The role of heterogeneity in spatial plant population dynamics

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Tag der mündlichen Prüfung:

I am a part of all that I have met;
Yet all experience is an arch wherethrough
Gleams that untraveled world, whose margin fades
For ever and for ever when I move.
How dull it is to pause, to make an end,
To rust unburnished, not to shine in use!
As though to breathe were life. Life piled on life
Were all too little, and of one to me
Little remains: but every hour is saved
From that eternal silence, something more,
A bringer of new things; and vile it were
For some three suns to store and hoard myself,
And this grey spirit yearning in desire
To follow knowledge like a sinking star,
Beyond the utmost bound of human thought.
[…]
Tho' much is taken, much abides; and though
We are not now that strength which in old days
Moved earth and heaven; that which we are, we are;
One equal temper of heroic hearts,
Made weak by time and fate, but strong in will
To strive, to seek, to find, and not to yield.

Lord Alfred Tennyson

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List of Abbreviations

Abbreviation	Description
Area.max1	Largest gap area
Area.max2	Second largest gap area
Area.max3	Third largest gap area
cont.water	Sum of contained water in first 10-50 cm soil
CSR	Complete Spatial Randomness, Homogeneous Poisson Process
DBH	Diameter at Breast Height [cm]
DEM	Digital Elevation Model
diff.soil1	Contained water in first 10 cm soil
diff.soil2	Contained water in first 10-20 cm soil
diff.soil3	Contained water in first 20-30 cm soil
diff.soil4	Contained water in first 30-40cm soil
diff.soil5	Contained water in first 40-50 cm soil
DUS2_1	Dry weight of upper soil in July
DW1_1_1 – DW1_1_9	Dry weight of upper 0-10 cm …- upper 80-90 cm soil in May (Pürckhauer)
DW2_1_1	Dry weight of upper 10 cm soil in July (Pürckhauer)
DW2_1_2- DW2_1_9	Dry weight of upper 10-20 cm …- upper 80-90 cm soil in July (Pürckhauer)
DW3_1_1 – DW3_1_9	Dry weight of upper 0-10 cm …- upper 80-90 cm soil in March (Pürckhauer)
DWUS2_1	Fresh weight of upper soil cm in July (Pürckhauer)
FW2_1_1	Fresh weight of upper 10 cm soil in July (Pürckhauer)
FW1_1_1 – FW1_1_9	Fresh weight of upper 0-10 cm …- upper 80-90 cm soil in May (Pürckhauer)
FW2_1_2 - FW2_1_9	Fresh weight of upper 10-20 cm …- upper 80-90 cm soil in July (Pürckhauer)
FW3_1_1 – FW3_1_9	Fresh weight of upper 0-10 cm …- upper 80-90 cm soil in March (Pürckhauer)
FWUS2_1	Fresh weight of upper soil cm in July (Pürckhauer)
GCSIplot.median	Median of Gap Shape Complexity index of three
GSCI.max1	Gap Shape Complexity index of largest gap
GSCI.max2	Gap Shape Complexity index of second largest gap
GSCI.max3	Gap Shape Complexity index of third largest gap
MD1_1	Maximum soil depth in May
MD2_1	Maximum soil depth in July
MD3_1	Maximum soil depth in March
mean_depth	Mean soil depth over three sample periods
nFK or PAW	Plant Available Water
Perim.max1	Largest gap perimeter
Perim.max2	Second largest gap perimeter
Perim.max3	Third largest gap perimeter
pF1_8	Field capacity: Fresh weight when saturated with water (pF 1.8 bar)
PPA	Point Pattern Analysis
sd_depth	Standard deviation of soil depth between samples
SPPM	Spatial Point Process Models

Abbreviation	Description
TWI	Topographic Wetness Index
var_depth	Variation in soil depth between samples
wF.spec	Wetness indicator value weighted by species cover
wK.spec	Continentality indicator value weighted by species cover
wL.spec	Light indicator value weighted by species cover
wN.spec	Nitrogen indicator value weighted by species cover
wR.spec	Acidity indicator value weighted by species cover
wT.spec	Temperature indicator value weighted by species cover

Abstract

Ecological theory names interacting mechanisms that allow competing species to coexist in limited available space, some of them are perceive as antagonistic. Most prominent are niche differentiation, heterogeneity and neutrality (ecological equivalence). Species similarity is also influenced by two mechanisms: Habitat filtering selects for ecologically similar species, while niche differentiation reduces competitive pressure and thus prefers ecologically different species. The spatial arrangement of abiotic resources can determine the spatial pattern and competition framework for a pre-selected tree species ensemble. Spatial occurrence patterns of trees are formed by dispersal, growth and mortality which are influenced by the interacting abiotic and abiotic conditions. The relative impact of these mechanisms are underresearched in temperate forest trees, especially in Europe.

We analysed a data set of a temperate old-growth forest with spatially explicit information about more than 15 000 individual trees of six tree species (90 % beech admixed with Ash, Hornbeam, Sycamore, Norway Maple, and Wych Elm) located in the central region of the Hainich National Park in central Germany.

We tested space-related coexistence mechanisms under heterogeneous conditions.
For this, we employed Point Pattern Analysis for testing several ecological hypotheses on inter- and intraspecific interactions of the species, varying from randomness to strict ecological niche. In order to identify the critical components of possible niches, we collected field data on the abiotic conditions such as the availability of water and light, and considered topography using a Digital Elevation Model. These field data were used for fitting suitability surfaces depending on tree species identity using spatial interpolation methods such as Kriging and Generalised Additive Models. We used Spatial Point Process Models to reconstruct the spatial distribution processes composed of purely biotic, abiotic or mixed covariates of the tree species.

We found that spatial heterogeneity was important in all aspects we studied. Both, tree density and the distribution of the abiotic habitat components varied in space. Especially when species interacted with beech, abiotic heterogeneity played an important role: beech outcompeted the admixed species under most prevailing abiotic conditions.

This way, beech influenced the spatial pattern of the six studied species by limiting available (niche) space via inter- and intraspecific competition. Here, Beech proved to be the superior competitor with no pronounced abiotic niche, but is mostly excluded from slopes. The remaining available niche space was often occupied by ecologically similar species, which formed typical associations in subregions of the study area less suitable for beech. We found spatial segregation between the three most abundant species Beech, Ash, and Hornbeam, coexistence by niches seem to be rather trait based rather than based on abiotic preferences. Habitat suitability and spatial distribution of Ash, Sycamore, and Norway Maple were more affected by the abiotic environmental condition than Beech, Hornbeam, and Elm. This indicates that the coexistence of rare species seems to be mediated by heterogeneity.

Our study revealed that the difference in abiotic conditions, such as soil depth and plant-available water were relevant for habitat suitability at small spatial and temporal scales.

When simulating the distribution pattern of the surveyed species, it became apparent that biotic interactions play an important part in shaping the scales at which aggregation or segregation happen in the abiotic environment. Beech and Sycamore both showed endogenous heterogeneity. For both species, point processes models incorporated several different interaction scales of intraspecific interaction. The interspecific interaction played only a minor role compared to the intraspecific one.

All results together seem to underline that niche differentiation happens at the level of the individual allowing ecologically similar species to interact *de facto* neutrally within their niche space and thus, to coexist in presence of a strong competitor.

"The world is a patchy place." (Dale 2001)

0 Introduction

Standing on the brink of the sixth mass extinction (Ceballos et al. 2015), it seems more important than ever to understand the mechanisms that allow species to form stable populations and co-exist with other species. Although ecologists have been aware of the importance of heterogeneity for species coexistence for decades, e.g. (Holt 1984), statistically evaluating its impact is still a major task under field conditions where not all processes within the environment are known (Pélissier and Goreaud 2001). Here, I aim to study spatial heterogeneity and species coexistence in a near-natural forest to fill this gap.

The more species of a guild are present in a habitat, the higher the probability of overlapping niches (Gravel et al. 2006). Such a niche-overlap would allow for neutral population processes (Hubbell 2006). In this case, species can be considered ecologically equivalent and the species identity would be of minor importance relative to stochastic processes (Hubbell 2001). Also, abiotic heterogeneity would not drive species assembly because the abiotic habitat would not differ in its impact on the different species. However, there is evidence, that especially in temperate regions, niche processes seem to predominate over neutral processes (Gilbert and Lechowicz 2004, Zhang et al. 2014). Niches are the result of competition, selecting individuals towards minimal competition pressure (Gause 1934; Hardin et al. 1960).

There has been a focus on explaining species coexistence by the differences between species. Driven by the classic understanding of species ecology as a mixture of traits and requirements, the habitat filtering hypothesis (Keddy 1992) states that coexistence depends on the suitability of site conditions while the habitat heterogeneity theory proposes the diversity of site conditions as the main driver (Tilman 1982, Potts et al. 2004). However, Hubbel argues, that most of the coexistence patterns can be reproduced with the sole assumption of stochastic events in population dynamics given a certain species pool even with ecologically equivalent species (Hubbell 2001, 2006).

There are two main categories of processes that determine spatial forest patterns a) tree-habitat interactions and b) tree-tree interactions. Habitat interactions include processes such as water uptake or nutrient depletion. Depending on the species ecology and the individuals' life stage, and given an abiotic resource pool, these interactions result in suitable and less suitable patches within the habitat. In tree-tree interactions, competition and facilitation are the major biotic processes. While facilitation is an enhancement usually by provision of nutrients or water (Callaway 1997), competition in forests is mainly a light-driven process (Kohyama 1993). Species' light requirements are thus the major driver of succession. Shade tolerance determines the degree of (self-)thinning in the juvenile phase as well as the ability to outlast adverse light conditions until a gap opens (Whitmore 1989, Kobe et al. 1995).

Virgin old-growth forests are ideal for studying these dynamics. These forests are rare in central Europe because this region is densely populated, thus, most forests have been cut and land put to agricultural use for a long time, and most of the remaining forests are managed (Peterken 1996, Bengtsson et al. 2000). One of the largest deciduous forest areas that have been under no intense use for several decades is the National Park Hainich (Thuringia) in the Hainich-Dün region. The study area Hainich National Park, central Germany, is remarkable in several ways. First, several competing species co-occur under near-natural conditions (Butler-Manning 2008), in a higher proportion of admixture to a Beech forest than known from other National Parks (Commarmot et al. 2005, Parviainen 2005). This is especially interesting, as beech is also known to be highly competitive over a variety of abiotic conditions (Leuschner and Ellenberg 2010a). Second, while topography shows little variation on small scale, soil conditions are known to be heterogeneous (Mund 2004). Thus, abiotic heterogeneity may impact co-occurrence of species on different scales and across different resource types in this forest.

The key goal of this dissertation is to investigate the prevailing mechanisms in the study region that might allow tree species to coexist. For this, we 1) characterised the spatial patterns of the tree species with respect to inter- or intraspecific interactions and niche behaviour 2) investigated to what extend abiotic heterogeneity influences habitat suitability for the individual tree species 3) identified spatial biotic and abiotic interactions that influence the tree species patterns.

Study area

Location

The study area is located in the Hainich National Park in the Hainich-Dün region. The forest is part of one of the largest continuous broad-leaved forests in Europe, covering about 13,000 ha (Großmann 2001). The forest type is a mixed beech forest on shell limestone (*Muschelkalk*), typical of low mountain ranges. The study plot ("Huss plot", Figure 0-1) is located in the "Weberstedter Holz" in the core zone I of the National Park and is part of the UNESCO world heritage area by the. It is a 28.5 ha large area within an old-growth mixed beech forest of trees up to 250 years old. The climate is suboceanic to subcontinental with a long-term mean annual precipitation of 750 to 800 mm (320 to 370 mm during growth season) and mean air temperature of 7.5 to 8 °C. The plot lies at an elevation of 425 to 455m with a gentle slope of mostly 1° to 5°. In the north-east is a gully area where slope can locally increase to 17 °.

The predominant parent material is shell limestone. Mund (2004) classified the soil conditions as calcareous rendzina or brown rendzina covered by a layer of loess, whose thickness varied at small scales, but tended to be thicker in the central and north eastern area. Springs and areas of occasional water logging lead to a highly variable hydrology in the plot area (Klaus and Reisinger 1995).

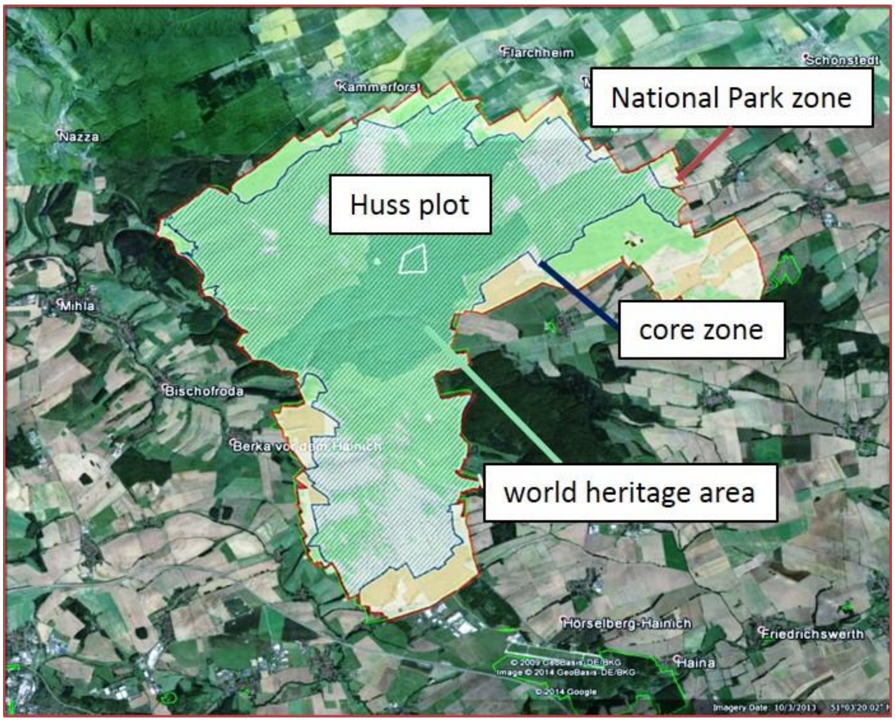


Figure 0-1 The study plot ("Huss plot", outlined in white) is in the world heritage area of the core zone of the Hainich National park.

History

Although information concerning the history of the Hainich in past centuries is scarce, the reconstructed history (Mund 2004, Butler-Manning 2008) is as follows: From 12th to 15th century, the area was used by local people to their needs as cattle pastures (*Hutewald*) and later (16th to 19th century) turned to a coppice forest or coppice with standards. At the end of the 19th century, the study area was put to intense selective cutting. During the two world wars, the management was unordered. Around 1930 the forest was possibly used as a beech selective forest (Huss 2005). In order to promote rejuvenation, gap cuttings were increased in the following 30 years within a selection forest system. From 1965 to 1990 the Weberstedter Holz was used as a military training site by *the Nationale Volksarmee* of the German Democratic Republic. Because the forest served as a buffer region between shooting sites, human access was very limited for several decades. When the area became a National Park in 1997, all management stopped. With little to no human interference over the last 50 to 100 years, the spatial structure of the forest in this core zone can be considered to be comparable to virgin beech forests in other parts of Europe (Peterken 1996 p. 15).

Species composition and stand structure

The forest is dominated by beech (*Fagus sylvatica L.*), accounting for 90 % of all trees. The past regimes of forest pasture and coppice management resulted in a high proportion of high quality timber species (Ash, Hornbeam, oak, lime and wild service tree). Ellenberg indicator values classify the species as different in their preferences (Table 0-1). The forest was classified by Hofmann (1965) as a *Hordelymo-Fagetum* (*Waldgersten-Buchenwald*).

Table 0-1 Study species and Ellenberg indicator values *(Ellenberg et al. 1991) on a gradient along a nine point scale, abbreviates according to German names (L=light, T=temperature, K=continentality (Kontinentalität), F=wetness (Feuchte), R= soil acidity (Reaktion), N=soil productivity/Nitrogen. x mark indifference, i.e. broad tolerance towards environmental factor.*

Species name		**Indicator values**					
Latin	**English**	**L**	**T**	**K**	**F**	**R**	**N**
Acer platanoides	Norway maple	4	x	3	5	5	5
Acer pseudoplatanus	Sycamore maple	4	x	4	6	x	7
Carpinus betulus	hornbeam	4	6	4	x	x	x
Fagus sylvatica	European beech	3	5	2	5	x	x
Fraxinus excelsior	European ash	4	5	3	x	7	7
Ulmus glabra	Wych elm	4	5	3	6	7	7

Point pattern analysis and spatial heterogeneity

Point pattern analysis is increasingly applied in ecology for characterising spatial arrangements of individuals/point-like entities and understanding the pattern forming processes (Wiegand and Moloney 2014). It is based on the assumption that an observed point pattern within a region is generated by a point process. Ecological processes leave an imprint in the spatial arrangement of individuals and can therefore be reconstructed by analysing spatial patterns (Velázquez et al. 2015). In sessile organisms like trees, the spatial pattern is a direct result of reproduction, dispersal, growth, competition, and mortality. For example, if the position of all individuals in a given forest area is mapped, the cumulative result of these processes within this area can be evaluated and inference on the single components (e.g. competition) can be drawn. There are several summary functions that characterise different aspects of spatial point patterns (Wiegand et al. 2013), the most common of which are Ripley´s K(Ripley 1977), the pair-correlation function(Stoyan and Ohser 1982, Stoyan and Stoyan 1994a), the empty-space function (Diggle 1983), and the nearest neighbour distribution (Hanisch 1984) function These will be introduced in Chapter 1.

All these functions aim at detecting deviations from demographic noise, i.e. true spatial trends within the mapped census. If there are no or neutral, i.e. stochastic, interactions between individuals, a random and independent spatial distribution is to be expected. This is called Complete Spatial Randomness (CSR) and modelled by a homogeneous Poisson process (Figure 0-2a). In cases of negative interaction, e.g. competition, a regular pattern (Figure 0-2b) is to be expected, because the distance between events is maximised. If there are positive interactions, e.g. facilitation, clumping will occur (Figure 0-2c). These patterns can be less easily detected under heterogeneous conditions (next section).

If all individuals (in this thesis, trees) are considered to be equal in all qualities, they can be treated as an unmarked point process. To take differences in qualities, e.g., species identity or size into account, a mark can be assigned to each point or individual (Penttinen et al. 1992). These marks can then be used to make an inference on the impact of the observed qualities by comparing the spatial patterns of events within (univariate) or between (bivariate) classes of marks.

In this thesis, species identity is used as a mark to study the spatial interactions between the species. In addition, for beech we also analyses differences between life-stages based on DBH-size classes. Size classes can also influence the spatial structure of a forest because differences in the physiological properties of life stages lead to differences in critical scales. This is considered in Chapter 1.

Heterogeneity and habitat suitability

Taking heterogeneity (Figure 0-2d) into account complements the point pattern approach with concepts adapted from the classic approach of spatial ecology, species distribution or habitat suitability models (Elith and Leathwick 2009, Wiegand and Moloney 2014). Habitat suitability can influence ecological processes by increasing establishment probability, growth, or mortality (Hirzel and Le Lay 2008). Given that species show different ecological traits, their habitat preferences or ecological potential differs. Abiotic conditions can favour the performance of different species while limiting the growth of the dominant species. Thus, large-scale abiotic heterogeneity the potential of allowing species to co-exist even if one species predominates the other (Chesson 2000). At the same time, physiological properties of life stages lead to differences in critical scales, e.g. a larger tree may integrate over several less suitable patches, while those sites are unsuitable for a smaller tree, to which such patches appear disconnected. Juvenile stages tend to be more shade tolerant. As a consequence, while seedlings of a particular species may grow under a closed canopy, there may be no adult trees in the canopy layer of that species because a later stage exhibits little shade tolerance.

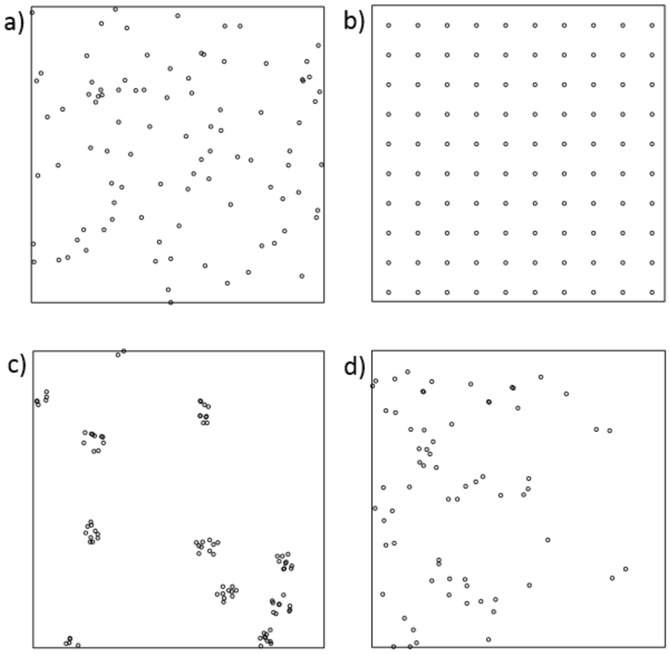


Figure 0-2 Point patterns showing contrasting mechanisms: a) Complete Spatial Randomness, b) regularity (repulsion) c) clumping (aggregation), d) randomness with a spatial trend (anisotropic), showing heterogeneity.

