_{DB} \cdot c_D - c_B) - c_W \cdot m_{WF} \cdot (1 - m_{BB}) - (1 - m_{BB}) \cdot m_{DF} \cdot c_D}{m_{BB} \cdot m_{FF} - m_{FF} - m_{FB} \cdot m_{BF} - m_{BB} + 1} \\ B^* &= \frac{(1 - m_{FF}) \cdot c_B - m_{FB} \cdot (-m_{WF} \cdot c_W - m_{DF} \cdot c_D - c_F) - c_W \cdot m_{WB} \cdot (1 - m_{FF}) - (1 - m_{FF}) \cdot m_{DB} \cdot c_D}{m_{BB} \cdot m_{FF} - m_{FF} - m_{FB} \cdot m_{BF} - m_{BB} + 1} \\ W^* &= c_W \\ D^* &= c_D \end{aligned} \quad \text{Eq.15.}$$

The conditions for stability and spiralling are the same as in case study 3 (Eq. 13, 14) because the lower half of the interaction matrix contains only zeros. The existence of an equilibrium is not affected by changes in base values *c*, it can only be influenced by the interaction matrix *M*. This means a potential tipping point for forest collapse only depends on interaction strength, not on base values. With the parameter estimates of Tab. 1, an equilibrium exists and small changes in the parameters do not change this. We can identify critical values of interaction strength by a systematic variation of m_{BF} and m_{FB} (Fig. 2). The higher one of the interaction parameters the narrower is the possible range for the other one maintaining stability. With the given values of the exemplary temperate forest disturbances approach the equilibrium smoothly (Eq. 14). Spiralling can only occur if the interaction parameters have different signs (Fig. S3).

The disturbance regime R_t without and with interactions differs due to positive interactions. For those disturbances not influenced by others, e.g. windthrow and drought, there is no difference whereas the values for bark beetles and fire increase due to positive interactions (Fig. 3). This leads to a rank reversal compared to the base values. The total disturbed forest at equilibrium for the ‘current’ values given in Tab. 1 increases from 8.5% without to 15.3% with the effect of interactions.

As a further experiment the base values of the disturbances are increased systematically having in mind the impact of climate change (Fig. 3). At the maximum for all disturbances their base values sum up to 14% (Tab. 1) and the fraction of disturbed area increase to 27% due to interactions. The results demonstrate that the increase of each disturbance is amplified due to positive interactions but forest still persists. Especially forest are disturbed by bark beetles increases considerably due to their positive interactions leading to a rank reversal compared to the base values *c*.

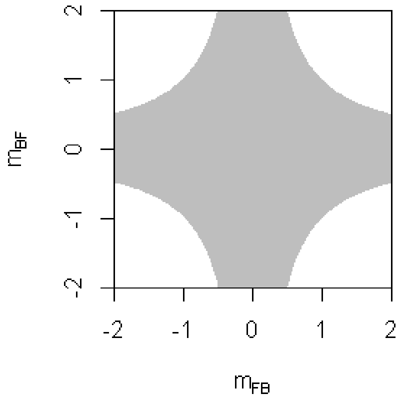

Fig. 2: Visualization of the stability condition (Eq. 13) for case study 4 (conceptual framework) with varying m_{FB} and m_{BF} for constant self-feedbacks given in Tab. 1. For both interaction parameters smaller than one an equilibrium generally exists.