Null-models

Observed point patterns are usually compared to the expected outcome of the summary function. This expectation is formulated in null-models. These null-models are used to infer on the link between the observed spatial pattern and the pattern generating process. Null-models can be used to define an expectation or to separate mechanisms of the underlying processes even if the outcome is similar (s. Table 0-2). Depending on the hypothesis, null-models can vary in their complexity. The simplest null-model assumption is CSR, which assumes no interaction between habitat or trees. In cases of heterogeneity in the abiotic habitat, the underlying null-model should include the anisotropic influence of the habitat on the species (Wiegand and Moloney 2014 p. 87). Thus, we would assume a spatial trend, and for example, incorporate a limiting resource (Shen et al. 2009, Lin et al. 2011). If there are interactions between trees, e.g., they facilitate each other, or dispersal is clumped, assuming a cluster process will be more appropriate as an underlying assumption than a Poisson process without this biotic interaction (Baddeley et al. 2015 p. 449). As many processes occur at the same time, the application of more than one null-model can help to disentangle involved processes (Johnson and Omland 2004, Wiegand and Moloney 2004).

Table 0-2 Link of pattern, ecological hypothesis and null-model. *Grey scenarios are not applied in this thesis.*

Observable spatial pattern	Mechanism/ Hypothesis	Null-model
Clustering		
of one or multiple species	Heterogeneous habitat suitability leads to clustering in suitable patches and gaps or lower densities in less suitable or unsuitable patches	Remove clustering by using heterogeneous Poisson process, i.e. tree or, if known, resource density as null-model for redistribution
between species	Resource partitioning of species allows spatial coexistence	Heterogeneous Poisson process including niches (species-specific large trees). If null-model sharpens repulsion patterns this hints towards niche differentiation, if it does not, it may hint towards density dependence or *de facto* neutrality.
in particular species	Heterogeneous habitat conditions limits specialist species to sub-habitats	Underlie critical resource density or species density as proxy
in particular species	Species reproduces in clusters (e.g. small dispersal kernel)	Use cluster process, e.g. Cox
between species	One species facilitates the other	Bivariate random labelling: Pattern of species 1 fixed, randomisation of pattern 2
between life stages	Dispersal limitation leads to clustering between juvenile, and subsequently, small trees. If dispersal e.g. via nuts, usually also clustering around mature/ large trees	Random labelling, case/control design to model a two-step process, where one process produces the pattern and the second the life-stages.

in dead trees	Scramble competition leads to cluster-wise mortality due to resource depletion, Random mortality hypothesis (Kenkel 1988)	Random labelling where the first process distributes the trees and the second the alive/dead labels
Randomness		
between species	Species interact neutrally, thus showing independence or randomness towards the occurrence of the other	CSR to check for randomness. Under homogenous conditions: toroidal shift to test for independence between patterns of species 1 and species 2. Under heterogeneous conditions: pattern reconstruction to produce heterogeneous, but random, reference patterns
Ubiquity in space	Broad ecological niche allows generalist to occur in whole observation area	CSR at large scales, intraspecific patterns still can show small-scale repulsion
Repulsion		
Spatial segregation	Former competition lead to different niches, that are spatially segregated (larger time scale), or competition-driven mortality eradicated one species from the area of the other. Competition past	Heterogeneous Poisson process testing including niches to look for niche differentiation. Toroidal shift under homogeneous conditions to check for independence between species patterns
Repulsion within species	Intra-specific competition (self-thinning)	Heterogeneous Poisson process (under heterogeneous conditions, otherwise homogeneous)
Repulsion within species	competition leads to minimum distance	Include hardcore process (, e.g. Gibbs) or softcore (with rare small distances) process
Repulsion between life stages of same species	Contest competition between life stages forms regular pattern. Random mortality hypothesis (Kenkel 1988)	Random labelling where the first process distributes the trees and the second the life-stage labels
Repulsion at small scales	Competition between individuals	Heterogeneous Poisson Process, removable by using hard-core processes

Thesis rationale and structure

The aim of this thesis is to analyse and model the effect of environmental heterogeneity on spatial tree patterns. Particular focus lies on the tracing of effects that indicate neutrality (stochastic interaction between species), niche effects (species-specific effects) or the response to heterogeneity (response to topography or resources).

Chapter 1

The spatial pattern within and between the six studied species in the study area are analysed with regard to heterogeneity and niche structures with standard point pattern analysis (PPA). Chapter 1-3 formatted according to requirements of target journal Ecography.

Chapter 2

Afterwards, I will introduce indicators of abiotic spatial heterogeneity. They are based on information derived from a Digital Elevation Model (DEM) and measurements done in the field. I combined these indicator variables to derive a spatially explicit habitat model of the prevailing heterogeneity.

Chapter 3

In Chapter 3, I used the derived spatially explicit model of the abiotic habitat and to fit abiotic null-models for point process models. The accuracy of the point process models were compared to the results of the null-models used in Chapter 1, which based on e.g. heterogeneous point processes and were not derived from field measurements. Moreover, I added neutral and species specific biotic interaction between the species. The comparison of abiotic, species indifferent, species specific models, and models including abiotic and biotic covariates will be used as hypotheses on the relative impact of abiotic and biotic interactions for the species.

Chapter 4

In the last step, I shifted the focus from the spatial patterns to the implications of neutral species interaction in conservation practice (here, formatting is according to target journal Conservation Biology).

1 Chapter 1: Spatial analysis of coexistence in a heterogeneous environment

Abstract

Within and between species, there is an omnipresent competition for resources. Only few sets of conditions seem to allow stable coexistence with ongoing competition. Known coexistence mechanisms are for example differences in resource utilisation, or spatial heterogeneity of environmental conditions.

In order to test space-related coexistence mechanisms under heterogeneous conditions, we analysed a temperate old-growth mixed-beech forest in central Germany that is considered to be near-natural in its spatial structures. To describe the overall spatial pattern of multiple species and characterise the nature of inter- and intraspecific interactions, we employed inhomogeneous pair-correlation, nearest neighbour, and empty-space functions. We used three null-model assumptions to relate the spatial arrangement of the environmental conditions to the spatial tree pattern. The first null-model assumed homogeneity, giving each location the same suitability for all tree species. The second null-model assumed heterogeneous abiotic conditions and that tree species were equal in their environmental preferences. The third null-model also assumed heterogeneity but allowed separate niches for the species. Homogeneity was rejected for all univariate species-interactions except Norway Maple, and Elm.

Spatial heterogeneity of environmental conditions describes the spatial pattern of the trees best whenever the interaction with beech was considered. Our results suggest that in a temperate forest, spatial segregation and spatial niche differentiation are evident within the three main species beech, sh, and hornbeam. Beech and hornbeam show density-dependent spatial patterns, while for ash, sycamore, and Norway maple, the null-model assuming niches performed better. Beech proves to be a strong competitor in interaction within and between the species.

1.1 Introduction: Species coexistence mechanisms in space

To identify and explain the mechanisms behind species coexistence is one of the fundamental tasks in ecology (Sutherland et al. 2013). The concept of limiting similarity predicts that species evolve distinct niches because they need to be sufficiently different to coexist. Thus, the coexistence of species with very similar ecology in spatial proximity (Simberloff and Dayan 1991) seems to challenge the concept of distinct niches. But to prove or disprove the existence or quantify the importance of niches is challenging (Adler et al. 2010). This difficulty stems from practical reasons: First, considering niches in Hutchinson‘s sense as n-dimensional (Hutchinson 1957) implies that the sufficient difference might lie in any of these dimensions. Second, while dynamics of populations with short generation times are observable (Turner et al. 1996, Meyer and Leveau 2012), slow population dynamics as for example in forests are not easily detectable. Moreover, usually only two species are considered, because of the challenges of a full-factorial analysis for many species. While recent theory-based coexistence studies (Plotnick and Gardner 2002, Snyder and Chesson 2003) or studies located in the tropics made considerable advances (Hubbell 2001, Chave 2004, Wiegand et al. 2012), the mechanisms in temperate forests still deserve some study (Mart’ınez et al. 2013, Zhang et al. 2013).

While it has been acknowledged for a long time that space plays an important role in species interaction and population dynamics (Duarte et al. 1998; Snyder and Chesson 2004; Amarasekare 2003), interpreting spatial patterns is not trivial. Spatial tree patterns result from a number of processes of population dynamics, such as dispersal, growth, and mortality. These processes are influenced by abiotic and biotic interactions: Abiotic interactions refer to trees interacting with their abiotic environmental conditions, e.g. resource availability. These conditions may vary over space and thus may form patches that are more or less suitable, with suitability also depending on species preferences. Ultimately, heterogeneous abiotic conditions change the population dynamics (Oliver and Larson 1996) and, thus, the spatial patterns of plants (Huston and DeAngelis 1994; Getzin et al. 2008). Biotic interactions constitute the second type of interaction. While competition and density-dependent mortality cause spatial repulsion between individuals, facilitation and dispersal may lead to spatial aggregation (Stoyan and Penttinen 2000a). However, these biotic interactions are likely influenced by abiotic conditions and the spatial arrangement of the abiotic conditions.

Spatial heterogeneity itself can change competition patterns within the population (Day et al. 2003). For example, the growth of the dominant species can be locally limited by less suitable abiotic conditions. This, in turn, can favour the performance of a suppressed species. As a consequence, large-scale heterogeneity has the potential of allowing species to coexist even if one species predominates the other (Chesson 2000a). An additional layer of complexity is added by considering both, intra- and interspecific competition as intraspecific competition that produces regular patterns. For example, competition can disperse the clumping effect of heterogeneity that leads to aggregation on suitable patches. Thus, multiple processes affect spatial tree patterns and these patterns are influenced by a combination of abiotic and biotic interaction types that act with different strength.

1.1.1 Niches

The interactions of all required abiotic resources and tolerances of a species define the fundamental ecological niche of a species (Hutchinson 1957). However, individuals of species with similar fundamental niches have to compete for the available resources, leading to realised niches that are smaller than the physiologically possible, fundamental niche (Begon et al. 2006). Unless the intraspecific competition outweighs the interspecific competition, interspecific competition results in an exclusion of species (Lotka 1907, Wilson et al. 2003). Because species with the same requirements are likely to find the same habitats suitable they show spatial co-occurrence. Thus, the spatial arrangement of abiotic resources can pre-define the species ensemble (Fauth et al. 1996), and determine their spatial pattern (gradual decline vs. patchy occurrence) and competition framework.

1.1.2 Coexistence mechanisms

The competition mechanisms outlined above imply that most forms of coexistence between species are unstable (Huston 1979). However, species coexistence can be expected to be either stabilised if intraspecific limitation is more important than interspecific interactions or populations can be equalized in their performance, if differences between species are reduced (Chesson 2000a). There are several more mechanisms that can stabilise or precondition species coexistence: Pacala et al. (1996) found that spatial coexistence due to spatial segregation over evolutionary time scales works via the ecological mechanism of forming conspecific clusters through spatially separating heterospecific individuals by repeated exclusion of single individuals. Thus, spatial segregation can be a sign of a former competition (Connell 1980).

In contrast to spatial segregation, if species evolve niche differentiation, these species can spatially coexist with no or little competition (Hardin and others 1960, Whittaker 1965). Niche differentiation can be found due to resource partitioning that may occur in time or space or due to morphological adaptation that allow the use of a common resource in different ways. Moreover, the differentiation may lie in the utilisation of a resource depending either on the varying abiotic conditions or on the lowest limit for survival in a combination of resources (R^*, (Tilman 1980, 1982)).

At local scales, stable coexistence can have its cause either in different ecological niches or neutral mechanisms (Chave and Leigh 2002). However, in temperate forests niche differentiation can be especially pronounced for water and light (Coomes and Grubb 2000), and competition mechanisms are mostly light-mediated (Pacala et al. 1996). Therefore, in temperate forests, niche differentiation seems to be of greater importance than neutral processes (Kohyama 1993, Gilbert and Lechowicz 2004, Zhang et al. 2014).

1.1.3 Spatial patterns

Spatial environmental properties form the competition landscape for plants and, *vice versa*, competition patterns result in spatial plant patterns. However complex the processes leading to the spatial patterns may be, there are still only three spatial interaction types extractable from point pattern analysis: Clustering, randomness, or repulsion. The same spatial pattern can result from different ecological processes (Wiegand et al. 2000). Thus, even under scale-explicit pattern analysis, the interpretation of spatial patterns can be disputable. An appropriate interpretation depends on incorporating the critical ecological processes under the assumptions that are represented in the null-model. For example, a species can show a clustered pattern because of clustered dispersal, because suitable abiotic conditions occur patchily or both. To test this, a null-model that takes habitat suitability into account would for example be appropriate because it mimics the abiotic conditions and thereby isolates effects of clustered dispersal. Here, we describe the spatial patterns and identify the pattern-forming processes in a near-natural temperate forest dominated by beech trees:

Aim 1: Characterise the uni- and bivariate spatial pattern of the six co-occurring species.

Hypothesis 1: Beech (*Fagus sylvatica*) shows repulsion patterns with all species and within life stages, because beech is a supreme competitor.

Aim 2: Test the importance of niches under near-natural conditions in a heterogeneous, multispecies set-up.

Hypothesis 2: Spatial randomness occurs both when regarding heterogeneity and when regarding niches as a null-model, but assuming niches shows stronger patterns of deviation from randomness. This follows the assumption that in temperate forests both neutral and niche mechanisms occur (Chave 2004), but niche mechanisms prevail (Gilbert and Lechowicz 2004, Zhang et al. 2013).

Hypothesis 3: *Fagus* occurs everywhere randomly, whereas *Fraxinus* and *Acer sp.* are clustered. The generalist *Fagus* should be less sensitive towards a change of environmental conditions than the specialist species that can outperform beech in suboptimal patches.

1.2 Material and Methods

1.2.1 Study area

In order to investigate the natural mechanisms of coexistence in a temperate multi-species forest, we used data collected in a 28.5 ha area ("Huss plot", Figure 1-1) in the core zone of the National Park Hainich, Thuringia, Germany. The first census was conducted in 1999, the second in 2007. Trees were mapped with: coordinates (Easting, Northing), species identity, and viability. The sampled area is part of a continuous beech forest (*Hordelymo-Fagetum*) with beech accounting for 90% of all trees, admixed with ash, hornbeam, sycamore, Norway maple, Wych elm, and few individuals of seven other tree species. However, only the named six species occurred in large enough numbers for statistical analysis (Table 1-1). The area is an old-growth forest of little and further decreasing human influence over the last 60-150 years (Butler-Manning 2008). For a more detailed description of mapping method and data set see Butler-Manning (2008).

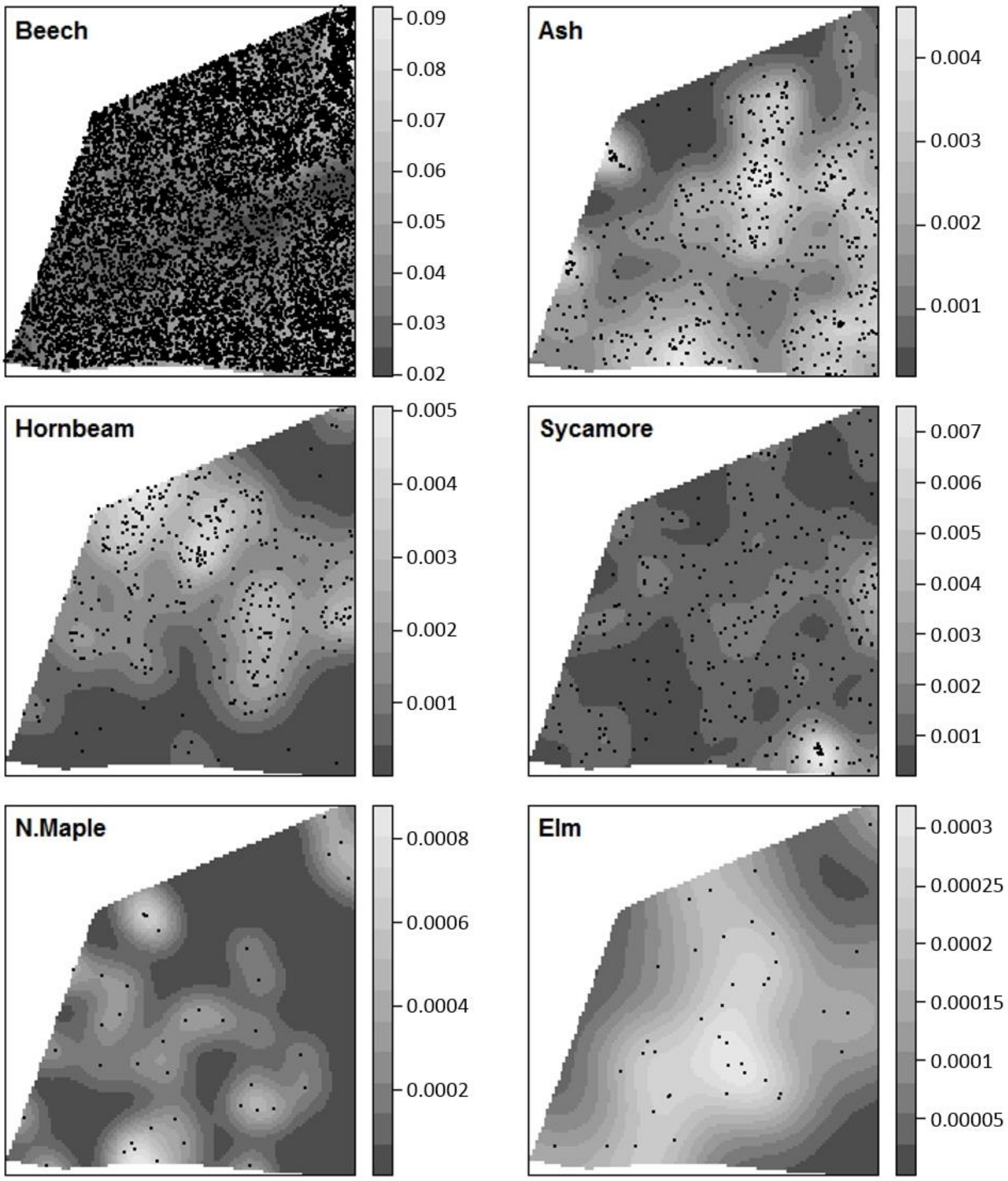


Figure 1-1 Spatial distribution of the density of the six most abundant species *in the 28.5 ha-sized study plot in the core zone of the Hainich National Park, Thuringia, Germany****.*** *Legend shows intensity in individuals per square meter (light colour means high intensity). Note that the densities have different scaling between the species. Black dots mark the position of trees*

Table 1-1 Abundance of species in the plot (total area 28.5 ha) in 2007: *total and divided in size classes according to diameter at breast height (DBH). The second column also gives the total number of trees in 1999 in parentheses.*

Species	**total 2007 (1999)**	**small (0 - 10 cm)**	**medium (>10 -30 cm)**	**large (>30 cm)**
beech *(Fagus sylvatica)*	12191 (13307)	6098	3434	2658
ash *(Fraxinus excelsior)*	527 (550)	5	16	505
hornbeam *(Carpinus betulus)*	361 (389)	2	77	282
sycamore *(Acer pseudoplatanus)*	345 (321)	38	10	297
Norway maple *(Acer platanoides)*	40 (44)	0	6	34
elm *(Ulmus glabra)*	39 (69)	5	6	28
sum	13503 (14680)	6148	3549	3804

1.2.2 Spatial analyses

Mund (2004) and Butler-Manning (2008) observed spatial heterogeneity in soil conditions that seems to influence the tree layer. In the present study, we characterized the abiotic environment indirectly, via density of large trees (details in section 2.3, see also Baddeley et al. 2000). We used the intensity function of all tree species for a global estimate of habitat heterogeneity, and the intensity function of individual species for species-specific estimates of habitat heterogeneity.

Biotic interactions were analysed at species level. Interactions at species level give information about the competition patterns between the species and thus allow conclusions about the stability of coexistence. Here, univariate analyses gave information on intraspecific interactions, and bivariate analyses on interspecific interactions.

In order to analyse the effect of recruitment on stand dynamics, we conducted uni- and bivariate analyses at size-class level. However, only beech occurred in large enough numbers to be analysed at the intraspecific level of size classes (Table 1-1).

Therefore, we conducted uni- and bivariate analyses within and between size classes of beech (small: ≤ 10 cm, medium: > 10 cm and ≤ 30 cm, large: > 30 cm). For the other five species, we restricted the analyses to the species level. All results shown in the main text refer to the 2007 census. All spatial analyses were conducted using the statistical software R 3.2.2 and the *spatstat* package 1.46-0 (Baddeley and Turner 2005).

1.2.3 Summary statistics

Wiegand et al. (2013) argued that only a combination of spatial summary statistics may capture all characteristics of a complex spatial pattern. Therefore, we used three summary statistics: 1) pair-correlation function (Stoyan and Stoyan 1994b) for explorative pattern detection and scale identification, 2) nearest neighbour distribution (van Lieshout and Baddeley 1996; Baddeley et al. 2000) to characterise the direct, short-range spatial interactions, and 3) the empty-space function (Lieshout and Baddeley 1996) to identify clustering. These summary statistics serve for measurements. The null-models used to investigate Aims 1 – 3 given in the Introduction are given in Section 2.3. Briefly, our null-models were variations of homo- and heterogeneous Poisson processes. We applied homo- and inhomogeneous versions of functions 1)-3) to simulations of these processes and as well as to field data.