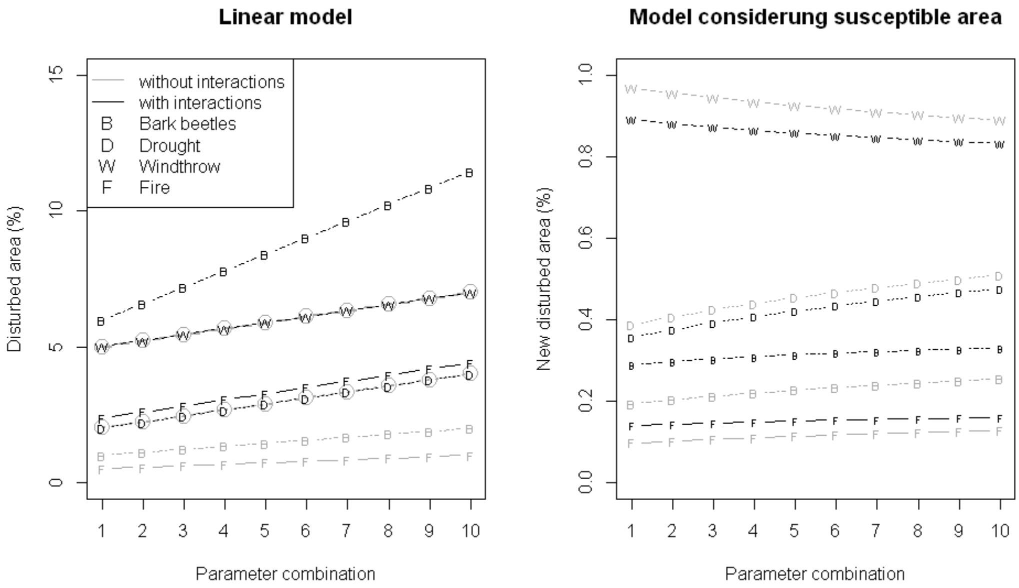

Fig. 3:Disturbance regimes for increasing base values for case study 4 (conceptual framework): Base values were increased systemically in ten equidistant steps from the minimum (=‘current’) to a maximum value (Tab. 1) for both, the linear and the non-linear model. Grey lines in the figure for the linear model constitute the base value combinations 1 to 10. Disturbance regimes were calculated with and without interactions to show the importance of their consideration and quantification for estimations of future disturbance regimes.

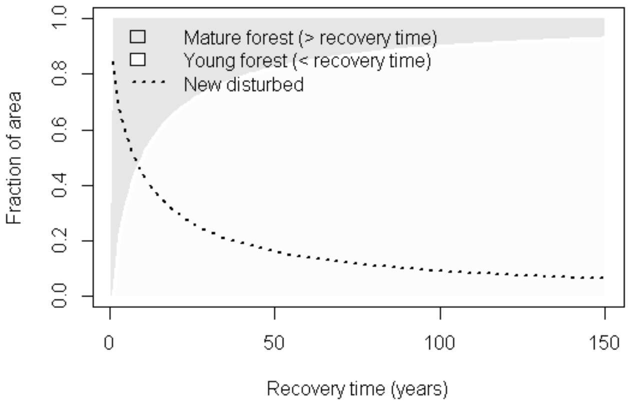

Fig. 4: Disturbance regimes and resulting fraction of forest area considering recovery time. The fraction of mature forest (older than recovery time τ) decreases while young stands become more frequent. Fraction of new disturbed area becomes less with increasing recovery time.

Non-linear model considering regeneration time

Simulations with the non-linear model considering regeneration time result in the same general behaviour regarding equilibria and the condition for the existence of an equilibrium, thus the tipping point. However, mature forest naturally decreases with increasing recovery time τ while young stands, i.e. younger than τ increase. Subsequently, the fraction of newly disturbed area also decreases with increasing recovery time to more realistic values (Fig. 4). For the parameter values chosen in case study 4 (Tab. 1) and a recovery time of $\tau = 50$ time steps, 18% of the total area remains mature forest (= forest older than 50 time steps). The rest of the forest is younger than 50 time steps or newly affected by disturbance. At each time step 1.7% of the total forest is newly affected by one of the four disturbances. Interactions cause a share of 1.9% of these disturbances.

In the scenario with maximal base values only 12% mature forest remains while each time step 1.8% of the forest is disturbed. Interactions cause a share of 0.9% of these disturbances. In the model considering recovery time the increase of total disturbances in each time step in the climate change scenario is less than in the linear model due to the effect of susceptible area (Fig. 3).

Besides of the total amount of disturbances R_t the model outcome differs also in the resulting order of disturbance abundances. Whereas in the model without recovery time the abundance increases from drought, fire, windthrow to bark beetles, here the abundance increases from fire, bark beetles, drought to windthrow. Remarkably, windthrow decreases despite an increasing base value. This is caused by the interplay of direct interactions (M) and the indirect effect of a reduction of susceptible forest (S, τ).