Considerations on the interaction scale

We attributed deviations from a given null-model at small distances to direct tree-tree interactions and deviations at large scales as outcome of a heterogeneous environment. Stoyan and Penttinen (2000) suggest the use of 10 m as a general distance threshold, but as there are crown diameters of 15 m and more for canopy trees in our study plot (Jacob et al. 2010), we considered up to 15 m as direct interaction range for large trees. We accordingly chose a general distance threshold of 15 m, or in other words a kernel width sigma of 30 m, arguing that this reflects the ecological window for grasping both meaningful heterogeneity and the interaction scale of large canopy trees. However, we are aware that sigma is a sensitive parameter.

Intensity function $\lambda(x)$

The intensity function describes the number of points per unit area (density distribution function $\lambda(x)$ (Wiegand and Moloney 2014). Here, intensity was calculated as the number of tree individuals per species per square meter.

Ripley's K and Pair-correlation function $g(r)$

For an observed pattern, Ripley's K (Ripley 1976) calculates point densities within the entire circle of a given radius *r*, it is thus a cumulative distribution function.

$$K(r) = 2\pi \int_{t=0}^{r} \mathrm{g(t)tdt}$$

The pair-correlation function $g(r)$ (Stoyan and Stoyan 1994b) describes the number of expected points of type *i* at distance *r* around a typical point of type *j*. Here, *i* and *j* could represent species or size classes. The analysis is univariate if *i=j*, and bivariate otherwise. The pair-correlation function is related to the derivative of Ripley’s K-function (Ripley 1976), but is, in contrast, non-cumulative.

$$g(r) = \frac{dK(r)}{dr} \Big/ 2\pi r$$

Wiegand et al. (2012) found that the pair-correlation function is the most powerful function in characterising a spatial pattern and it is recommended for exploratory data analyses to identify critical scales of deviation from the null-model (Illian et al. 2008; Perry, Miller, and Enright 2006; Wiegand and Moloney 2014). Deviations of the observed patterns that show lower values than predicted by the null-model are interpreted as repulsion. Observed values higher than predicted are considered to show a spatial clumping, whereas observations that are within the null-model prediction are considered to be random within the null-model assumptions.

Cumulative nearest neighbour distribution function $G(r)$

The nearest neighbour distribution function (G-function (Diggle 2003)) describes the probability distribution of one individual having its k^{th} -closest neighbour at distance r. It is an appropriate function for considering short-range interaction patterns.

$$\lambda g(r) 2\pi r = \sum_{k=1}^{\infty} G^2(r)$$

Observations below the null-model prediction show shorter nearest neighbour distances, and thus, clumping. Similar to the pair-correlation function, the nearest neighbour distribution function is point-based, i.e. it describes spatial correlation between individuals. Here, we summarize the function by reporting the distance at which 90% of the trees have their nearest neighbour.

Empty space function (spherical contact distribution function)

The empty-space function is location-based, i.e. it describes the spatial distribution of individuals relative to random locations, not between individuals. The spatial distribution is described in terms of a frequency distribution of distances between random locations and the nearest tree. If the observed pattern is below the null-model prediction, the observed empty space is smaller than expected. This indicates regularity. Observations above the predicted values show large empty spaces and thus, indicate clustering in presence of also short empty-space distances. Please note that for Poisson processes nearest neighbour and empty-space functions are the same function (Stoyan et al. 1995). Thus, if no deviations from the simulated Poisson process are observable, empty space and nearest neighbour distribution look the same. Here, we summarize the empty-space function by reporting the distance for which for 90% of random locations there is at least one tree found at or within this distance.

1.2.4 Choice of null-models

Null-Models are usually used to produce simulated randomised reference patterns of spatial characteristics that are anticipated in the absence of specific ecological processes (Gotelli and Graves 1996). Rejection of a null-model then indicates the presence of the respective ecological processes. Taking the opposite perspective, null-models can also be seen as representing a particular spatial process such as Complete Spatial Randomness (CSR) or clustering. Then, the non-rejection of a null-model indicates that the process represented by the null-model could be the main driver of the observed pattern (Wiegand and Moloney 2004). Here, we thus consider as the best null-model the one that produces simulation envelopes with the smallest deviations in respect to the observed pattern, for an example graphic, see Figure 1-2.

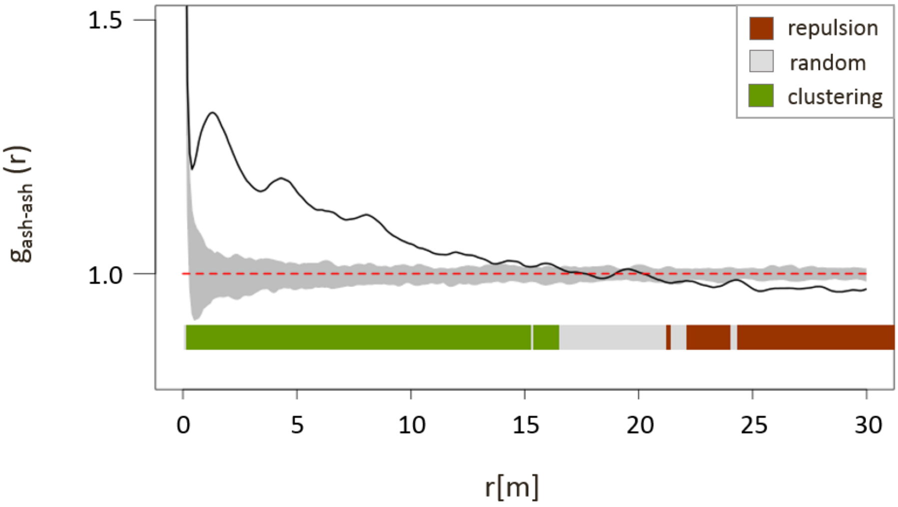


Figure 1-2 Example (Ash-Ash) result of a pair-correlation function and presentation as quantum plots. *The results of the pair-correlations will be presented as the lower coloured plot (quantum plot) only. Deviations from the simulation envelope towards clustering are green, deviations towards repulsion are red. If the function follows the envelope, the quantum plot is grey. Therefore, the null-model that shows where the pair-correlation function shows little deviation from the envelope will have a mostly grey simulation envelope.*

Complete Spatial Randomness (CSR)

The above mentioned CSR is the simplest null-model. CSR assumes the absence of all spatial pattern-generating ecological processes that could lead to anisotropy or non-stationarity (Baddeley et al. 2015 p. 409). It corresponds to a homogeneous Poisson process (Cressie 1993 p. 586). In our particular study, the assumption of CSR implies that all locations have the same suitability for tree occurrence and thus the same probability of holding trees (Specific Hypothesis 1, short SH1, null-model: CSR ($null_{ubiq}$) with homogeneous pair-correlation function g_{ubiq}).

Including heterogeneity

However, heterogeneity was observed for soil properties (Mund 2004). Thus, we investigated if this heterogeneity also showed in the spatial tree patterns (technically, by rejecting SH1) and then separately applied two null-models to include two different forms of habitat heterogeneity: The first assumed species do not differ in their reaction to abiotic heterogeneity (Aim 2), the second allowed for differences depending on species identity (Aim 3). In lack of an explicit habitat model that included influential abiotic field-measured variables, we characterized habitat heterogeneity by tree density, considering tree density as the indirect outcome of differences in habitat suitability (Baddeley et al. 2000). To support the null-model choice and deal with the difficulties of estimating first and second order properties from the same model, we included ecological pre-knowledge (Diggle and Ribeiro Jr 2007). The deliberate inclusion of explicit pre-knowledge also promotes the possibility of separating between clumping due to heterogeneity, due to niche properties or due to tree-tree interactions. We assumed that large trees (> 30 cm DBH) are mature trees and that their differences in density indicated differences in abiotic habitat suitability. These trees had already survived the thinning process caused by adverse abiotic conditions. Following the approach of Getzin et al. (2008), we first hypothesized that suitability is equal for all species (Specific Hypothesis 2, short SH2, null-model: heterogeneous Poisson process ($null_{equal}$) with inhomogeneous pair-correlation function g_{equal}).

However, depending on species identity, abiotic habitat heterogeneity may have a different impact on occurrence probability. Indeed, Zhang et al. (2013) observed that niche effects seem to be more important than stochastic processes in a temperate forest. Thus, as an alternative to assuming equal habitat suitability for all species, we secondly hypothesized species-specific suitability. To this end, we characterised species-specific experienced habitat heterogeneity based on tree density of large trees (> 30 cm DBH) of each species individually (Specific Hypothesis 3, short SH3, null-model: inhomogeneous Poisson process ($null_{niche}$) with inhomogeneous pair-correlation function g_{niche}).

Using a non-parametric approach, we estimated the intensity $\lambda(x)$ of the spatial distribution of mature trees overall and species-wise for the two null-models SH2 and

SH3, respectively, by applying a moving window approach combined with an Epanechnikov kernel as suggested in Stoyan and Stoyan (1994b, 2008) and Getzin et al. (2008). Following Baddeley et al. (2000), technically, the intensities $\lambda(x)$ are not part of the null-models but are used as thinning surfaces to adjust the pair-correlation function (g_{equal} or g_{niche}).

1.2.5 Construction of simulation envelopes

In order to evaluate significant departure from the null-model under consideration, we performed 199 Monte-Carlo simulations of the respective null-model process, using the highest and lowest 2.5% simulation values in order to get an approximately 5%-error-probability of the constructed simulation envelopes. In order to consider the multiple-testing problem of simulation envelopes (Loosmore and Ford 2006) of the used point-wise envelopes, we also conducted a goodness of fit test for significance of deviations from the simulation envelope in steps of r <10 m, 10-20 m and 20-30 m (Stoyan und Penttinen 2000). Whenever the observed pattern deviated from the simulation envelope we conducted a goodness of fit test. Only statistically significant deviations from predicted patterns were included in the graphics, discarding insignificant differences.

1.3 Results

1.3.1 Interactions at species level – univariate and bivariate

The pair-correlation function characterises the overall spatial pattern with respect to the null-model and the critical scales of deviation, if present. When assuming homogeneous habitat suitability (SH1, CSR; $null_{ubiq}$ with homogeneous g_{ubiq}), there were large scale deviations towards aggregation in univariate pair-correlation functions except for Norway Maple and Elm (see Appendix A.7-1,). To identify the influence of heterogeneity and niches, two further null-models were applied (Figure 1-3). Assuming equal suitability for all species in the intensity estimation (heterogeneity without niches; Inhomogeneous Poisson process $null_{equal}$ with inhomogeneous g_{equal}), the univariate interactions were largely random (Figure 1-3a, plots on main diagonal). Exceptions with a small scale intraspecific clustering were beech at < 2m and ash with clustering at ≤ 8 m, and repulsion at > 16 m.

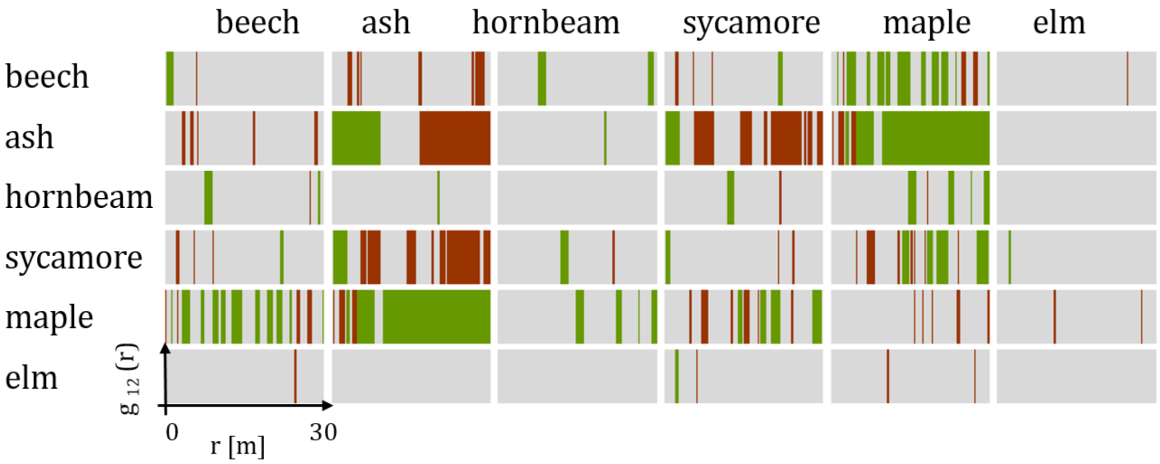
For analysing the niche effect, only the density of conspecific large trees of the particular species of interest were used in the pair-correlation function for including habitat heterogeneity (heterogeneity with niches; inhomogeneous Poisson process $null_{niche}$ with g_{niche} Figure 1-3b, plots on main diagonal). Here, the univariate interactions were random for Elm and the *Acer* species. Beech showed clustering from 0 m to almost 20 m. Ash showed small scale clustering up to 8 m.

For bivariate (between-species) interactions, under SH1, there were large-scale deviations in all bivariate interactions with beech except for elm. Under SH2, there were no deviations from the simulation envelopes for most species combinations (Figure 1-3a, off-diagonal plots). Exceptions to this were combinations of the *Acer* species with Ash and beech. The only bivariate attraction is observed in beech aggregating around Ash at a very small scale. In fact, under SH3, interspecific interactions showed repulsion patterns in g_{niche}, almost over the whole range of scales from 0 m to 30 m. In all combinations of the three most abundant species, beech, ash, and hornbeam, strong repulsion patterns occurred. Thus, the assumption of niches removed all interspecific attraction processes, in some cases to the extent of adding interspecific repulsion. There was a strong positive correlation between Ripley's K and the number of large trees per species (Fig 1-4a, showing $K(r = 30\text{ m})$), with beech being a clear exception.

The Nearest neighbour distance distribution function gives information about the spatial co-occurrence of species and their evenness in space. While in intraspecific combinations the nearest neighbour distances were the shortest, there were significant deviations from a heterogeneous Poisson process in all combinations of the three most abundant species (Figure 1-4b). Beech, ash and, hornbeam exhibited strong repulsion patterns under the assumption of a heterogeneous Poisson process (SH2). Amongst all species, beech showed the shortest distances to its inter- and intraspecific nearest neighbours (s. Appendix Table A7-1) and the highest asymmetry in its interspecific distances, especially towards Sycamore. Moreover, while still being clumped, beech comes closest to a random nearest neighbour distribution of large trees (Figure 1-4b).

The empty-space function is suggested to be more sensitive towards the detection of clustering than the nearest neighbour distribution, as the detection of large empty spaces indicates gaps between conspecific clusters (Dixon 2002)**.** The observed empty space was in all cases larger than expected within a species both under homogeneity (not shown) and heterogeneity (Figure 1-4c). This implies a tendency towards clumping with conspecifics. Beech comes closest to a random empty space distribution of large trees. Please note that there is no bivariate version of the empty-space function.

a) SH2 - $g_{\mathrm{equal}}(r)$



b) SH3 - $g_{\mathrm{niche}}(r)$

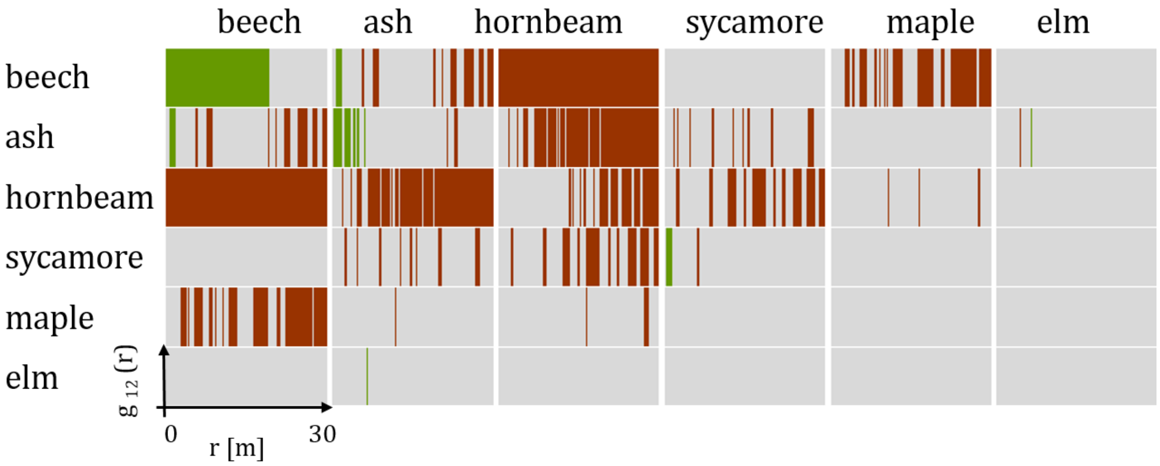
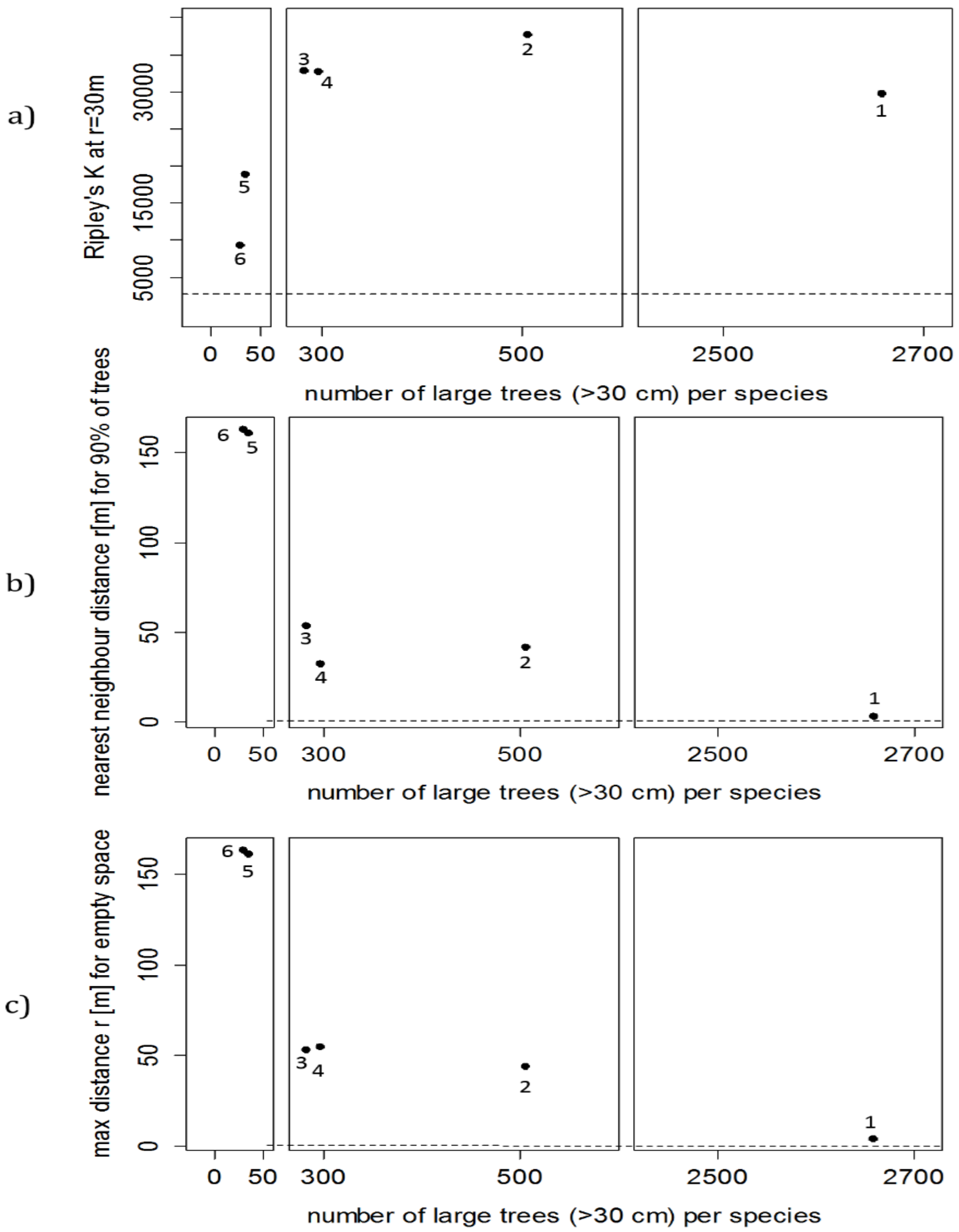


Figure 1-3 Univariate (plots on main diagonal) and bivariate (off-diagonal plots) pair-correlation functions within and between species for two null-models: *a) SH2 - equal heterogeneity, b) SH3 - niche heterogeneity. Diagonal plots show the results of univariate (intraspecific) pair-correlation functions, the off-diagonal plots of bivariate (interspecific) pair-correlation functions. Rows: focal species, columns: neighbouring species* g_{equal}*: simulation envelope created by heterogeneous Poisson process using large-tree density to characterize heterogeneity.* g_{niche}*: using species-specific large-tree density. Red= repulsion, grey= randomness or neutral interactions, green= clustering, bandwidth of smoothing kernel* σ*= 30 m. See Figure 2 for an illustration of how the colour code is derived.*



1= beech, 2=ash, 3=hornbeam, 4=sycamore, 5= Norway Maple, 6=elm

Figure 1-4 Number of large trees and the applied three summary functions a) *Ripley's K (the expected number of trees within r=30, normalised for density),* ***b)*** *the distance r where trees had a 90% probability to have their conspecific nearest neighbour,* ***c)*** *maximum distance r between a random location and the nearest tree for 90 % of the particular species (empty space). Dashed line: expected value under Complete Spatial Randomness (CSR; homogeneous Poisson process), calculated as* ***a)*** $\lambda\pi r^2$ *and* ***b), c)*** *expected value following Stoyan (2006, S. 140).*

1.3.2 Interaction between size classes within beech (SH 2)

The spatial patterns differed both within and between the size classes of beech. In the univariate pair-correlation-functions, i.e. within their size class, small and medium trees were clumped at small scales (< 15 m). In contrast, large trees showed repulsion at small scales (≤ ca. 8 m; Figure 1-5, plots on main diagonal). The bivariate cases, i.e. between size classes, the differences were more consistent. Between small and medium trees, there was a repulsion across all scales (Figure 4). Between small and large trees, there was also repulsion at almost all scales, except for clumping at small distances (ca. 2 m; Figure 1-5). Medium and large trees showed small scale repulsion (≤ ca. 8 m; Figure 1-5) and distributed randomly at larger scales.

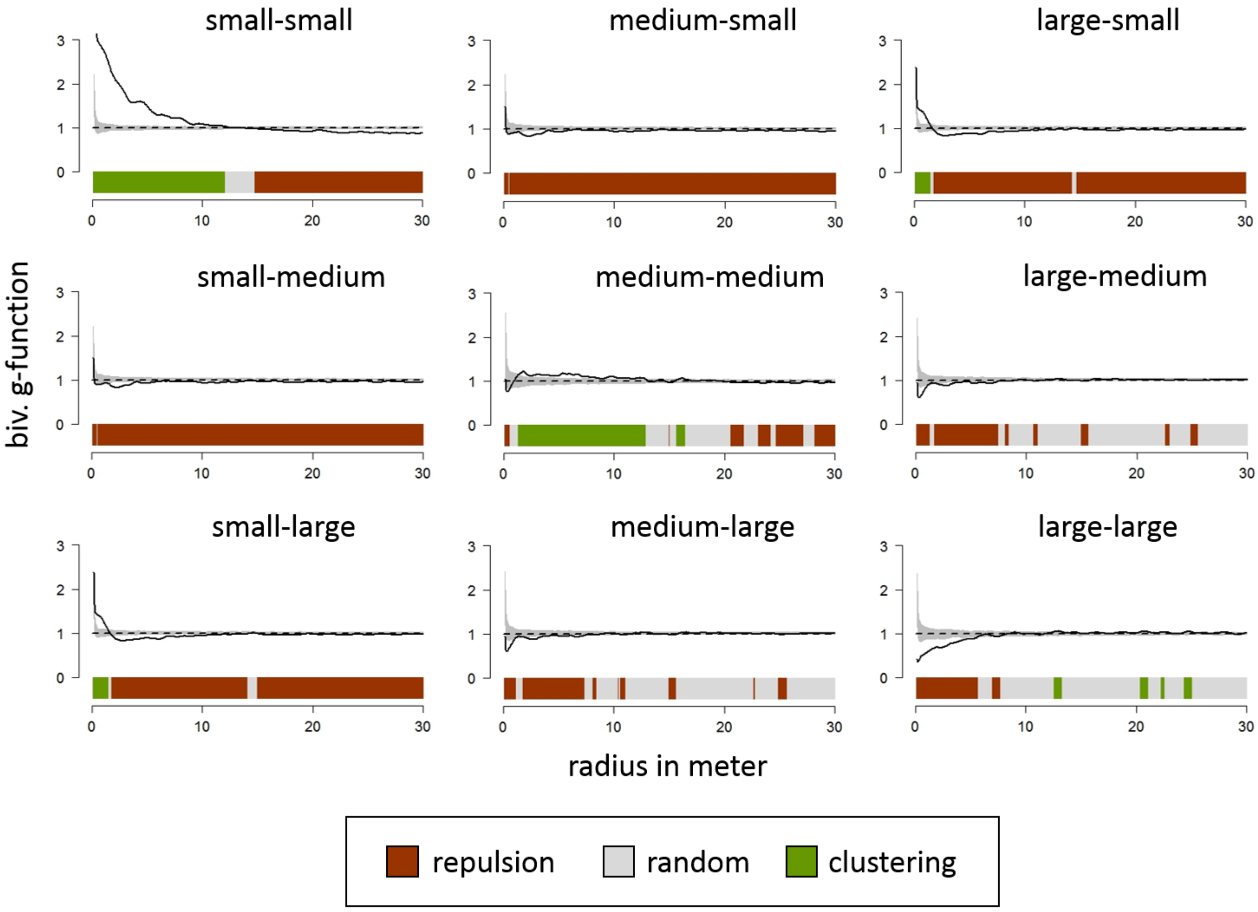


Figure 1-5 Bivariate intraspecific pair-correlation functions between the three size classes within beech under heterogeneity (SH2) *across all six species. Small trees DBH <10 cm, medium trees DBH 10-30 cm, large trees DBH >30 cm.*

1.3.3 Null-Model implications

We judged the adequacy of the null-models by their ability to capture a pattern as a random realisation of the modelled process. The assumption that habitat heterogeneity is experienced equally by all species as described by the large tree density of all species (SH2, $null_{equal}$ - g_{equal}) led to more random patterns than the assumption of global suitability (SH1, CSR; $null_{ubiq}$; Figure 1-3a). Assuming a species-specific habitat heterogeneity (SH3, $null_{niche}$ - g_{niche}) seemed to reproduce the point process only for the three more rare species: Sycamore, N. Maple, and Elm (Figure 1-3b). In most species and over most scales, the assumption of species-specific habitat heterogeneity poorly captured the patterns of the three most abundant species, indicating that for abundant species the null-model of species-specific habitat heterogeneity (SH3) does not mimic the pattern-creating process well.

At the level of interspecific interactions, the assumption of niches (SH3) sharpened the differences in the spatial distribution. Between the spatial distribution patterns of the three main species, comparing results under SH2 and SH3, assuming niches (i.e. SH3) moved the pattern towards stronger repulsions for the bivariate interaction of beech with hornbeam and of beech with maple (Figure 1-3a vs. Figure 1-3a). There was clear repulsion in the interactions between ash and hornbeam at scales above 10 m. At small distances the spatial distribution of ash and hornbeam fell within the simulation envelope as one realisation of the niche-assuming spatial process. With Maple, there was a switch from clustering in $null_{equal}$ (SH2) to repulsion in $null_{niche}$(SH3).

1.4 Discussion

In our detailed spatial analysis of coexistence mechanisms in a near-natural old-growth temperate forest, we found that spatial patterns were not homogeneous for four of the six studied tree species. Heterogeneity of spatial patterns was particularly apparent when intra- and interspecific interactions involved beech, the most common species in our study area. Thus, the necessary condition for resource competition is met, because heterogeneity is a factor in competitive interactions (Pielou 1961; Dovčiak, Frelich, and Reich 2001). In classic ecological theory, species that co-occur in spite of niche overlap either outcompete one another, segregate, or evolve towards character displacement (Chesson 2000a). We found evidence of segregation for the three most abundant species in our study, because interactions of beech, ash and, hornbeam showed repulsion under the assumption of niches. This fulfils the sufficient condition for competitive interactions and, in line with our first hypothesis, supports the status of beech as a supreme competitor. The spatial distribution of rare species was in accordance with the niche assumption, i.e. distributions of rare species were strongly determined by niche structure. Our second hypothesis concerning niche processes being more prevalent than neutral processes predominantly applies to the rare species of this study. Moreover, it agrees with our third hypothesis that rare species depend on safe sites, which was particularly apparent for light-demanding species such as ash.

Coexistence of the six species in the studied temperate forest is thus possible, at least theoretically, as it was indicated by the repulsion observed in the niche-based analysis. In practice, the natural coexistence potential between species can be difficult to identify because other processes co-occur, such as anthropogenic creation of admixtures as it was likely the case in our study plot (Butler-Manning 2008). Coexistence of different species is also promoted by density-dependent effects such as self-thinning (Clark and Clark 1984). Strong density-dependence indicates a concentration of intraspecific competition relative to interspecific competition (Cosner and Lazer 1984, Begon et al. 2006) and leads to monospecific clusters that are more likely to be attacked by pathogens. This effect seems to be more relevant in tropical forests (called Janzen-Connell-effect, (Janzen 1970, Connell 1971)). Here, we show strong density-dependence leading to coexistence also for a temperate forest, because density (SH 2, Figure 1-3a) was a better predictor than niches (SH 3, Figure 2b) for interactions with beech between the three most abundant species.

The asymmetric distances revealed in our nearest neighbour contingency analysis (Appendix Table A1) may be interpreted as evidence against species coexistence, because asymmetric competition over time necessarily leads to species exclusion. However, these analyses were done on a species level, so that species with different size structures were compared. For instance, ash that showed very little rejuvenation was compared with beech with diameters at breast height of less than 10 cm for most of the trees. This lack of saplings > 1.30 m in height in other species than beech is not necessarily an indication of species exclusion. In studies conducted in 2004, 2011, and 2012, plenty of trees with a height < 1.30m could be recorded (s. Chapter 2). There is heavy browsing damage by roe and red deer, which favour *Acer sp.*, ash, and hornbeam over beech. Ammer and Vor

(2013a) showed that asymmetric browsing puts ash and hornbeam at a disadvantage and leads to a higher proportion of beech. This also coincides with observations of Butler-Manning (2008) and our observations during field seasons 2011-2012 (Chapter 2).

The spatial arrangement between species seems to be driven by multiple processes, showing characteristics of density dependence as well as ecological distance. The number of large trees per species proved to be a good indicator for the order in nearest neighbour distances and empty space distribution functions. Here, Sycamore did follow that order, but seemed to form denser clusters than expected. This is in line with the assumption that rare species show higher clustering (Condit et al. 2000). The fact that we found a similar line-up of species depending on the numbers of large trees with respect to Ripley's K was unexpected as this index is already corrected for density. Here, beech showed less clumping than the other species at a given tree density. This might be due to strong intraspecific competition that leads to intraspecific repulsion effects. Alternatively, this intriguing dependence of spatial indices on tree density could also indicate that the studied tree species show a self-similar spatial distribution (Ostling et al. 2000). In this case, the strong competitive interactions between the three main species that we inferred from our analyses would be a result of numbers, not of ecological traits. However, there is no true evidence if this sorting according to numbers is either an ecological species effect or an effect of numbers.

Niche processes rather than neutral processes prevailed in the temperate forest under study. This is supported by the niche-based null-models that included species-specific heterogeneity. The three rare species were distributed randomly within their species-specific habitats in these models. However, this was not true for beech and hornbeam. Only for Ash, the niche-based null-model performed better than the one of equal heterogeneity. For these three most abundant species, assuming niches led to a full-scale repulsion pattern whenever they were considered in combination with each other. This seems to indicate that especially between the three most abundant species the repulsion effects (spatial segregation) becomes more pronounced during the interspecific thinning process. As we here only considered the density of large trees to reconstruct heterogeneity, we implicitly applied a space-for-time replacement, thus looking at a late point of a multi-species thinning process. This allows for the conclusions that niches do exist and are tangible by spatial analyses. Although, if present, full spatial co-occurrence or even complete spatial overlap could be detected with the applied method, the results stressed contrasts between the three most abundant species. The spatial separation of species was revealed even without further knowledge of the prevailing environmental conditions. These results suggest that niches in temperate forests are detectable by comparison to suitable heterogeneous null-models. If interactions are not strong, species-specific large-tree densities allowed reproducing the point process over several scales. However, if interactions are strong (i.e. in the case of competition), assuming niches led to a repulsion at all scales. The trees form only monospecific clusters, apart from a few small scale attractions between beech and ash. These seem to result from indifference of the large canopy Ash trees towards smaller beech trees and an attraction of beech towards the lighter canopies of ash. All in all, our findings strengthen the hypothesis that in a temperate forest system niches are important.

This analysis, although clearly indicating the existence of niches, does not reveal the properties that form the differences of the species' niches. For this, additional sampling on prevailing abiotic conditions especially concerning topography, light- and water availability is necessary.

1.5 Conclusions

Niches are detectable in temperate forests by describing species-specific habitat heterogeneity based on the spatial distribution of conspecific large trees. Furthermore, there are strong indications of density effects that might promote multi-species coexistence in these forests. We believe that this study is a step towards measuring and quantifying niche differentiation between coexisting and competing species. Moreover, our result that niches seem to be more pronounced in abundant than in rare species may hint at processes that are driven by frequency and less on species identity in a temperate forest context that merit further investigation.

1.6 Acknowledgements

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2 Chapter 2: The effects of spatial heterogeneity on abiotic niche separation in a semi-natural forest

Abstract

Most tree species compete for the same set of optimal conditions. If there is a niche overlap in species, habitat heterogeneity can still allow for species coexistence. While adverse conditions filter for similar species traits, competition drives evolution towards species differing in their traits. Our first aim was thus, to characterise abiotic conditions in a temperate forest under near-natural conditions. Our second aim was, to identify abiotic covariates that were critical for niche separation as well as abiotic covariates that were subject to niche overlap. We used a data set of almost 15,000 trees in the Hainich National Park in a mixed beech forest. We sampled the abiotic conditions on the study plot (28.5 ha) and used GAMs for predicting the abiotic covariates that would influence habitat suitability for each of the six studied species. Our results showed that the studied species indeed differed in the abiotic covariates that were important for modelling their size distribution in space. It is striking that species-specific habitat suitability was most affected by factors that were not facilitating but inhibiting, for example, beech was most influenced by slope. The critical variables of differentiation were small-scaled, e.g. in soil layers that were only 10 cm apart. This might indicate that while habitat filtering acts at larger scale (e.g. excluding beech from steep slopes), niche differentiation is small-scaled where competing species co-occur.

2.1 Introduction: Spatial heterogeneity, indicator values and species dominance

The spatial patterns of commonness or rarity of species over different scales play a key role in ecology (Chesson 2000b, Chave 2004). A general pattern is that there are few abundant and many rare species (McGill et al. 2007). The persisting presence of rare species is puzzling, especially in cases of rare species that persist in the presence of strong competitors despite niche overlap. Theory attributes the persistence of these rare species to specialisation, reduction of niche overlap, and to rare-species advantages such as lower intraspecific competition in small populations (McGill et al. 2007), or in neutral theory, be the result of ecological drift (Hubbell 2001). The persistence of species in general and the abundance of species in specific can be affected by a number of factors acting over different temporal scales. At the scale of a few generations, species may persist due to local adaptation to environmental conditions, due to competitiveness relative to co-occurring species, and due to intraspecific regulation, due to density dependence in competing species or by stochasticity. At evolutionary time scales, individuals of a species are selected towards stabilising the fundamental niche (Pearman et al. 2008) of the species in heterogeneous landscapes(Holt and Gaines 1992). Classic niche theory predicts that species may co-occur if they tend to differ in their requirements, i.e. in their niches (Kraft et al. 2008), resulting in niche differentiation. At the same time, habitat filtering might limit the suite of species that can occur at any one location (Keddy 1992), resulting in a species ensemble of ecologically similar species. Both mechanisms, niche formation and habitat filtering, form opposing poles of species similarity in space (Scheffer and van Nes 2006; Hardy and Sonké 2004). Scheffer and van Nes (2006b) proposed to consider the slow replacement of species by similar competitors as an additional mechanism of coexistence, explaining the co-occurrence of similar species in spatial clusters. By acknowledging transient coexistence, they softened the contrasting requirements for coexistence that species either need to be different enough or similar enough to coexist (Vergnon et al. 2012).

Niche availability is variable in space because habitat properties show spatial patterns. Some abiotic habitat properties tend to form larger continuous patches (e.g. topographic habitats), while other properties tend to vary at smaller scales (e.g. water availability). Due to these complex patterns, few individuals grow at their maximum growth rate because most individuals occur in non-optimal conditions. They survive because they can still show higher growth rates than other individuals of other species for which a certain location is even more suboptimal (Ellenberg et al. 1991; Blanco 1993; Leuschner and Ellenberg 2010).

Previous studies have linked the spatial patterns of trees to the prevailing differences in topography (Pelissier 1998, Harms et al. 2001, Itoh et al. 2003, Punchi-Manage et al. 2013). However, these studies address tropical forests whereas in temperate broadleaved forests, topography is rarely distinct enough to form disjunctive sub-habitats and explain the observed heterogeneity in the spatial pattern of tree species distribution. Topography is an indirect descriptor of habitat properties and in absence of pronounced variation in topography one can expect changes in habitat properties to be more subtle as well.

Therefore, different approaches are necessary to explain spatial patterns of trees in temperate broadleaved forests. In order to link spatial patterns of trees and environmental properties, it seems thus necessary to combine directly measured abiotic variables under field conditions and statistical analysis of the relationship between spatial tree distributions (Wang et al. 2011).

We tested this approach of directly linking abiotic and biotic patterns in the temperate broadleaved forest of Hainich National Park. Chapter 1 showed that heterogeneity in overall abiotic conditions (derived from the spatial distribution of all species) was a useful explanatory variable of the spatial pattern of most species (except Ash and Sycamore, and its combination) and of their spatial patterns of co-occurrence. Thus heterogeneity in abiotic conditions can be expected to be an important driver of these spatial coexistence patterns. In the Hainich, first steps in this direction have been taken, however, using indirect measures of the abiotic environment only. Ratcliffe et al. (Ratcliffe et al. 2015) found that topography-derived estimators of abiotic conditions have little power to predict tree growth patterns. Instead, individual tree growth in the Hainich is sensitive to diversity and composition of neighbouring trees (Ratcliffe et al. 2015), and mortality links tree growth with tree density (Holzwarth et al. 2012). As there are indications that the observation of a non-homogeneous tree pattern may result from abiotic heterogeneity (Getzin et al. 2008, Wang et al. 2011, Shen et al. 2013), we aim at uncovering the links between the prevailing abiotic conditions and spatial patterns of tree distribution in this multi-species setting.

Thus, our first aim (Aim 1) was to describe potential abiotic drivers of spatial pattern formation in the tree layer. This was done to identify properties that characterise sub-habitats that are especially suitable for one particular or several species. In the Hainich, the proportion of admixed species is higher than usual for old-growth National Parks with beech as a main species (Tabaku 2000, Butler-Manning 2008, Leuschner et al. 2009, Trotsiuk et al. 2012). Although most of the admixed species have been favoured by previous management (Butler-Manning 2008), environmental heterogeneity still allows a continued coexistence of the dominant and admixed species, and Aim 1 specifically asks for the sub-habitats that allow for growth of the admixed species.

Our results in Chapter 1 indicated that during succession in the temperate broadleaved forest of Hainich National Park, the three most common species (beech, ash and hornbeam) would exhibit patterns of spatial exclusion, presumably due to competitive interactions and niche processes. In contrast, the three locally rare species (sycamore, Norway maple, and elm) showed patterns of spatial randomness or spatial patterns of heterogeneity in tree density. Thus, our second aim (Aim 2) was to assess whether divergent patterns of locally common and rare tree species are an effect of competitive exclusion or of different habitat requirements, i.e. if differences in the fundamental niche along the gradient of abundant, intermediate, and rare species lead to spatial exclusion among abundant species.

In order to describe the abiotic heterogeneity (Aim 1) potentially critical for the persistence of admixed species, we followed three approaches. First, similar to studies of tropical forests, we described topography using a Digital Elevation Model (DEM) from high-resolution LiDAR data. Second, we additionally measured physical and chemical conditions, to describe e.g. light and soil properties. Third, we determined indicator values (Ellenberg et al. 1991). Indicator values are ordinal classifications of ground vegetation along gradients reflecting light, temperature, continentality, moisture, soil pH, fertility, and salinity. They integrate over temporal variations at a location and thereby relate measurements to plant-perception (Jongman et al. 2002). We applied both approaches (two and three) to be able to compare such direct and indirect measurements for niche construction.

We characterised the abiotic environment (Aim 1) to characterise the abiotic heterogeneity for the whole study area. We used generalised additive models (herein GAMs) as a spatial interpolation method between sample points. First, each measured abiotic covariate was interpolated and we chose the spline type that would produce the most accurate fit for each abiotic covariate. Second, to infer on the impact of the abiotic environment on the tree layer (Aim 2), we used GAMs to explain the tree size of each species by combining abiotic covariates and thus delineating the abiotic conditions that determine habitat suitability and, ultimately, the (realised) abiotic niche of the tree species. We were interested whether the spatial segregation observed in Chapter 1 could be attributed to differences in utilised abiotic components or the impact of the abiotic environment on the tree layer.