Discussion

Currently, the results of disturbance interaction studies are difficult to consolidate and quantitative comparisons are prevented because of differences in observed parameters, considered time scales and statistics between existing empirical studies. However, such quantification would mark substantial progress towards evaluating the ecological and economic relevance of interactions for example in climate change studies. As one step towards this goal we formulate a concept of disturbance interactions and define its components. At the example of temperate forests and with the help of a mathematical model the possible consequences of this concept are assessed. The main findings of this study are the following:

1. Temperate forests persist even when all disturbance interactions are positive. When interaction parameters and self-feedbacks are less than one the equilibrium condition is fulfilled for most cases, even with exclusively positive interactions. There is evidence from empirical studies, that these parameter ranges apply to temperate forests despite our parameter estimates only represent one possible scenario. At the same time the model illustrates that a tipping point for interaction strength necessarily exists – under the assumed model structure. This tipping-point exclusively depends on the interaction strength and not on base values. This is particularly interesting in case the interaction strength is not constant as assumed within this study but changes positively with disturbance abundance (plug in functions depending on R_t or S_t in matrix M instead of constants). The finding that interaction strength determines a possible tipping point for forest stability complements the question if forests could suffer a regime shift due to an increase of disturbance rates due to changes in physical features like climate.

2. The conjoint effect of direct and indirect interactions can lead to counter-intuitive changes in disturbance regimes. The non-linear model incorporating forest regeneration time helps to clarify the difference between direct interactions between disturbances due to e.g. increased host material for bark beetles, and the naturally negative interaction due to the amount of susceptible forest. The decrease of windthrow despite all base values increased, also the one for windthrow, can be attributed to the effect of reduction of susceptible forest. In this example setting the strong increase of base values of bark beetles and fire (c_B, c_F) in conjunction with positive mutual feedbacks (m_{BF}, m_{FB}) leads to an increase of these disturbances and a reduction of susceptible forest (although assuming negative self-feedback of fire m_{FF}). In contrast, windthrow decreases relative to the total forest because the increase in its base value c_W cannot compensate for the effect of reduced susceptible area. Thereby, the effect of the negative interaction mediated by susceptible area even causes a rank reversal in disturbance regimes compared to the model without susceptible area. This shows

the importance of an explicit definition of the susceptible forest area relative to the total area particularly when comparing studies, e.g. at different sites or for time periods. This further motivates research on stand age dependence of susceptibility to each disturbance to be able to quantify the susceptible area.

3. The share of disturbances caused by interactions (and not by their base values) is rather low and depends not only on interaction strength but also on recovery time. In the given example a share of 1.9% of disturbances can be attributed to disturbance interactions and not to the physical and vegetational causes (climate, forest structure). This share becomes lower when longer recovery times are assumed. In the scenario for increasing disturbance base values ('climate change') the disturbance share caused by interaction even decreases. According to our parameter estimations and concept of disturbance interactions, they have low importance compared to changes of disturbances due other factors. However, in the model no feedback is included that leads to a change of interaction strength with increasing disturbances.

Besides the three main findings this study provides a definition of 'interaction strength' and thereby a way of quantification. Quantification is needed to enable comparisons between findings of different empirical as well as simulation studies and to make projections for changed conditions. Interaction strength is here defined by a parameter which is identical with the 'slope'-coefficient of a linear regression (like in Schroeder and Lindelow 2002). We choose a linear interaction characterized by one single parameter because the principle of parsimony seems to be reasonable in the face of little knowledge about the true character of disturbance interactions (e.g. about possible shapes of a more complex function). Additionally, a linear regression has the advantage that it can be calculated with very few data, in the most extreme case with as few as two data points. Another finding relevant under the aspect of quantification is that interactions observed at a particular time step might depend on the system state. Because disturbances could spiral towards the equilibrium if one interaction parameter for a mutual interaction is negative the observed interaction between to time steps could be negative. Finding interaction strength and equilibrium of a real disturbance regime (e.g. the long term mean of disturbed area) can therefore be complicated, specifically in short time series, and it should be discussed in the analysis and interpretation of empirical data.

The above described results are based on several model assumptions entailing deficiencies which is unavoidable in ecological modelling. In the following we discuss the main shortcomings of our disturbance interaction model and at the same time urge future research opportunities.

- Most apparent is the linearity of interactions (parameters in *M*) causing constant interaction strengths over all disturbance rates. To represent disturbances that interact non-linearly (Jactel et al. 2012) functions could be used instead of the static interaction matrix *M* (Eq. 4). This would allow for the influence of one disturbance on another to increase or diminish with increasing disturbance intensity. However, this would substantially complicate the parametrization of the model for a real ecosystem.

- Susceptible forest area could be calculated for each disturbance separately accounting for differences in susceptibility to each disturbance during successional stages. Furthermore, regeneration time differs among forest types and disturbances influencing the amount of susceptible forest by the rate of regrowth.