2.2 Material and Methods

2.2.1 Study area and ecological properties of the studied tree species

This study was conducted in a 28.5 ha area of an old-growth mixed-beech forest in the Hainich National Park (51° 06’ N, 10° 31’ E), Thuringia, Germany. The study area has a gentle slope of <1°, except for a gully area, where the slope is about 8° degrees and the soil is considerably wetter. In contrast to the slope, soil type, and soil depth are highly heterogeneous (Mund 2004). Triassic limestone bedrock is covered by layers of loess varying in their depth at small spatial scales (Mund 2004). *Rendzina* or *Terra fusca* soil types dominate where the loess layer is very thin, and various brown soils (*Braun*- and *Parabraunerde*) or *Cambisols* to *Luvisols* are found in locations with a thicker loess layer (Mund 2004). All trees were mapped in 1999 and 2007 (Butler-Manning 2008). Within the study area, beech accounts for about 90% of the trees. It is the only tree species that shows noticeable successful recruitment (Huss and Butler-Manning 2006).

Beech (*Fagus sylvatica*) is largely considered a highly dominant species as it has a large niche breadth (Pignatti et al. 1996, Leuschner and Ellenberg 2010a). However, the occurrence of beech can be limited by late frost, sunburn, and dry and wet soils. Less competitive species can thus outperform beech in habitats prone to the occurrence of these limiting conditions (Leuschner and Ellenberg 2010a). Ash (*Fraxinus excelsior*) is the second most abundant species, with most of the Ash individuals being large-canopy trees (Butler-Manning 2008). Ash changes its light preference from being fairly shade tolerant in juvenile stages to light demanding as adult trees (Dobrowolska et al. 2011). Hornbeam (*Carpinus betulus)* shows ecological preferences similar to beech, but is less shade tolerant and culminates early in height and diameter growth (Lockow and Lockow 2009). However, hornbeam can outperform beech on soils that show a high content of loam or clay (Schmidt et al. 2011).

Hornbeam and Sycamore (*Acer pseudoplatanus*) occurred in almost equal numbers. Sycamore is light-demanding but can tolerate wetter and steeper habitats than hornbeam or beech. In other conditions, sycamore is inferior competitor to beech (Roloff 2009). Norway maple (*Acer platanoides*) was in 1999 the rarest of the six studied species. It can tolerate drier and wetter sites than sycamore with lesser nutrients and poorer aerated soils. However, Norway maple is light-demanding, sensitive to late frosts and of limited height (Hein et al. 2009). *Fraxinus* and *Acer* species are known as specialists of alluvial and slope forests. We thus expected especially wet and steep subareas to influence the distribution of these admixed species. Elm (*Ulmus glabra*) prefers half-shade conditions on nutrient-rich, deep soils without consolidation (Schmidt et al. 2011). Being more abundant than Norway maple in 1999, elm lost almost half its individuals between 1999 and 2007.

2.2.2 Digital Elevation Model (DEM) and Topographic Wetness Index

A DEM derived from data surveyed on a LiDAR flight (Schulze, unpublished data) was used as continuous topography data. The resolution was 0.5 m by 0.5 m and covered the whole study area. SAGA GIS and RSAGA (Olaya 2004, Cimmery 2010, Conrad et al. 2015) were used to calculate the abiotic covariates from the DEM (Tab. 1). The TWI (Topographic Wetness Index) describes the amount of water at a location depending on the upslope area and the slope and can be used to characterise hydrological conditions (Kopecky and Cizkova 2010). Due to nutrient leaching and erosion, the TWI can also be an indicator for nutrient availability (Chapin, Matson, and Vitousek 2011). Hill Shading gives information on the direction of incoming light and the Cross Sectional Curvature (Zevenbergen and Thorne 1987) gives information of the divergent or convergent character of the water flow, thus is can detect areas without drain.

Table 2-1 Topographic variables estimated from LiDAR data

Name	**Description**
Aspect	Horizontal direction that the ground faces
Catchment area	Upslope area (m^2)
Curvature	Rate of change of the slope
Cross Sectional Curvature	Convergent or divergent character of the flow
Elevation	Height above sea level
Hill Shading	Direction of incoming light
Slope	Inclination of the ground
Topographic Wetness Index (TWI)	ln(a/tan(b)), where a is the specific upslope area (catchment area) and b is the slope

2.2.3 General sampling design and data collection

Information on tree position, tree species identity, and tree size was collected in 1999 and again in 2007. We used a modification of the 50 m × 50 m sample grid established in 1999 in the study area (Figure. 2-1, (Butler-Manning 2008) to characterise spatial heterogeneity in terms of physical and chemical conditions as well as indicator values. We established a coarser sampling grid within the study area. Each grid cell was 100 m by 100 m. We took our measurements in each corner of the grid cell plus at the grid cell centre (sample plots). We marked a 10 m × 10 m (100 m^2) sample area around each centre point of our sample plots. Within the 62 resulting sample plots, all physical measurements, and vegetation relevés were conducted (not including the LiDAR data).

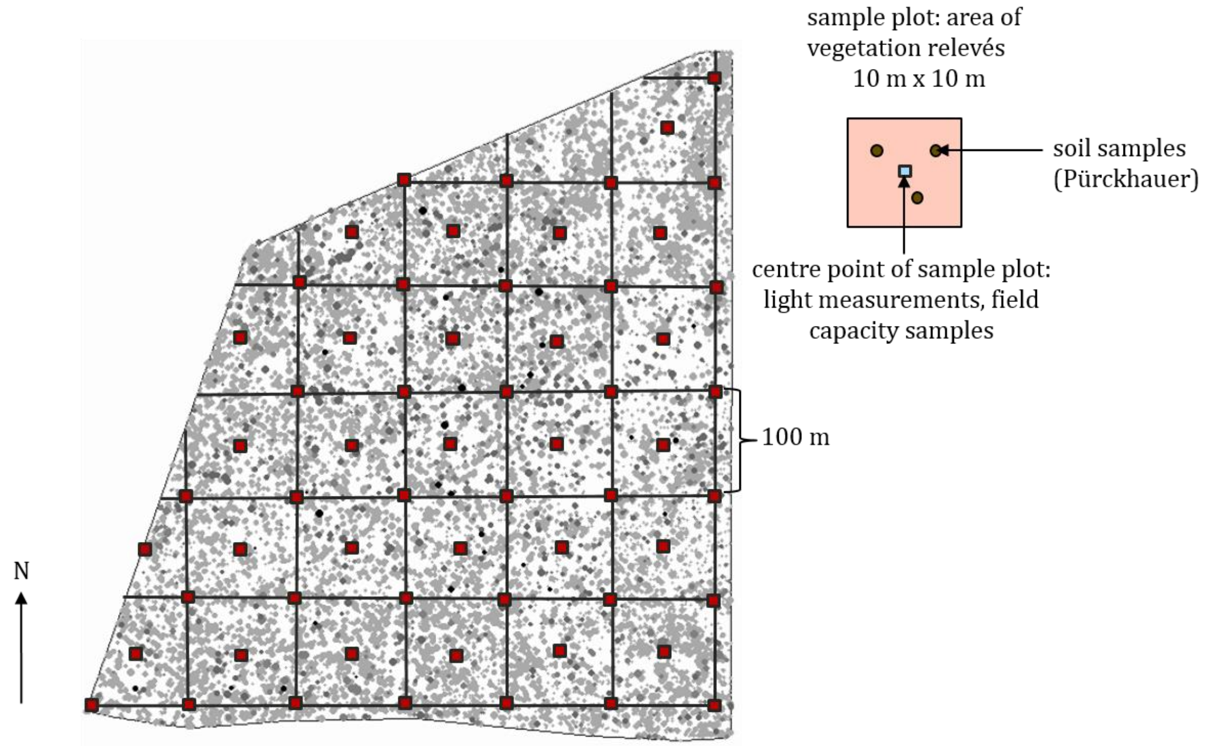

Figure 2-1 Sample design*. Grey outline: study plot. Dots: tree positions in 2007. Black lines: transects forming the 100 x100 m grid. At each intersect and in the grid cell centre: red square: sample area (10 m x10 m) of vegetation relevés and soil samples brown dots: soil samples within sample area (up to three soil samples per sample period, three sample periods in total, blue square: centre point of sample plot*

2.2.4 Soil samples and water content

Pürckhauer soil samples were taken in all 62 sample plots in early May 2011, end of July 2011, and March 2012. In order to include information on soil conditions before and after budburst as well as in full foliation, we conducted a series of soil core sampling and field capacity measurements.

Before sampling, the litter layer was removed. Soil samples were taken at the coarse grid scale with a gauge auger (Pürckhauer) of 100 cm core length and inner diameter of 18 mm. The auger was driven into the soil with as few strikes as possible. The end was defined by making no progress for a maximum of three powerful strikes to ensure that smaller obstacles e.g., small roots or stones, would be destroyed.

Total soil depth was defined as the depth from the top of the mineral soil (A-horizon) down to the transition zone to the bedrock (C-horizon). Sampling was repeated twice within 50 cm of the first sample if a) no bedrock was visible in the soil core, b) a root or a smaller rock seemed to have stopped the auger, and c) soil depth was greater than 100 cm.

In order to minimise soil compaction or dislocation, the auger was pulled out as straight and smoothly as possible, avoiding rocking or rotating the tube if at all possible. After taking the sample, sampling depth was determined and the extracted core was divided into 10 cm pieces to gain information on the spatial water distribution. Each sub-sample was kept in a sampling paper bag. In order to minimise transpiration, each paper bag was enclosed into three layers of plastic bags. All samples were kept in the shade and transported with cooling. Weight measurements were conducted on the same day as the sampling, with samples stored in the fridge (< 7 °C) as soon as possible. After determining the fresh weight, samples were dried at 105 °C for at least 24 hours. Afterwards, soil samples were returned into the oven and re-weighted up to three times within one week until weight no longer changed. The final weight was considered as dry weight. We defined water content per 10 cm piece as the difference between fresh weight (FW_sampledepth/10) and dry weight (DW sampledepth/10). Total soil water content was defined as the sum of the water content of all pieces within one sample. A high content of clay and stone in the soil prevented us from extracting undisturbed samples. As a consequence, we determined gravimetric water content, but not volumetric water content.

2.2.5 Soil water storage and plant-available water

Soil samples for field capacity measurements were taken in March 2012. Water availability depends on physical soil properties, such as grain and pore sizes. The matrix potential of a given soil determines how difficult it is for a plant to extract water from this soil. The smaller the grain and pore size (i.e. the greater the clay content), the more difficult water extraction becomes while soil water storage ability increases. Consequently, water content can differ from plant available water. Thus, we determined both water storage ability of the soil and plant-available water.

The soil sample ring for measuring soil water storage ability had an inner volume of 100 cm^3 (internal dimension 57.0 mm x 40.5 mm). These samples were taken at the coarse grid scale after removing the litter layer. We calculated plant-available water as:

$$PAW = FC - PWP$$

where *PAW* is the plant-available water, *FC* the field capacity (180 kPa), which is the contained water two days after saturation when excess water has run off, and *PWP* is the contained water at permanent wilting point (20 kPa). The measurements of field capacity were conducted after two days of soil water saturation, increasing pressure each week in the steps 180, 200, 250, 300, 350, 370, and 420 kPa and weight measurements after sampling, and after drying.

2.2.6 Light availability and canopy photos

We took hemispherical photos for light measurements with a NIKON (D90 camera and AF-S DX NIKKOR 10–24 mm 1:3.5–4.5G ED lens, effective angular field 109°) at the centre pole of the sample areas when foliation was complete (July 2011). The camera was turned skywards, a bubble level ensured a horizontal position photos at a height of 130 cm. To account for underestimation of leaf coverage due to overexposure (Glatthorn and Beckschäfer 2014), we took photos with automatic exposure as well as underexposed pictures with exposure value -3.0 (Zhang et al. 2005). Photos were taken against a cloud cover as uniform as possible, preferring overcast days to avoid scattered light (Seidel 2011). In cases where taking photos at the centre of the sample areas prevented by a blocking tree or low large branches, photos were taken at each of the four corners of the sample area. We took high resolution pictures (4288 x 2848 pixels) with ISO set to 200 and focus ring set to infinity (Jonckheere et al. 2005). The photos were converted into binary pictures (Jonckheere et al. 2004) and further analysed with the freeware image tool ImageJ (Abràmoff et al. 2004). We calculated the mean gap area, perimeter and shape of all gaps larger than 10 pixels for all plot photos. In cases where photos were taken at the sample plot corners, these statistics were calculated as the mean over the four positions. Where manual exposure yielded a higher value for vegetation cover than automated, these photos were used. From these extracted values, we calculated the gap shape complexity index GSCI of all gaps, and median GSCI considering the three largest gaps (Getzin et al. 2012).

2.2.7 Species composition and indices

The vegetation relevés were conducted from May to June 2011 at the 62 sample plots of 100 m^2 size (Muller-Dombois and Ellenberg 1974). Vegetation cover of all vascular plants < 130 cm was estimated per species in steps of 5% and estimated on a modified Braun-Blanquet scale (Reichelt and Wilmanns 1973, Wilmanns 1989). If species cover was below 5% (Londo 1976), individuals were counted. Ellenberg's indicator values (Ellenberg et al. 1991) describe the occurrence probability of species along the gradients of several abiotic habitat properties on a nine level scale (Ellenberg et al. 1991). As these values describe the realised niches of the understorey, we used these realised niches of the species from the undergrowth layer to infer the conditions that may form the fundamental niches for the tree layer. We expected to find the most pronounced differentiation in light and wetness; we thus focused on these two abiotic factors. For these two, we considered several aspects, whereas we represented other abiotic environmental variables by indicator values only.

2.2.8 Statistical methods

Environmental variables were sampled at 62 sample plots spread over the whole study plot. Afterwards, we conducted a sequence of statistical analyses: 1) Data interpolation, 2) choice of variables for abiotic habitat model, and 3) building of tree model (Figure 2 - 2). Our first step was spatial interpolation of the variables sampled in grid mode to cover the whole area.

Because our previous analyses suggested a highly non-linear relationship between abiotic covariates and tree layer (Saefken et al. 2013), we used generalised additive models (herein: GAMs). We chose the spline type that would produce the most accurate fit for each abiotic covariate. We chose the most suitable model based on lowest AIC and highest R^2-values (Wood and Augustin 2002).

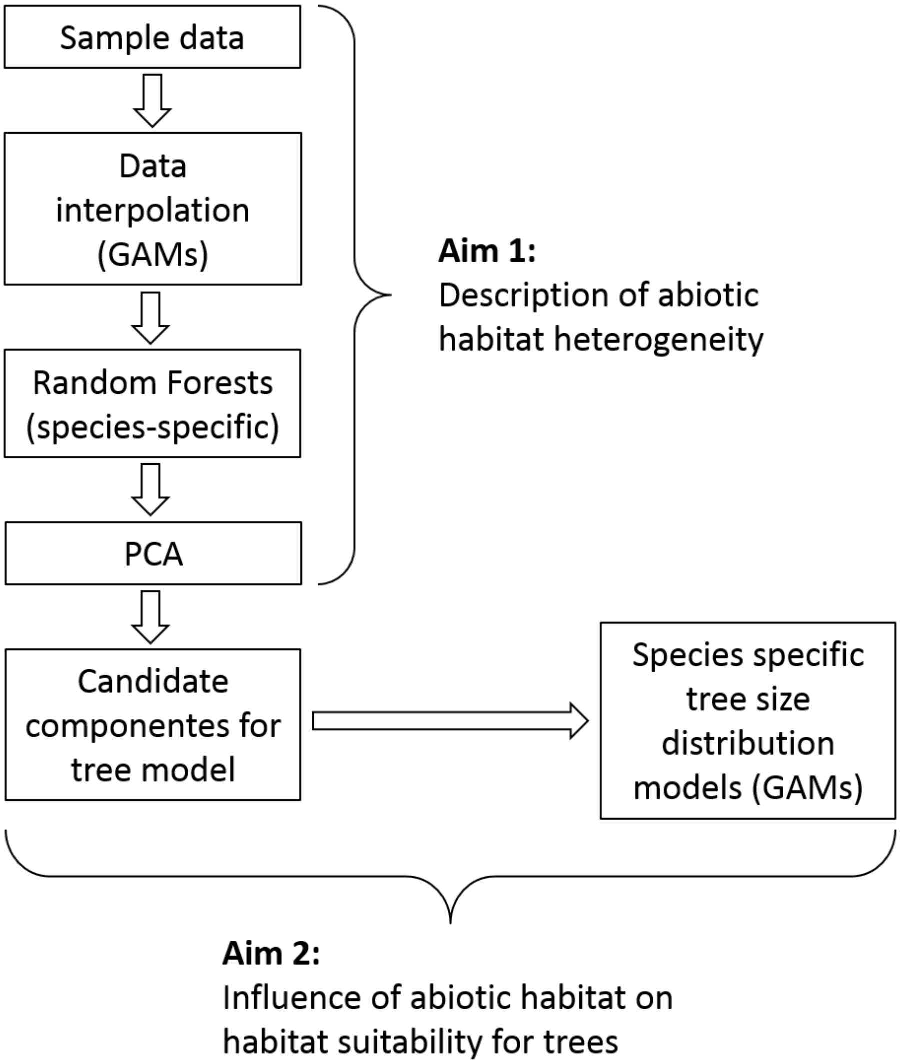

Figure 2-2 Work flow of statistical analysis *from field data to habitat description (Aim 1) to an abiotic model for tree size distribution (Aim 2).*

Most of the abiotic covariates did not share the same units and moreover, they could not be assumed to occur in isotropic formations. We therefore used anisotropic tensor products for smoothing, (Wood 2006), allowing different units and the unsymmetrical smoothing kernel shape, because spline shape is estimated in x- and y- direction separately. The interpolation results were used to describe the spatial distribution of abiotic conditions, thus characterising the habitat conditions (Aim 1) for each species.

Aim 2 was to identify suitable sub-regions as suggested by DBH-distribution. From the total of 101 sampled possible variables plus 10 derived from topography, we needed to reduce the number of variables considered as candidates for an abiotic habitat model. For this, we used Random Forests (Breiman 2001), implemented in the R-package randomForest (Liaw and Wiener 2002). Random Forests is an ensemble learning method for classification. It gives estimates of what variables are important in the classification by growing multiple independent decision trees from randomly selected subspaces of data. Classes or mean predictions that are chosen with the highest frequency over all grown trees are used. A further advantage for using Random Forests on field data is that it can handle missing data well and is insensitive to noise (Biau 2012). Random forests correct for overfitting to their training set (Breiman 2001). For the tree model, we used the abiotic covariates identified as important by the classification method as a point of departure for a backward selection. This was possible for beech, ash, hornbeam, and sycamore, while Norway maple and elm had too few individuals compared to the possible variables influencing them. For the two latter species, we did a backward selection when implementing the GAMs based on the common variables chosen in the models for beech, ash, and sycamore.

In order to account for possible multicollinearity, we conducted PCAs to check whether related covariates (Graham 2003) were successfully avoided in the Random Forests approach. Within the correlated variables we ensured that the variable that showed the higher coverage for variance, i.e. the one contributing most to the axis, was included in the candidate model. Log-transformation was performed on gap metric values. By log-transforming these values we avoided gap area being chosen as highly influential due to their high variance alone.

When the set of possible, non-correlated variables was determined, we applied GAMs to link tree patterns with spatial patterns of environmental variables. We chose GAMs as there were no indications for assuming a linear relationship between the spatial pattern of tree sizes and the abiotic variables. We used tree size as a response variable and the previously interpolated values of the environmental variables at the tree position as explaining variables. While tree density is used more frequently than tree size as a response variable (Clark and Clark 1984, Chesson 2000b, Bagchi 2007), we decided not to use tree density because in our study area tree density is likely to be influenced by strong interaction links, such as competition, that may cause mortality (Bagchi et al. 2011, Holzwarth et al. 2013). We also included space into the tree model where it performed better than the non-spatial equivalent. Because Elm had too few individuals for this analysis, we were restricted in the tree size model for Elm to identifying the amount explained by the two most influential covariates.

Thus, this general model (hereafter called tree model) for modelling the DBH structure was adjusted depending on the best suitable abiotic covariates for the different tree species:

$$DBH_{species\ i}(x, y) = f(x, y) + f(abiot_{1(x,y)}) + \ldots + f(abiot_{n(x,y)}) + \varepsilon$$

The species specific DBH was predicted for each location by using the predicted values for topographic and measured covariates for this location. The best model was chosen based on AIC and R^2. All statistical analyses were carried out in R 3.2.2 (R Core Team 2015) using the *mgcv* package (Wood 2006).

2.3 Results

2.3.1 Abiotic covariates and their interpolation (Aim 1)

Our first aim was to describe and characterise their spatial distribution of the prevailing abiotic conditions which the different tree species experience in the study area. We therefore measured or calculated in total 101 abiotic environmental variables (see Table 2-2) at a regular grid of 62 sample plots covering the whole study area. The measured environmental variables included information on soil depth, the vertical distribution of water at a 10 cm resolution, and differences in water content per 10 cm as well as the whole sampling core. The differences in space were observable within the vertical distribution of water. Typically, the mid-parts of the soil cores would include the least water, the upper levels would show the highest variability within time and the lowest parts were less variable. Usually, the clay content increased in depth above 60 to 70 cm. Sampling the soil was conducted three times in roughly two month intervals, resulting in a description of the seasonal variation in time. Soil moisture varied both in space and time (see Table 2-2 and Figure 2-3) but with no obvious trend.