- Feedback on the disturbance base values is not considered. While the effect of physical features is tested in the ‘climate change scenario’ by increased but constant base values, an interaction with the vegetation was not considered. An example for changes in vegetation and feedback on the disturbance regime are Mediterranean fire adapted and fire facilitating pine forests (Fernandes and Rigolot 2007).

- The interaction model does not consider different duration of disturbance events and contact times (Sanchez et al. 1995). All disturbances are modelled at the same time scale. As time step (of disturbance events, contact times and regeneration) one year is selected although it is known that the duration differs among disturbances. Windthrow events for example happen almost instantaneously, while bark beetle outbreaks can last several years. Another reasonable choice of time step would be the contact time, thus the time which the disturbance event continues to have an effect. Since contact time differs between disturbances this leads to a more complex model which we decide to avoid for the benefit of comprehensibility.

- The interaction model is not spatially explicit. Thereby, we subsequently assume, like usually in spatially non-explicit models, that all disturbances influence each other over the entire landscape (well-mixed system). Actually, this is not exact; the influence rather declines with distance. Consideration of a decline in the influence of one disturbance to another with increasing distance attenuates the interaction strength and thereby the total abundance of disturbances at the landscape scale. With increasing size of the assumed landscape the ‘characteristic scale’, e.g. a radius discussed by de Roos et al. (1991), is passed and a consideration of space becomes more important. This could be assessed by converting the model into a grid-based simulation model. Examples of how explicit considerations of space might alter the predictions of ecological models have been summed up for example by Tilman and Kareiva (1997). Despite space is one important property of disturbances, within this study we decided to avoid making additional assumptions on how interaction strength declines with distance (exponentially, linearly etc.).
- An arguable assumption is the choice of a deterministic model. Stochasticity could cause the disturbance regime to fluctuate around equilibrium. The effect of stochasticity could be assessed in further studies by analysing a equivalent stochastic discrete-time model (Wilson 1998, Allen and Burgin 2000).

Within this study we keep all other processes governing disturbance regimes simple despite interactions, and relegate to simulation models which constitute a promising approach to overcome shortcomings of conceptual, mathematical models, unfortunately at the cost of transparency. Simulation models such as the forest landscape model LandClim (Schumacher et al. 2004, Schumacher et al. 2006) can account for the complexity and multitude of processes and dependencies in real ecosystems, such as stand structure and species composition, spatial patterns of affected and susceptible area and more. There is an increasing number of modelling studies on disturbances employing landscape or gap models. Unfortunately, until now most of them do not explicitly analyse interactions between disturbances. Seidl et al. (2007), for instance, combined the forest patch model PICUS v1.4 (Seidl et al. 2005) with the bark beetle model PHENIPS (Baier et al. 2007) and aimed at adding windthrow in future model versions facilitating an assessment of disturbance interactions in further studies. Schumacher and Bugmann (2006) already assessed the conjoint effect of tree growth, climate and the large-scale disturbances fire, windthrow and management on forest dynamics using the forest landscape model LandClim but did not quantify interaction strength. Based on the forest model LANDIS the interaction of forest pest insects and fire were recently assessed (Chen 2011, Chen et al. 2011) and a significant mutual interaction between larch caterpillar and fire was found but no effect size reported. A further study conducted by James et al. (2011) assessed interactions among fire, spruce budworm, and logging. They found that their combined effect is greater than the sum of their individual effects but unfortunately also did not report the effect sizes of their ANOVAs which could be used as measure for interaction strength. A nice example enabling a quantitative comparison was published by Simard et al. (2011) who combined empirical data with the fire behaviour model NEXUS.

Nevertheless, while the above issues warrant further research, our model already in its present form gives us valuable lessons. Only when quantifications are given similarities and differences among studies regrading underlying concepts can be identified and findings of simulation and empirical studies can be consolidated. This helps to increase the understanding of disturbance regimes, to improve estimations of interaction strength and their importance relative to other drivers. Reasonable projections of disturbance regimes under current and changed environmental conditions like expected due to climatic changes are the basis of well-grounded management.