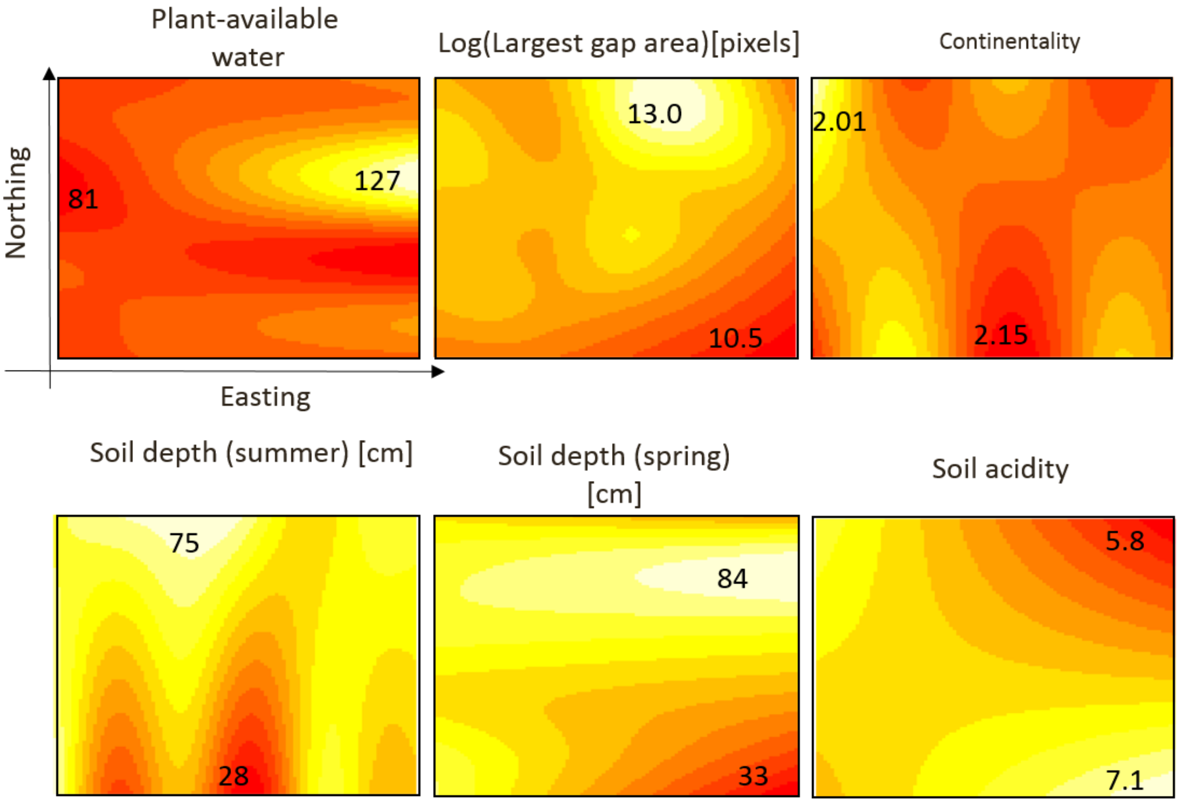

***Figure 2-3 Best interpolation results of the sampled abiotic covariates** that were most influential for predicting tree size. The lighter the colouring the higher the predicted values. Note that interpolations in each picture has its own scaling and different units. Continentality is a measure of the range of temperatures that tend to occur, it is a good indicator for variations in the difference between January and July temperatures.*

Gap properties varied largely between the plots. Some plots contained gaps a hundred times larger than the largest gaps of other plots (Appendix Table 9-1). Moreover, we computed seven abiotic Ellenberg indicator values based on Ellenberg (1991) with the plant information from the vegetation relevés (Table 2-3). We identified 65 different plant species on our sample areas, eight of which were tree species. The range of species richness was 5 to 28 species per 100 m^2 with a mean of 12 (±4) species. The indicator values showed a small range and little variation between the sample plots (Table 2-3).

Table 2-2 Abiotic variables *calculated from field capacity and field measurements (soil samples, hemispherical photos)*

Variable name	Description
wL.spec	Light indicator value weighted by species cover
wT.spec	Temperature indicator value weighted by species cover
wK.spec	Continentality indicator value weighted by species cover
wR.spec	Acidity indicator value weighted by species cover
wF.spec	Wetness indicator value weighted by species cover
wN.spec	Nitrogen indicator value weighted by species cover
Area.max1	Largest gap area
Area.max2	Second largest gap area
Area.max3	Third largest gap area
GSCI.max1	Gap Shape Complexity index of largest gap
GSCI.max2	Gap Shape Complexity index of second largest gap
GSCI.max3	Gap Shape Complexity index of third largest gap
GCSIplot.median	Median of Gap Shape Complexity index of three largest gap
nFK or PAW	Plant available water
pF1_8	Fresh weight when saturated with water (pF 1.8 bar)
MD1_1	Maximum soil depth in May
MD2_1	Maximum soil depth in July
MD3_1	Maximum soil depth in March
var_depth	Variation in soil depth between samples
sd_depth	Standard deviation of soil depth between samples
mean_depth	Mean soil depth over three sample periods
Perim.max1	Largest gap perimeter
Perim.max2	Second largest gap perimeter
Perim.max3	Third largest gap perimeter
DUS2_1	Dry weight of upper soil in July
FWUS2_1	Fresh weight of upper soil cm in July (Pürckhauer)
DWUS2_1	Fresh weight of upper soil cm in July (Pürckhauer)
FW2_1_1	Fresh weight of upper 10 cm soil in July (Pürckhauer)
FW2_1_2	Fresh weight of upper 10-20 cm soil in July (Pürckhauer)
FW2_1_3	Fresh weight of upper 20-30 cm soil in July (Pürckhauer)
FW2_1_4	Fresh weight of upper 30-40 cm soil in July (Pürckhauer)
FW2_1_5	Fresh weight of upper 40-50 cm soil in July (Pürckhauer)
FW2_1_6	Fresh weight of upper 50-60 cm soil in July (Pürckhauer)
FW2_1_7	Fresh weight of upper 60-70 cm soil in July (Pürckhauer)
FW2_1_8	Fresh weight of upper 70-80 cm soil in July (Pürckhauer)
FW2_1_9	Fresh weight of upper 80-90 cm soil in July (Pürckhauer)
DW2_1_1 - DW2_1_9	Same as above for dry weight
diff.soil1	Contained water in first 10 cm soil
diff.soil2	Contained water in first 10-20 cm soil
diff.soil3	Contained water in first 20-30 cm soil
diff.soil4	Contained water in first 30-40cm soil
diff.soil5	Contained water in first 40-50 cm soil
cont.water	Sum of contained water in first 10-50 cm soil

Table 2-3 Summary of indicator values and number of species *< 130 cm height over all 62 sample plots (10 m x10 m). Ellenberg indicator values were weighted by species cover at the plot level. Weighted Ellenberg indicator values following standard German abbreviations : wL= light, wT=temperature, wK= Continentality (Kontinentalität), wF=wetness (Feuchte), wR=reaction, wN=nitrogen.* R^2 *= explained variance by best interpolation model of field data (GAM).*

Weighted indicator values	**Mean**	**Range (± standard deviation)**	R^2
wL	3.4	2.57-5 (±0.42)	0.19
wT	4.9	3.36-4.67 (±0.31)	0.27
wK	2.15	1.67-2.5 (±0.2)	0.11
wF	5.39	4.22-6.68 (±0.52)	0.25
wR	6.49	5.25-7.37 (± 0.52)	0.25
wN	5.07	4.06-6.25 (±0.45)	0.18
Num. species	11.94	5-28 (±4.34)	not applicable

In order to gain continuous spatial information, we interpolated all 101 different abiotic covariates (Appendix Table A7-2). In all interpolations of abiotic covariates, tensor product splines outperformed isotropic smoothers, except for the weighted indicator values for light and the logarithm of the gap area. The fit of the interpolation was generally low, usually explaining about 20% of the observed variance. R^2 varied from 0.03 for the differences in soil water content at 40 cm depth to 0.56 for the soil depth in July. In general, soil depth, mean values, and largest gap area were better predicted by our models than parameters with stronger fluctuations, such as contained water in soil and gap shape. Also, Ellenberg indicator values were predicted with low fit (R^2=0.11 to 0.27). Soil water content and soil depth differed in local values as well as in spatial distribution (Figure 2-3) between the three sampling periods. Differences in soil depth can be partly attributed to seasonal changes in water content that made it difficult to drive the auger deeper into the soil.

2.3.2 Modelling tree species diameter from the interpolated abiotic covariates (Aim 2)

Our second aim was to connect the abiotic environment to the tree layer. In order to analyse the fundamental niches of the tree species more closely, we tried to predict the DBH distribution in space for each species. Based on our analysis with Random Forests, tree size was influenced by multiple covariates (Table 2-4). The best performing tree models included more detailed variables, especially in soil information, than the respective PCAs. We did not include correlated variables in the final species models (Table 2-4). That reduced the variables for light to the logarithm of the largest gap and median GCSI. Included in the final tree size models were also variables derived from the DEM: Slope, TWI, Hill shading, and Cross Sectional Curvature (Table 2-4 and 2-5). The included variables for the model with the highest R^2 value and the lowest AIC are presented in Table 4 and 5 (R^2 of final model).

The PCA (Appendix Figures A 8-1 to A 8-3) showed that most measured variables have little shared variance. PCA had soil effects as a first principle component with the variance in soil depth over time contributing most. The second principal component can be characterised as describing water related summer conditions. This axis was loaded by plant-available water capacity, soil depth in summer, contained water in summer and Hill Shading. The PCA confirmed that the indicator values did not share variance but contain different information.

Tree species differed in the abiotic covariates that had the greatest influence (based on variable importance from Random Forests and R^2) on their size (Table 2-5). Including space into the model improved model predictions for Ash and Hornbeam, which were the second and third most abundant species. The best tree models included information that was specific to soil layer and time. Covariates that influenced water availability appeared to have the highest impact on most of the tree species. Fresh weight was identified to be more influential for tree size, although dry weight can be considered the more constant property. Before including topographic variables, species showed the abundance-dependent line- up as indicated from the spatial patterns of Chapter 1 (Appendix Table A9-5), meaning that the DBH of beech could be predicted with the least, Elm with the highest accuracy. However, including topographic variables improved the model fit, but dissolved the abundance-dependent pattern. Especially for beech, including topography improved the predictive power (cf. Table 2-5 to Appendix Table A 8-5). However, the tree size model of beech still had a low fit, although it was the most complex model.

Only Slope considerably influenced habitat suitability for beech, with only few beech trees growing into large trees on steeper slopes whereas the other covariates had relatively small influence. Soil information related to summer droughts were also influential. The tree size distribution of ash, sycamore, and Norway maple could be better predicted than for beech, hornbeam or elm by abiotic habitat information. This better model fit was not related to DBH distribution or species frequency. It coincided with one of the water-related covariates being most influential on the tree size of the concerning species. Predictions for beech improved when allowing for a higher degree of non-linearity i.e. increasing the number of nodes.

Predicting beech sizes required the highest number of abiotic covariates included into the model. We found evidence of the different tree species showing different realised niches in the subset of abiotic conditions (Table 2-4) that was most influential for their habitat suitability. Within the model, beech reacted particularly sensitive towards slope. Ash was sensitive to temporal variation in soil depth, and water content in the upper layers, especially in summer, and topography. The tree size of Hornbeam is also influenced by numerous factors, soil acidity being the most pronounced among them. Sycamore was most influenced by covariates that are related to light and water availability. The tree size of Norway maple could be explained best by water content in summer, slope and nitrogen. The low abundance of elm made tree size modelling difficult, as we could only account for two covariates at a time due to lack of data points. We identified slope and continentality to be the two most important determinants for tree size in Elm. The R^2-value for elm is thus a value for a model including only two covariates (cf. Table 2-5).

Table 2-4 Abiotic covariates included in the final species-specific tree size distribution model*. Note that, other than suggested by PCA, indicator values are suggested as contributing to prediction in all six species, whereas variance in soil depth is chosen only for beech and ash. The final species model can be read a combination of all variables marked with x in the particular species-column. The included covariates are a result of a backward selection based on AIC within the candidate GAMs for DBH-distribution with the results of Random Forests as a point of departure.*

Covariate	**beech**	**ash**	**hornbeam**	**sycamore**	**Norway maple**	**elm**
Analytical.Hillshading	x		x	x		
cont.water_1	x		x	x		
cont.water_2	x	x	x		x	
cont.water_3	x			x		
Cross.Sectional_Curvature		x				
diff.soil1_2		x				
diff.soil1_3		x				
DW1_1_4	x					
FW1_1_1		x				
FW2_1_1		x				
GSCIplot.median	x			x		
logArea.max1		x	x			
logArea.max2			x			
MD1_1	x		x	x		
MD2_1	x	x		x		
MD3_1	x		x	x		
PAW	x	x	x	x		x
Slope	x		x		x	
Space included	x	x	x			
Topographic_Wetness_Index		x				
var_depth	x	x				x
wF.spec	x		x	x		
wK.spec		(x)				
wL.spec	x			x		
wN.spec		x			x	
wR.spec	x		x			
wT.spec		x				

Table 2-5 Species identity, abundance and abiotic covariate in tree size distribution models *that influenced species specific tree size most (, i.e. resulted in highest R^2 as sole independent covariate)*

Species	**Number of individuals**		**R^2 Including topography**	**Most influential covariate**	**AIC highest - lowest**
	1999	**2007**			
beech *(Fagus sylvatica)*	13307	12191	0.17	Slope	107214.1-1064229
ash *(Fraxinus excelsior)*	550	527	0.32	Water content (spring)	4523.023-4507.443
hornbeam *(Carpinus betulus)*	389	361	0.16	Soil acidity	2709.013- 2698.533
sycamore *(Acer pseudoplatanus)*	321	345	0.55	Water content (summer)	2880.668-2849.574
Norway maple *(Acer platanoides)*	44	40	0.41	Water content (summer)	441.43-336.3
elm *(Ulmus glabra)*	69	39	0.24	continentality	862.94-854.81

2.4 Discussion

With this study on abiotic drivers of spatial pattern formation in forest communities, we rose to the call that more assessments of habitat suitability have to be done under field conditions to evaluate the role of niches for species coexistence (Pulliam 2000). Our study confirms and refines classic theoretical assumptions: Species coexistence has long been attributed to niche separation (Gause 1934, Hutchinson 1961). We found that species differed in the subset of abiotic conditions that had resulted in the most suitable habitat patches. The idea of niche separation was later augmented by acknowledging environmental heterogeneity (Levin and Paine 1974, Levin 1992a, Dale 1999). Our findings fit into this setting, where highly heterogeneous abiotic conditions were utilised differently between species, leading to spatial segregation (Chapter 1 and 3). This assumption of influential heterogeneity has been complemented by re-emphasising the influence of similarity for the spatial formation of coexistence patterns (Abrams 1975, 1976, Webb et al. 2002) and abundance (Condit 2006, Baldeck et al. 2013). However, delineating niches and conclusively assessing habitat suitability remains difficult. Our study highlights the need of comprehensive field data as well as the consideration of other species to reflect on the interaction between suitable habitat and available spaces in the light of competition (see Chapter 3).

In compliance with Aim 1, we have assembled a comprehensive data set on the spatial distribution of light, water availability, and topographic information in a near-natural forest. We found spatial and temporal variation in all measured data. This highlights the advantage of a constant habitat component like topography, which is often used for niche and habitat studies (Guisan and Zimmermann 2000, Wright 2002). However, the temporal and small scale spatial resource partitioning we found e.g. in soil also implies, that if explicit niche separation is a study aim, detailed and repeated sampling is necessary. We suggest that further studies should consider including samples that allow inferring at the scale of the individual tree within habitat patches. However, in order to be able to separate the suitable habitat between the different species, large scale heterogeneity proved to be valuable. We notice that despite the low fit at which abiotic covariates were sometimes interpolated, there is valuable information to be gained on the interaction between species and habitat. We therefore would like to encourage more field studies to complement existing data. There was no direct link between a covariate being influential on the tree layer and the quality of its interpolation (water content at high depth) or small differences (continentality). We conclude that subtle differences and weakly linked covariates can add valuable information, if supported by unambiguous data. The ability of tracing determining factors over a longer time frame merits the conclusion that the general framework allows an assessment of the abiotic environment with a longer time lag. However, further studies should consider sampling concurrent to the census and adding samples at finer spatial and temporal scales.

We used the interpolated abiotic data compiled for Aim 1 to attain Aim 2, which was to determine whether the differences in the spatial patterns of common and rare tree species (Chapter 1) were an effect of species' competitive abilities, i.e. result of competitive exclusion, or of differences in their fundamental niches. Here, we found that species did indeed differ in their fundamental niches. The number of relevant environmental variables differed (9 to 14, not considering Maple and Elm) as well as the abiotic habitat variables that were important.

We expect that differences especially in the link between soil conditions and tree pattern could be tighter, if there had been a typical dry period in summer. The year 2011 included a dry spring and a wet but warm summer (DWD 2011). In the summer 2011, soil samples could thus only be taken within a week without rain, but no more. This might mask typical trends. However, as weather is expected to change with climate change, there is a need of more investigation. Other studies predict short-term changes in the tree layer dynamics under severe changes of the environmental conditions (Jump et al. 2006, Lindner et al. 2010).

There seems to be a tendency that abundance influences the impact of abiotic covariates on tree size negatively, indicating that the abiotic niche restrictions seem to be less severe in this study. This seems not to be a mere artefact of sample size, but of species niche traits. We conclude this from the two Acer species occurring in different numbers but showed a similar impact of the abiotic environment on the species.

Abiotic niche covariates alone were not a good predictor for beech tree size. Even a large number of covariates included did not result in a particularly high model fit. This seems to indicate that beech was not restricted to a certain set of abiotic conditions and thus no limiting factor for beech was identified, as expected for a generalist species. As a shade-tolerant species, the best beech model did not include light covariates but only those that held information on topography and water content (Metz et al. 2016). Beech showed only small tree sizes on sites with a steep slope that exhibit shallow soil, low water availability while proposing an increased risk of wind throw. Thus, slope being the most influential covariate for beech is in line with beech being largely excluded ravine forests (Bartsch and Bartsch 2013, p. 44).

Surprisingly, while ash, the second most abundant study-species, is known to be highly light-dependent (Ellenberg et al. 1991; Leuschner and Ellenberg 2010) the resultant model did not include any of the light-related covariates. This could either mean that our methods were not able to grasp the true influencing light covariates or, that light is indeed not a limiting factor because Ash is mostly present in the canopy in our study area (Butler-Manning 2008). Ash seems to react to changes in deeper soil layers than beech, with deeper soil layer being included into the tree size model. Probably due to the higher wetness tolerance indicated by the higher occurrence of ash in the gully area, the TWI had a significant influence on the tree size of ash.

Analogously to the exclusion of beech by slope, the best predictive variable for the DBH of hornbeam was the Ellenberg indicator for soil acidity. Hornbeam is known to avoid acidic soils (Lockow and Lockow 2009) which our best predictive model confirmed. Additionally, hornbeam was influenced by gap area. This is in line with the observation that hornbeam requires canopy gaps to successfully compete against beech (Frech et al. 2003, Lockow and Lockow 2009).

Despite their difference in abundance, sycamore (intermediate numbers) and Norway maple (rare) showed similar spatial patterns (Chapter 1, Figure 1-3) and were similarly well modelled by the abiotic conditions based on R^2. Both sycamore and Norway maple responded strongest to water availability in summer. These results seem to support that trait similarity, abundance, and small phylogenetic distance can lead to spatial clustering (Scheffer and van Nes 2006; Hardy and Sonké 2004). The similar spatial and niche patterns of sycamore and maple despite their difference in number can thus be attributed to habitat filtering and the niche differentiation forced by beech as a strong competitor (Molofsky and Bever 2002a).

This seems to suggest, that for these species differences in fundamental niches allow coexistence, whereas for the other species (beech, hornbeam, and elm) competitive exclusion mostly determines the spatial distribution of suitable habitats. This process seemed to be driven by the competitive exclusion by beech, as species only occur in higher numbers where beech cannot reach dominance (see Chapter 1). However, Molofsky and Bever (2002a) demonstrated that positive frequency dependence between species combined with limited habitat suitability can maintain species diversity even in presence of a strong competitor such as, in our case, beech.

For Ash, Sycamore, and Norway Maple, the differences in the influencing abiotic conditions indicate niche separation. In this study, the tree size for these three was better explained by strictly abiotic models than those of beech, hornbeam or elm. Ash, sycamore, and Norway maple form a species combination known to the specialist habitat of ravine forests. This corresponds to the results of Wang et al. (2010)who hypothesised that species poor forests would show stronger species associations that species rich forests. The importance of niches in these results are in line with Chapter 1 (Figure 1-3) that Ash and the *Acer* species were mostly determined by abiotic conditions are also those that are best explained in their spatial distribution by niche processes. As we used tree size as an indicator for habitat suitability in the present analysis, this implies that Ash, Sycamore, and Norway Maple differ in their fundamental niches and can thus coexist. The probability of these species establishing large trees is more determined by abiotic covariates than beech, hornbeam or elm.

The validity of the indicator values is not universal (Barkman et al. 1964, Jongman et al. 2002). However, they were designed for the area in which we sampled, thus we believe they are appropriate for our case study. Despite very small variation within most indicator values, indicator values were clearly a useful proxy for the habitat conditions to model tree size. For instance, continentality in which the study species differed most (Ellenberg et al. 1991), differed less than one level between all plots, but influenced almost all species. Similarly, the topography showed little variability in our study area. Still, topography proved to be an important determinant for tree size distribution, especially as an excluding factor for beech.

While the species' tree models that did not include topography showed a clear line-up in model fit according to abundance, this pattern was dissolved when including topography. This allows the conclusion that self-similar patterns (Chapter 1, Figure 1-4) can be tied to abundance (Condit 2006). However, the reverse is not true: Abundances alone cannot be used to infer on the relative impact abiotic conditions have on habitat suitability for a species.

The commonness of species influences the per capita growth rates of species, because due to higher numbers common species more often encounter and compete with conspecifics than with individuals of other species. A growth reduction by intraspecific competition consequently is or becomes less severe if species are or become rare (Levine and HilleRisLambers 2009).

Due to a lower niche overlap, usually other species have less competitive impact on *per capita* growth. Moreover, there can be mechanisms working that allow rare species to persist in the presence of a strong competitor, such as strong self-limitation within the superior competitor species (Yenni et al. 2012).

This is in line with results showing that own and neighbour species identity determined growth patterns while neighbourhood diversity was unimportant (Jacob et al. 2010, Ratcliffe et al. 2015). This influence of neighbouring trees is also a possible explanation for the low model fit and shows the need to investigate the proportion of biotic interactions on growth patterns (see Chapter 3).

It becomes apparent that species differ in their sensitivity towards the different abiotic covariates. There seemed to be a negative impact of depth above 60 to 70 cm (Saefken et al. 2013), that seemed to be linked to the high clay content, which results in a high amount of water being stored, but inaccessible for plants. It seems that the best explaining variables for tree size for the particular species are interestingly not those that would facilitate the species, but those that are known to be adverse to a particular species. This stresses the influence of habitat filtering (Baldeck et al. 2013). The observed importance of fine spatial scales, e.g. differentiation happening at soil layers only 10 cm apart (e.g. 20 to 30 cm depth), or sensitivity to variation within a few months, may very well be the ecological answer to reconcile both contrasting mechanisms, niche separation, selecting for ecologically different species, and habitat filtering, which results in ecologically similar species while excluding non-similar species that are not adapted to the excluding abiotic conditions. Our results might imply that habitat filtering acts at coarser scales while niche differentiation can happen at small temporal and spatial scales (Peterson 1999, John et al. 2007).

This seems to support the suggestion that the supposedly opposing mechanisms of similarity and differentiation can –as a result- lead to emergent neutrality (Holt 2006; Vergnon, van Nes, and Scheffer 2012; Scheffer and van Nes 2006). The theory of emergent neutrality suggests that species can coexist when they differ ecologically so much that they minimise interspecific competition or they differ so little in their ecology that the outcome of competition is stochastic and they thus behave *de facto* neutral. Therefore, even in a setting that clearly contains niche structures, there seem to be subsets where neutral or *de facto* neutral interactions should be considered. This is the case, where niche overlap is large (Bewick et al. 2015) – as in our study setting– or species interactions do not result in different demographic rates (Hubbell 2001). Our results underline that niche and neutral processes can happen in parallel in a complex study system and should not be considered as mutually exclusive. The difference between species that are irrelevant under a certain set of conditions, may, however, be important under changing environmental conditions.

2.5 Conclusions

Habitat filtering and niche separation are stated opposing mechanisms in coexistence. This gradient seems to be a good explanation for species that react to heterospecifics either in dependence of the density of the interacting species or their ecological similarity. We found species association of ecologically similar species. Our results indicate that strong competitors, in our case beech, can influence the inferior species to occupy subspaces of the niches by competitive exclusion. Thus the density of beech seems to influence the other species. Niche differentiation in the abiotic conditions allows admixed species to occupy habitat outside the range of beech's optimal habitat. Habitat filtering pre-defines the traits required for existence in these marginal habitats. This filtering thus constrains the ecological differences between the admixed species. Our study demonstrates that a possible mechanism for coexistence is the differentiation in abiotic conditions at small spatial and temporal scales under a larger filtering mechanism.

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3 Chapter 3: Pattern to process in a near-natural temperate forest

Abstract

Ecological spatial patterns work as an archive of the processes that created them. It is one of the key questions in ecology to identify those processes. This is often difficult because several processes happen at the same time or influence later processes. Moreover, the individuals are influenced not only by other individuals, but also by their abiotic environment. Despite the recent advances on including field data, our study contributes to closing the gap on spatial processes that created the distribution pattern of species in a temperate forest. We used a data set from the Hainich National Park in Central Germany. The forest is beech dominated with admixed ash, hornbeam, sycamore, Norway maple and Wych elm. We included previously sampled and interpolated spatial data on abiotic condition, and topography. These information were included in ten different Spatial Point Process Models to infer on the relative importance of abiotic and biotic interactions, and on the scales of biotic interactions. We found that the intraspecific interactions influences the spatial distribution of all species most. Interspecific interactions influenced only the two rarest species, elm and Norway maple, and small beech. However, abiotic conditions play a role in the spatial distribution process in creating sub-habitats were competitive pressure, especially coming from beech, is lower. Moreover, we found an influence of small-scale abiotic heterogeneity (small areas without drain) that also influences small scale spatial patterns in ash. While the other four species were sufficiently modelled assuming little local interaction, the distribution process of sycamore (narrow niche) and beech (narrow dispersal kernel) were heavily influenced by small scale intraspecific interactions (Cluster processes), which indicates biotic heterogeneity. Our study suggests that small scale heterogeneity can result from many sources. Therefore, ecologists should act cautious when analyzing small scale interactions.

3.1 Introduction

Linking observed patterns and underlying drivers and processes is one of the fundamental issues in ecology and ecological point pattern analysis (Watt 1947, Dale et al. 2002; Velázquez et al. 2016; Genet et al. 2014; Law et al. 2009; Levin 1992). This link is especially difficult to uncover when several dynamic processes interact to shape the observed spatial pattern (McIntire and Fajardo 2009). Patterns are observations showing non-random structures (Grimm et al. 2005) they thus contain information on the processes that formed them over the course of time. However, information on spatial patterns is usually used only indirectly conclude about ongoing processes, such as competition, spatial segregation(Velázquez et al. 2016). This creates an ambiguity because patterns could be explained by abiotic heterogeneity or by biotic interactions. This mixture of information can only be separated by using real data directly taken from the abiotic environment. Up to now, this approach has been rarely taken (but see Uria-Diez, Ibáñez, and Mateu 2013; Zhang et al. 2011).

Spatial patterns of trees in a forest are formed by concurrent components (Chesson 2000). Abiotic components may refer to topography or soil type (Wang et al. 2012) and biotic components may refer to competition (Stoll and Bergius 2005) or dispersal (Kimmins 2009; Clark et al. 1999). Different abiotic conditions offer different resources and thus niches. This creates sub-habitats whose suitability varies depending on species identity (Hirzel and Le Lay 2008). Species tend to prefer similar conditions, which may result in niche overlap and thus greater competition. Depending on biotic factors such as competitive strength, species may exclude one another in space, evading to patches of suboptimal abiotic conditions where the inferior species might realise higher growth rates than the superior competitor species (Tilman 1982, Leuschner and Ellenberg 2010b). Thus, abiotic and biotic components can have varying relative importance for a particular species. In heterogeneous environments, the identification of the most important process components has to be spatially explicit (Beckage and Clark 2003): To derive the underlying processes from a particular spatial tree pattern, not only the critical abiotic and biotic process components need to be identified, but also their spatial arrangement (Levin 1992b, Rahbek 2004, Wang et al. 2012, Boyden et al. 2012). In addition, some components, such as resources, can be partitioned concerning space

(Schoener 1974, McKane et al. 2002), certain components of the abiotic environment, such as soil moisture (Le Roux et al. 1995, Weltzin and McPherson 1997), but also concerning temporal scales (Chesson and Warner 1981).

How abiotic resources are partitioned and how this influences biotic interactions such as competition is highly dependent on species traits (Gremer et al. 2013) and can change spatial assembly patterns (Chacón-Labella et al. 2016). These traits can refer to physiology (e.g. root shape), life history (e.g. switch in shade-tolerance) or typical rejuvenation patterns (e.g. in gaps or as clusters). Abiotic and biotic process components can thus be linked to the spatial pattern of trees in forests to uncover mechanisms of spatial forest assembly.

Point Pattern Analysis (PPA) provides powerful techniques for characterizing ecological patterns in the spatial distribution of individuals (points). The applications of PPA range from epidemiology(Bailey and Gilligan 2004) to ornithology(Cornulier and Bretagnolle 2006) and forestry (Stoyan and Penttinen 2000b, Wang et al. 2012). Recent advances in PPA have made it possible to include spatial information on abiotic covariates such as pH or elevation. To include these additional information can underpin the link between pattern and process, but requires both data on the spatial pattern and data on prevailing abiotic conditions.

Spatial point process models (SPPM) are stochastic models which are used to generate point patterns. SPPMs can be used to the establish the pattern-to-process-link by including processes assumed to have created the observed pattern into the model (Mø ller and Waagepetersen 2003, Illian et al. 2008). SPPMs can simulate the impact of ecological processes that form ecological point patterns. SPPMs can thus test data-driven null-models on the consequences of the ecological process. For example, SPPMs can be used to study how heterogeneity influences tree density (Chapter 1) by affecting the spatial distribution of habitat suitability for tree growth (Chapter 2). Although the technical methods are improving, the application of SPPMs in ecology seems to have been largely restricted to one- or two-species settings or disregarding species identity (Rathbun and Cressie 1994, Getzin et al. 2006), mostly did not account for heterogeneity (Velázquez et al. 2016), and are only recently combined with findings from abiotic field data (Zhang et al. 2011, Uria-Diez et al. 2013, Mi et al. 2014) .

In this paper, we carry out a comprehensive analysis of the patterns and processes in a near-natural temperate forest plot, consisting of over 13,000 tree individuals from six studied species. To characterise the abiotic environment, we considered 20 abiotic covariates (preselected in Chapter 2 from 101 abiotic covariates measured in the field). Patterns and processes were linked by building spatial point process models (SPPM) for the distribution of the tree species. Biotic covariates (nearest neighbour distances and local tree density) were considered. For each species pattern, we investigated ten hypothesis representing different combinations of the abiotic framework for the biotic interactions involved in the spatial distribution process. In order to assess the quality of the pattern-to-process-link, and based on the best hypothesis as selected by AIC, we simulated species specific point patterns and compared the results to the observed tree patterns. We were able to identify the biotic and abiotic factors required to reconstruct the spatial distribution process for all six species. Similar to previous investigations (Chapter 2) the resource separation between species happened at small vertical spatial scales. We found that no tree pattern depended on abiotic conditions alone, but also a purely biotic model sufficed only for the two rarest species, Norway maple and Wych elm. The distribution of beech and sycamore followed a cluster process, suggesting dependence between the trees, whereas all other species followed a Poisson process.

3.2 Methods

3.2.1 Study area

We chose a near-natural mixed-Beech forest area of 28.5 ha in the Hainich National Park (51° 06' N, 10° 31' E), Thuringia, Germany. The study area lies in the core zone of the National Park (Figure 0-1) and has experienced decreasing management in the last 150 years. Management ceased completely in 1997 with the foundation of the National Park. It is thus not a primary forest, but an old-growth stand (Mund 2004) with spatial characteristics very similar to virgin beech forest found in other parts of Europe (Butler-Manning 2008).

Within the study area, all trees taller than 130 cm were fully mapped in 2007, yielding data from 13503 individual trees of the six studied species (Figure 1-1). Beech (*Fagus sylvatica*) accounted for 90% of the individuals, with the admixed species ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*), sycamore (*Acer pseudoplatanus*), Norway maple (*Acer platanoides*) and, Wych elm (*Ulmus glabra*) .

3.2.2 Model covariates (abiotic and biotic)

We investigated the spatial process that formed the spatial distribution of the six studied tree species. To examine the effect of abiotic heterogeneity on the spatial distribution of each of the tree species, we included environmental covariates derived from topography (elevation, slope, hillshading, Topographic Wetness Index (TWI)) and measured in the field regarding light (Ellenberg L-Value, canopy gap area, and canopy gap shape), soil properties (Ellenberg F, R, N values, soil depth), and water availability (e.g. water contained per 10 cm soil layer, water content, seasonal variability). Topographic information was available at a 0.5 x 0.5 m scale, other abiotic information at a 75 x 75 m scale. In order to identify the crucial covariates required to recreate the spatial process creating the observed pattern, we used the interpolation surfaces fitted to the abiotic covariates (Chapter 2) and the estimated intensity functions of the species-specific point processes (Chapter 1).

3.2.3 Point Process Analyses

Results of Chapter 2 suggest that the spatial pattern formation includes the interaction of several abiotic and biotic covariates. Here, we developed several point process models to predict local tree density. A first set of models included only the abiotic heterogeneity. Second, both abiotic and biotic covariates were included. Here, we assumed that all tree individuals irrespective of size and species are equal in their impact. Third, in the combined abiotic and biotic models, we distinguished between conspecific and heterospecific individuals. For each tree species, we used the abiotic covariates identified in Chapter 2 (based on habitat suitability). For the biotic interactions, we considered two measures: nearest neighbor distance, which should be sensitive to the existence of clusters, and the density of trees in the neighbourhood, which should mirror density-dependent effects. In order to identify the most parsimonious model, we used both backward and forward selection of variables for the point process models.

To create the point process models, we used the inbuilt point process functions in R 3.3.0 {spatstat 1.4.2} (Baddeley and Turner 2005). This function was used to build linear additive models with the spatial covariates explained above and using the spatial distribution of trees observed in the field (Chapter 1) as response variable. These spatial models predict the number of expected points per unit area, i.e. the expected intensity at each location of the study area for each species (Baddeley et al. 2015).

For each species, we tested the AIC-performance of the following models, moving to the next model, if the inhomogeneous pair-correlation function of the observed pattern deviated from the simulation envelopes built from realisations of the point process model:

1) Neither abiotic nor biotic covariates drive tree density distribution. This corresponds to a homogeneous Poisson point process.
2) All abiotic covariates (identified in Chapter 2) drive tree density distribution (full model). This and the following models up to model 9) correspond to inhomogeneous Poisson point processes
3) Selected abiotic covariates drive process (selected via backward and forward selection)
4) as 3, but including interaction
5) biotic covariates (local tree densities and nearest neighbour distances) drive tree density distribution
6) as 4, but additionally allowing biotic interactions as represented by local tree density and nearest neighbour distance
7) as 6, but distinguishing between inter- and intraspecific local tree densities and nearest neighbour distances
8) Abiotic and separated inter- and intraspecific interactions (performing backwards selection and forward)
9) As 8, but including smaller bandwidth by using cross-validation algorithm (Diggle 1985, 2001, Berman and Diggle 1989) to select a smoothing bandwidth for the kernel
10) As 9, but including dependence between individuals in the distribution process of the trees. This corresponds to a LogGaussian Cluster process.

For each species, we used the AIC to evaluate the model performance, with lower AIC values indicating better performance. This means better ability to predict the observed intensity for the species in question. As a next step, we investigated the scale-dependent performance of the selected models. To this end, for each species we simulated the model selected by AIC and compared these simulated patterns to the observed tree point patterns. For each species, 199 simulations of the selected point process model for were used to construct a simulation envelope based on a 95% confidence interval. If the selected model describes the process forming the real tree pattern well, the (inhomogeneous) pair-correlation function calculated from the observed tree distribution should fall into the simulation envelope(Gotelli 2000, Potts et al. 2004).

3.3 Results

In order to identify the determinants of the spatial pattern forming process, we built species-specific Poisson or Cluster point process models (models 2– 10, cf. Methods) that potentially included a combination of biotic and abiotic covariates. For each species, we chose the Poisson point process model with the lowest AIC as the best, i.e. parsimonious, model.

The homogeneous Poisson point process was never selected (model 1). Species differed in the combination of factors included in their best-fitting model, i.e., that determined their spatial pattern forming process (Tables 3-1, 3-2). No two species shared a similar factor combination. From the abiotic variables, no variable was important for more than three species. From five investigated Ellenberg indicator values, only Light, Wetness, and Acidity (L,F, R) were included in any of the species' point process model.

3.3.1 Biotic interactions

The best point process model (Figure 3-1) for beech (DBH 10-30 cm), ash, hornbeam, and Norway maple included only intraspecific interactions, no interspecific interactions (model no. 8, 8, and 5). The models for small and large beech, sycamore and elm additionally included interspecific interactions (model no. 10, 10, and 5. respectively)). Only the models for the two rarest species, elm and Norway maple included biotic interactions only even after backward or forward selection (model 5). This is the case although a purely biotic model also had a lower AIC for ash, hornbeam, and big beech. To reproduce the spatial patterns, these models also required several abiotic covariates, corresponding to model no. 8 (Interactions between biotic and abiotic covariates, performing variable selection)

3.3.2 Abiotic interactions

Beech was the only species that was influenced by large topography (slope, hillshading) and gap shape (GSCI, (Getzin et al. 2012)). Beech density was influenced by water content of the whole sampled soil body. The beech-model included indicator values for wetness and acidity. Most variables included in the ash model refer to summer conditions. Ash density was best described by water contained in the upper soil, including small scale topography (as closed depressions) lead to a huge model improvement (AIC drop from 8626 to 526). Hornbeam is the only species where density was influenced by pure gap size (logArea.max). Sycamore is influenced by summer conditions (July), but by no further measured abiotic covariate. However, Ellenberg indicator values of light and water were included in the Sycamore point process model. The best point process model for the two rare species were including only biotic interactions (Norway Maple: inter- and intraspecific) and Elm (interspecific). All species except Norway Maple and Elm were dominated by variables that describe attributes of water-availability, e.g. plant-available water appearing in all other species point process models. In all models, residuals were larger where tree density increased. Except in explicit gap areas, tree density was overestimated. This underlines the importance of less suitable conditions for spatial pattern formation in trees.

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***Table 3-1 Abiotic variables and seperated inter- and intraspecific interactions** between trees remaining in the best-fitting Poisson point process model (models 2 – 9, cf. Methods), or cluster process model (model 10) based on AIC (Table 2). Variables were calculated/interpolated (Chapter 2). GCSIplot.median=Median of GapShapeComplexityIndex of three largest gaps in plot, logArea.max1= log(largest gap area), DW1_1_4=Dry weight in May in 40 cm depth, FW1_1_1= Fresh weight in May, upper 10 cm, FW2_1_1= Fresh weight in May, upper 10 cm, PAW= plant-available water, Cont.water: Sum of contained water in first 10-50 cm soil, diff.soil1_3= Contained water in May in first 20-30 cm soil, MD1-3= maximum soil depth (Pürckhauer), var_depth= Variation in soil depth between samples, wF, wL, wR= indicator value weighted by species cover for wetness, for light, or for soil acidity.*

Variables	**beech**	**ash**	**hornbeam**	**sycamore**	**maple**	**elm**
No. of best model	10	8	8	10	5	5
Topography						
Analytical Hillshading	x $^{s, m}$					
Cross-sectional Curvature		x				
Slope	x					
Canopy gap metrics						
GSCIplot.median	x $^{s, m}$					
logArea.max1			x			
Weight of soil samples						
DW1_1_4	x					
FW1_1_1		x				
FW2_1_1		x				
Contained or available water in soil						
PAW	x	x	x			

Continued Table3- 1

cont.water_May	x	x	x			
Variables	**beech**	**ash**	**hornbeam**	**sycamore**	**maple**	**elm**
diff.soil1_3		x				
Soil depth						
MD1_1	x		x			
MD2_1	x	x				
MD3_1	x		x	x		
var_depth	x	x				
Ellenberg indicator values						
wF.spec	x		x	x		
wL.spec				x		
wR.spec	x		x			
Biotic interactions						
intraspecific interaction[1]	$x^{s,m}$	x	x	x		x
small scale intraspecific	x			x		
interspecific interaction[2]	$x^{s,b}$	x	x	x	x	x

Included variables are marked by x. Beech was modeled in three size classes. Where covariates have not been included in all size classes, letters are given for the size classes the covariate was used in. s=small trees (DBH < 30 cm), m= medium sized trees trees (DBH 10-30 cm), b= big trees trees (DBH >30 cm).