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Supplement

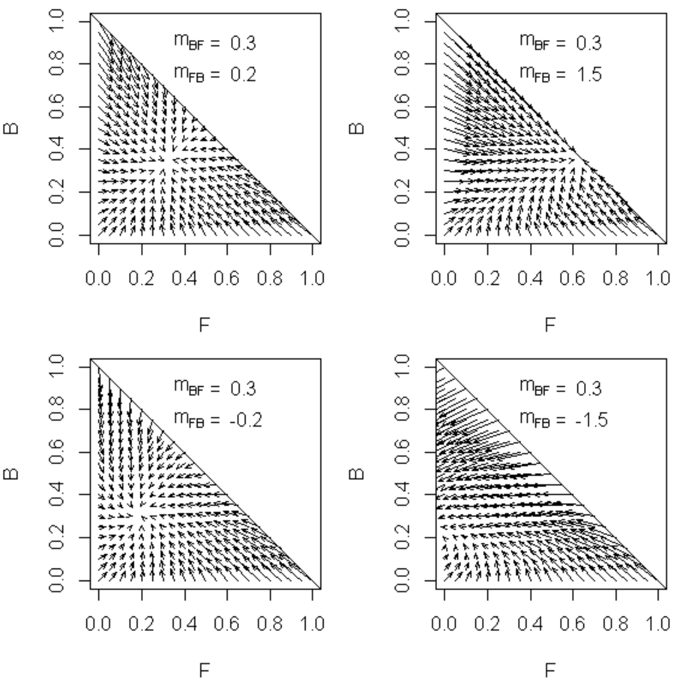

Fig. S1: Vector fields of the two way interaction model without self-feedback (case study 2) with $c_F = c_B = 0.25$. For $-1 < m_{BF} \cdot m_{FB} < 1$ an equilibrium exists despite mutual positive feedbacks in the first example. For $|m_{BF} \cdot m_{FB}| > 1$ no equilibrium exists. In the positive case the disturbances affect the entire landscape, in the negative case the disturbance with negative response approaches to zero.

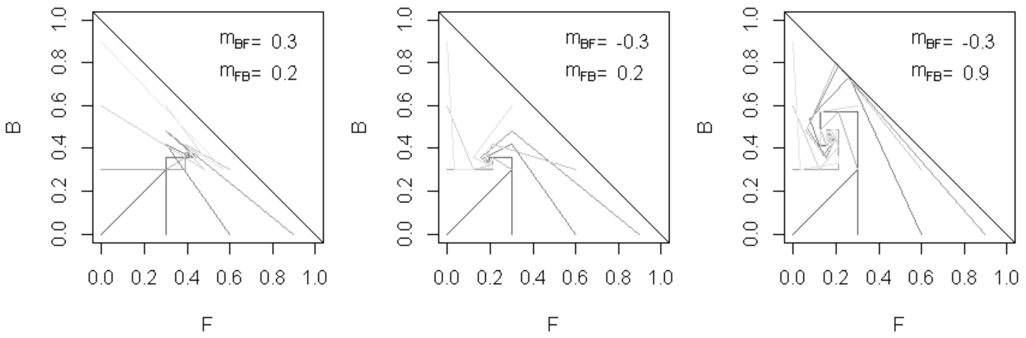

Fig. S2: Phase space graphs for nine different starting values for c_F, $c_B = 0.25$ and three different interaction scenarios for the two-way interaction model without self-feedback (case study 2). In the first case the system approaches its equilibrium smoothly whereas in the other two cases it spirals toward the equilibrium. R-Code in Supplement 1.

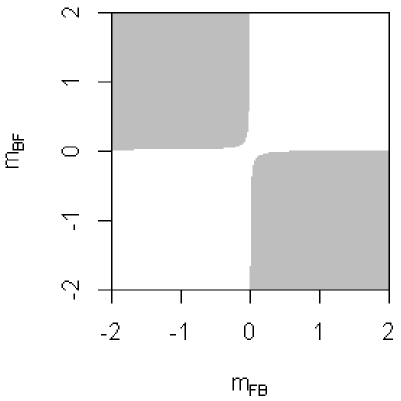

Fig. S3: Visualization of the condition for spiralling (Eq. 14) for case study 4 (conceptual framework) with varying m_{FB} and m_{BF} for constant self-feedbacks given in Tab. 1.

Supplement 1: R-Code of the model function for calculating time series.

```
### INTERACTION MODEL
model <- function(state=c(F=0, W=0, D=0, B=0), baseValues, M,
timesteps=10){

  # Arguments
      # state:  Fraction of disturbed area. Vector of length 4 with
entries for
      #         fire, windthrow, drought and bark beetle affected area.
      # baseValues: Ecosystem susceptibility due to environmental
factors.
      #         Importance of each disturbances before interaction. Same
order
      #         as state.
      # M:      Interaction matrix. 4 x 4 matrix with values for the
interaction
      #         strength in the order given by state.
      # timestep: Number of timesteps to be calculated.
  #  Value
      # result: Matrix with 4 columns with the state in each timestep.

  result <- matrix(NA, nrow=timesteps, ncol=4,
    dimnames=list(NULL, c("F", "W", "D", "B")))
  result[1,] <- state
  for(t in 1:(timesteps-1)){ ### MODEL FORMULA: state <-
cbind(baseValues, M) %*% c(1, state) if(sum(state) > 1) state <-
state/sum(state) result[t+1,] <- state }

  result
}

### EXAMPLE
M <- matrix(0, nrow=4, ncol=4, dimnames=list(c("F", "W", "D", "B"),
   c("f", "w", "d", "b")))
M["F",] <- c(0, 0, 0, -0.3)
M["B",] <- c(0.2, 0, 0, 0)
```

```
start <- expand.grid(F=seq(0,1, by= 0.3), B=seq(0,1, by= 0.3))
start <- start[rowSums(start)<1,]


for(i in 1:nrow(start)){
  res <- model(state = c(start[i,"F"], 0,0, start[i,"B"]),
     baseValues = c(0.3,0,0,0.3), M = M, timesteps=50)
  if(i == 1) { plot(res[,"B"] ~ res[,"F"], type="l", ylim=c(0,1),
xlim=c(0,1), xlab="F", ylab="B") abline(1,-1) }
else { lines(res[,"B"] ~ res[,"F"]) }

}
```

Supplement 2: R-Code of the model considering forest recovery time τ.

```
### INTERACTION MODEL CONSIDERING RECOVERY TIME
model.recovery <- function(state=c(F=0, W=0, D=0, B=0, G=0), baseValues,
M, timesteps=10, tau=1){

 # Arguments
      # state:  Fraction of disturbed area and recovering/insusceptible
area.
      #         Vector of length 5 with entries for fire, windthrow,
drought
      #         and bark beetle affected area and additionally recovering
area.
      # baseValues: Ecosystem susceptibility due to environmental
factors.
      #         Importance of each disturbances before interaction. Same
order
      #         as state.
      # M:      Interaction matrix. 4 x 4 matrix with values for the
interaction
      #         strength in the order given by state.
      # timestep: Number of timesteps to be calculated.
      # tau: Recovery time. Time needed until a disturbed forest patch
becomes
      #         susceptible again.
  #  Value
      # result: Matrix with 5 columns with the state in each timestep.

  result <- matrix(NA, nrow=timesteps, ncol=5,
    dimnames=list(NULL, c("F", "W", "D", "B", "G")))
  result[1,] <- state
  for(t in 1:(timesteps-1)){ disturbedArea <- sum(state) recovery <-
(1/tau) * disturbedArea ### Recovery susceptibleArea <- 1 -
(disturbedArea - recovery) ### MODEL FORMULA: state[1:4] <-
cbind(baseValues, M) %*% c(1, state[1:4])* susceptibleArea state[5] <-
disturbedArea - recovery if(sum(state) > 1) state <- state/sum(state)
result[t+1,] <- state }

  result
}
```

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Supplement

List of manuscripts and specification of own contribution

Comments and inputs from discussions with the co-authors are covered under ‘concept and discussion’. ‘Analysis/programming’ covers data handling, statistical analysis and the programming of simulations models. ‘Writing’ is understood as the actual formulation of sentences and paragraphs.

Manuscript 1

Thrippleton, T.[#], Dolos, K., Perry, G. L. W., Groeneveld, J., Reineking, B. (accepted). **Simulating long-term vegetation dynamics using a forest landscape model: The post-Taupo succession on Mt. Hauhungatahi, North Island, New Zealand**.

Concept and discussion 30%, analysis/programming 25%, figures 0%, writing 10%, first submission in October 2012 (accepted in New Zealand Journal of Ecology)

Manuscript 2

Mette, T.*, Dolos, K.*, Meinardus, M., Bräuning, A., Reineking, B., Blaschke, M., Pretzsch, H., Beierkuhnlein, C., Gohlke, A., Wellstein, C.[#] (in review). **Climatic turning point for beech and oak under climate change in Central Europe**.

Concept and discussion 40%, analysis/programming 40%, figures 40%, writing 40%, first submission in November 2012 (in review in Ecosphere)

Manuscript 3

Dolos, K.[#], González, J. M., Zavala, M.À. de, Reineking, B. (in prep.). **Symmetric and asymmetric competition in forests along the aridity gradient throughout the Iberian Peninsula**

Concept and discussion 85%, analysis/programming 100%, figures 100%, writing 90%

Manuscript 4

Dolos, K.#*, Thiel, D.*, Wellstein, C., Beierkuhnlein, C., Reineking, B., Kreyling, J. (in review). **Ecotype mixing as climate change adaptation in forests: The interplay of self-thinning and the portfolio effect**.

Concept and discussion 70%, analysis/programming 90%, figures 90%, writing 70%, data collection 0%, first submission in March 2013 (in review in The American Naturalist)

Manuscript 5

Dolos, K.#, Reineking, B. (in review). **Towards a better understanding of forest disturbance interactions: Lessons from a strategic model**.

Concept and discussion 90%, analysis/programming 100%, figures 100%, writing 90%, first submission in January 2012 (in review in Canadian Journal of Forest Research)

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Presentations on this research

15.04.2010	BayCEER Workshop 2010, Bayreuth Poster: Forest disturbances under climate change: Interactions of bark beetle outbreaks with fire, windthrow and drought (2nd place poster award)
23.04.-25.04.2010	Annual Meeting of the Young Modellers in Ecology, Wallenfels Oral presentation: Forest disturbances and climate change
30.08.-03.09.2010	GfÖ 40th Anniversary Meeting 2010, Giessen Oral presentation: The significance of intraspecific trait variability in modelling forest growth Poster: Bark beetle outbreak patterns – A theoretical study of dispersal distances and aggregation strength
22.09. - 24.09.2010	Forstwissenschaftliche Tagung 2010, Göttingen Oral presentation: Forest disturbances and their mutual interactions
15.04.-17.04.2011	Annual Meeting of the Young Modellers in Ecology, Wallenfels Oral presentation: Interactions of bark beetle outbreaks with fire, windthrow and drought
5.09.-09.09.2011	4st Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GFÖ), Oldenburg Poster (Co-Author): The role of disturbances for long-lived pioneer species in New Zealand’s forests (2nd place poster award)
19.09.-21.09.2011	10th Workshop on Vegetation Databases, Freising Poster (Co-Author): Assessing climate change effects on tree-growth based on forest inventory data from Bavaria
25.09.-29.09.2011	12th EEF Congress, Ávila Oral presentation: Interactions of bark beetle outbreaks with fire, windthrow and drought
30.04.2012	Colloquium of the Dept. Forest Ecology, ETH Zürich (Prof. Harald Bugmann) Oral presentation: Forest growth in dynamic environments – The effect of climate and disturbance interactions

Non-refereed periodicals

Dolos, K., Reineking, B. 2011. Walddynamik im Klimawandel - Modellstudie zeigt: Innerartliche Variabilität und Störungsinteraktionen haben bedeutenden Einfluss auf die künftige Waldentwicklung. – LWF aktuell 85.

Falk, W., Dolos, K., Reineking, B., Klemmt, H. J. 2012. Baumarteneignung im Standort-Leistung-Bezug: Klimarisikokarten werden in Zukunft standortsabhängiges Wachstumspotential berücksichtigen. – LWF aktuell 90.

Further publications

Dolos, K., Rudner, M. 2011. Seasonal variability and phenology of dwarf rush communities in southern Spain. – Ecologia Mediterranea 37(1).

Steinbauer, M., Dolos, K,. Reineking, B., Beierkuhnlein, C. 2012. Current measures for distance decay in similarity of species composition are influenced by study extent and grain size. – Global Ecology and Biogeography 21(12).

Erklärung

Hiermit erkläre ich an Eides statt, dass ich vorliegende Arbeit selbständig verfasst habe, andere als die von mir angegebenen Quellen und Hilfsmitten nicht benutzt habe und die den benutzten Werken wörtlich oder inhaltlich entommenen Stellen als solche kenntlich gemacht habe.

Hiermit erkläre ich an Eides statt, dass ich weder die vorliegende noch eine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden habe.

Klara Dolos im April 2013