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[1] For intraspecific interactions nearest neighbour distances and densities of the separate size classes of beech were included: for Norway Maple and Hornbeam only included the densities. Beech included both, distances and densities: small beech: density of all three size classes; for medium: density of small and big trees; for big beech: density of all three size classes

[2] Same as for intraspecific, but heterospecifics not divided into size classes

***Table 3-2 AIC selection process of the 10 different model hypothesis**. Bold= best model. More than one selected means that the one with higher AIC performed better when evaluated with the pair-correlation function.*

Point process type	**model hypothesis**	**beech**	**beech. small**	**beech. medium**	**beech. big**	**ash**	**hornbeam**	**sycamore**	**N. maple**	**elm**
homogeneous Poisson	**1. Randomness**	127898.2	59030.5	37186.9	30145.7	8827.3	6330.7	6081.4	846.8	859.3
inhomogeneous Poisson	**2. All abiotic**	127322.3	57851.8	36836.6	30040.9	8760.2	6214.9	6026.9	851.4	862.9
	3. Abiotic selection	127320.8	57847.1	36832.7	30029.3	8751.6	6210.9	6019.6	846.8	859.3
	4. Abiotic Interactions (selections)	126563.2	57279.3	37074.3	30064.7	8631.2	6093.2	5981.8	844.4	854.8
	5. Biotic interactions only (selection)	99579.3	56608.9	36674.3	**27670.9**	**7475.4**	**5281.0**	5196.3	**767.5**	**750.9**

Continued Table 3-2

Point process type	**model hypothesis**	**beech**	**beech. small**	**beech. medium**	**beech. big**	**ash**	**horn-beam**	**sycamore**	**N. maple**	**elm**
	6. Abiotic + Biotic (all equal) inter-actions	126568.6	57101.6	37105.8	30143.1	8827.9	6331.8	6074.7	847.2	860.2
	7. All covariates, separate inter+ intra	126523.1	56791.6	36772.9	29971.8	8638.6	6098.0	5966.5	848.1	858.7
	6. Abiotic + Biotic (inter+ intra) selection	126511.8	56786.2	36763.8	29961.4	8626.6	6087.1	5957.8	844.4	854.8
	9. include small scales	**99499.3**	**565450.0**	**36628.1**				**4864.3**		
inhomogeneous Cluster process	**10. use Cluster process[3]**	**23360991**	**15041132**	**6889235**	**4638540**			**114254.7**		

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[3] The given cluster process models are a new model type. Thus, the given AIC is not comparable to the AIC from the Poisson process models. The given AIC is the lowest AIC amongst the tested cluster process models.

3.3.3 Spatial evaluation of the point process models

For elm, Norway maple, hornbeam, and ash, the pair-correlation function fell into the simulation envelopes built from the best-fitting Poisson point process model (Fig. 3-1). However, for beech, ash, and sycamore species, the pair-correlation function of the observed pattern deviated from the simulation envelopes at small distances (Fig. 3-2). The largest deviations occur at distances < 15 m. At farther distances, for all species, the pair-correlation function fell into the built SPPM. To simulate the small scale spatial pattern at distances < 15 m, ash required adding small-scale heterogeneity (cross sectional curvature) to recreate the spatial pattern forming process. To recreate the small scale spatial pattern of beech and sycamore required the assumption of dependence between trees (cluster process) while the other four species could be modelled in their distribution without explicitly including paternal trees (Poisson process). Moreover, sycamore and beech both required a fine-scale spatial resolution in neighbourhood density which did not smooth over individual trees. The repulsion pattern at small distances between large beech trees could not be recreated in any of the built point process models. In all species distribution models, residuals were larger where the species occurred in higher density (Figure 3-3).

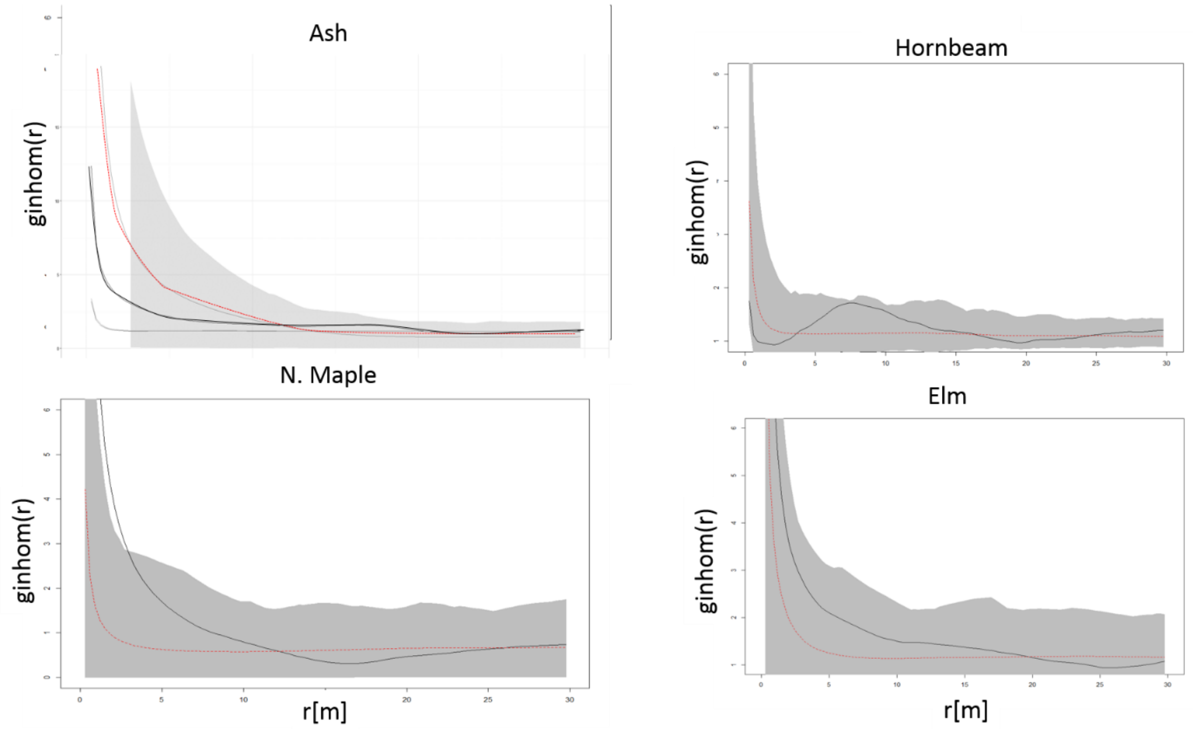

Figure 3-1Results of best Point Process Models: Heterogeneous Poisson point process models including biotic and biotic interactions*. Radius r ranges from 0 to 30.). Black line= observed pattern evaluated with inhomogenous pair-correlation function, red = mean model assumption, grey envelope: created from 199 random realisation of the point process*

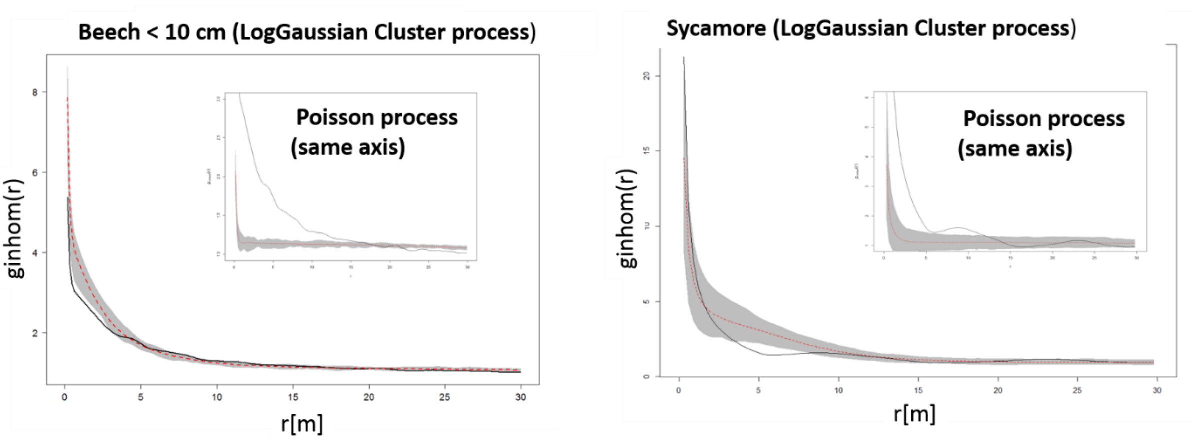

Figure 3-2 Results of LogGaussian Cluster process. *Radius r ranges from 0 to 30. Small inner graphics also share these axis. Graphics for medium and large beech trees included in Appendix Fugure A 10-1.*

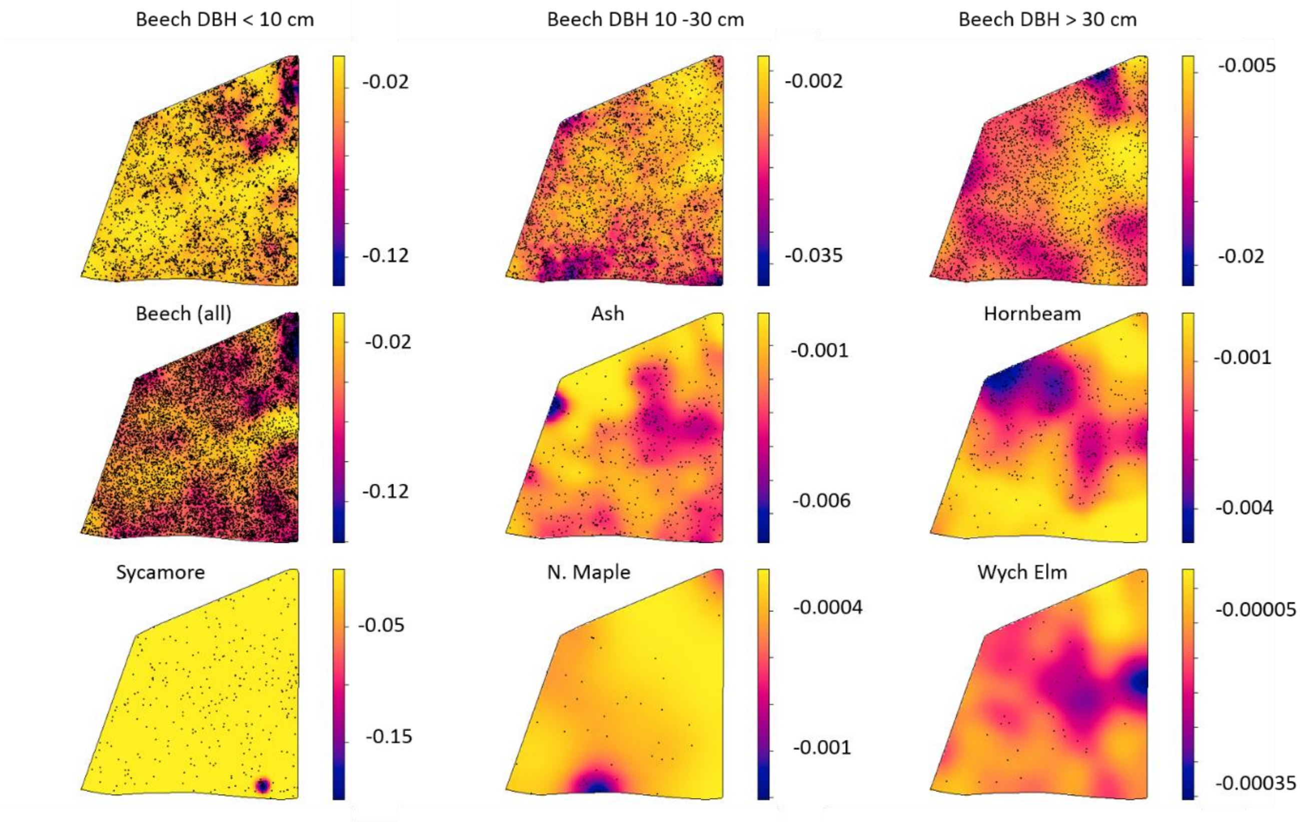

***Figure 3-3 Spatial distribution of residuals from best-fitting SPPM**. Lighter colours indicate higher residual values. Black dots: tree positions. Note that the scaling of the colour gradient differ between species and size classes.*

3.4 Discussion

We were interested in linking the observed spatial distribution patterns of six tree species in a near natural forest to the prevailing abiotic conditions, while taking biotic interactions within and between the species into account. For this link, we built several Spatial Point Process Models (SPPMs) that included different assumptions on the influencing covariates that shape the distribution process of the six species. Our assumptions were built along a gradient from random distribution (CSR) over purely abiotic and purely biotic models to models including abiotic and biotic components (model 1-10). In all cases, those models that included biotic interactions performed better than purely abiotic models. This was especially true for beech, which was sensitive to different scales of biotic interactions. Only when models that took biotic interactions into account came close to fitting the observed patterns. However, abiotic components were necessary to account for deviations that were not included in biotic interaction (e.g. small-scale heterogeneity in increased soil moisture influenced ash). The identities of the abiotic components included in the point process models differed between all six species. While the distribution of beech and sycamore could be reconstructed applying Log-Gaussian-Cluster-Processes (model no. 10), the other four species followed Poisson point processes.

Influence of the biotic environment

For all species, the spatial point process models improved dramatically and were further improved when a distinction was made between con- and heterospecific neighbourhood interactions, so that it was possible to exclude either intra- or interspecific interactions. For all species, the spatial distribution was best predicted if conspecific neighbours were taken into account. This is in line with the assumption that self-limitation (Pacala and Deutschman 1995, Chesson 2000b) reduces the speed of exclusion even in the presence of a strong competitor (Molofsky and Bever 2002b, Scheffer and van Nes 2006a).

The distances to (or densities of) heterospecific neighbours were only important for beech, sycamore, and elm. This is unexpected for beech. As a superior competitor (Otto 1994), beech should not depend on the distribution of other species. However, the other species might enable a better spatial description of the beech distribution as they delineate those areas that are unsuitable for beech, as they can only here realise a higher growth rate (Pignatti et al. 1996, Leuschner and Ellenberg 2010a). This is in line with Chapter 1 where the large trees of the three main species showed a spatial segregation against each other.

The scale of interactions/ endogenous heterogeneity

Local-scale interactions may lead to heterogeneous spatial patterns. In other words, heterogeneous spatial patterns can be of endogenous or biotic origin. In splitting the abiotic from the biotic interactions, it became apparent that some aspects of the heterogeneous spatial patterns could not be attributed to the abiotic environment. Interestingly, beech and sycamore were the only species that required a high spatial resolution and a spatial cluster process in their best fitting models. This indicates the importance of local interactions at the level of individual trees. For beech, this may emphasize the overarching importance of short-range dispersal for spatial pattern formation, because Beech produces nuts as seeds and is the only studied species that is not wind dispersed. As a strong competitor, previous studies also found evidence for the dominating effect of intraspecific interactions (Ratcliffe et al. 2015). For sycamore, spatial clustering in when co-occurring with beech was observed in previous studies (Janík et al. 2016). As a wind-dispersed species this clustering seems to occur rather driven by its ecological potential (*sensu* (Otto 1994)), than by a narrow dispersal kernel. These results also indicate that the biotic interactions within sycamore and beech are very strong, introducing a biotically-generated, or endogenous, heterogeneity that cannot be represented at levels beyond the individual tree (Pacala and Levin 1997) .

Niches often have only few important dimensions, such as light availability or topography that dominate the species interactions because. This influence of few dimensions is owed to competitors resource consumption can reduce them to a level where environmental requirements of the competitors are no longer met and thus limit their occurrence (Tilman 1980, 1982, Leibold 1995). However, niche separation in the studied species must have evolved in several dimensions, because the components that influenced the distribution of the studied species differed in all considered resource aspects, i.e. type, spatial distribution and temporal distribution of resources. These resource aspects formed species-unique combinations.

The species seemed to have separated with respect to root allocation (e.g. beech vs. ash) as well as the period of time they are most sensitive to (summer: sycamore and maple, spring: ash). Moreover, ash seemed to respond to small-scale heterogeneity in topography which had an aggregating effect. Thus, the results of this study indicate multi-dimensional niche separation.

Influence of the abiotic environment

Physiology

The influence of the abiotic environment is often linked to certain physiological traits of the studied species. For instance, differences in the root system may influence which soil layers are more important to the particular species. The distribution of beech was mostly influenced by variables describing the water content of the total soil depth available. This is probably related to the heart root system (Büsgen 1897) of beech. Beech roots have a maximum density between 5-10 cm (Rust and Savill 2000), but roots regularly are found at soil depths > 50 cm (Schmid and Kazda 2001). In contrast to beech, ash was sensitive to parameters that referred to water content of shallower soil depths. This corresponds to the differences in the root system, since Ash builds surface roots, where most of them at 0-5 cm (Büsgen 1897, Rust and Savill 2000).

Life stages

Life stages may differ in their response to abiotic variables, so that the relative importance of abiotic variables changes across the life stages of trees (NakAshizuka 2001). In this study, this was particularly apparent for beech. The distribution of small beech trees was best described with models including several parameters for light. This is not surprising, because light is the typical target variable of aboveground competition and self-thinning (Coomes and Grubb 1998). Furthermore, light parameters were almost absent in the models for larger beech trees. This change of parameter importance indicates different selection determinants over the life-history of beech.

Competitive ability

Interestingly, only the Hornbeam model included canopy gap area (Table 1). This relates to the analyses in Chapter 1 where Hornbeam showed spatial segregation in combination with large trees of all species except the two least frequent species. However, it is surprising that none of the more light demanding species, such as Ash or Acer included gap area in its distribution. One reason for this abstinence from gap areas may be that these species lack rejuvenation (Huss and Butler-Manning 2006, Butler-Manning 2008), so that only trees that are part of the canopy are included in the data set. Instead, the shape of gaps (GSCI) seems to have an influence on the spatial pattern of Hornbeam, Ash and *Acer sp.* (Huss and Butler-Manning 2006), possibly influencing the success of establishing in the understorey (Getzin et al. 2012).

3.5 Conclusions

As the methodological contribution, our study highlights that point process models based on field data can indeed be connected to species traits (e.g. their physiology). In this way, they can be used to gain more detailed insights into ecological processes, such as niche separation.

In ecological terms, this study highlights the importance of considering small-scale endogenous heterogeneity in spatial patterns of trees. We show that clustering at scales of less than 8 m could be fully explained (i.e., the observation falls into the simulation envelope) or turned into repulsion (i.e., the observation is below the simulation envelope) by including small-scale heterogeneity in the analysis. This might imply that ecologists have to act cautiously when interpreting small-scale deviations as a result of second-order pattern properties and interactions. Instead, small-scale abiotic heterogeneity (which is a first-order property of patterns) may be much more important in shaping small-scale spatial patterns.

3.6 Acknowledgements

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4 Neutral theories of biodiversity and conservation practice

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Abstract

Neutral theories of biodiversity have been heavily debated in ecology, but their application potential for conservation practice is unclear. Neutral theories assume that species establishment success in a community does not depend on the differences between species, but is mostly a stochastic process. On the contrary, niche theories highlight the importance of species differences for establishment success, because specialization of species leads to higher conspecific than interspecific competition and thus coexistence. Our review shows that neutral theories have rarely been used in conservation research. This is probably due to their lack of species-specificity or their less intuitive assumptions and lower acceptance than niche theories. This is the case although models based on neutral theory proved to be useful in biodiversity hotspots, which are especially prone to conservation action. Moreover, models based on neutral theories often subdivide space into local community and metacommunity, which reflects concepts such as metapopulation dynamics, which are commonly used in conservation science. We propose that neutral theories can serve as a valuable null-model to reduce complexity, account for stochasticity, and, where appropriate, can serve as a starting point for conscious stepwise addition of niche structure and other non-random processes. Alternatively, recent integrative concepts that combine aspects of neutral and niche theory such as the stochastic niche or emergent neutrality may provide a promising foundation for future conservation practice.

4.1 Introduction

Neutral theory has sparked controversy among ecologists (e.g. Ricklefs 2003; Nee 2005) when it was suggested as a unified theory to explain biodiversity without the need to refer to niches (Hubbell 2001). However, thus far, Hubbell's neutral theory and its modifications have not been discussed very much in the field of conservation biology. On the one hand, this is not surprising, since neutral theories assume that species are ecologically equivalent, whereas conservation often focuses on species-specific differences. On the other hand, neutral species assembly has critical consequences for conservation goals, especially in its implications for species protection and invasive species management. Moreover, most successful tests of Hubbell's neutral theory originate from species-rich tropical ecosystems (Wiegand et al. 2012), which are often hotspots of conservation concern. In this review, we compile studies that explicitly or implicitly address the implications of neutral theories for conservation, often in the form of neutral models. These case studies can be used to identify further conservation settings in which the assumption of neutrality might be reasonable. We also compare these studies to the established perspectives on conservation purely based on niche theory (MacArthur 1972; Tilman 1982; Gause 2003), but also on more intermediate concepts such as the stochastic niche theory (Tilman 2004), the continuum theory (Gravel et al. 2006) and the concept of emergent neutrality (Scheffer & van Nes 2006).

Conservation decisions are rarely explicitly based on theoretical considerations, but theory influences the viewpoints that are adopted in conservation biology and applied ecology. The few existing investigations of the conservation value of ecological theories cover mainly niche theory (Tilman 1982), stability theories related to resilience and multiple stable states (Gunderson 2000; Scheffer et al. 2001), and spatial theories such as the metapopulation (Hanski & Gilpin 1991) or island biogeography theory (MacArthur & Wilson 1967). These studies address, for instance, biodiversity loss in economic models (Eppink & van den Bergh 2007) and conservation concepts for forests (Schulte et al. 2006) and for ecosystems in general (Driscoll & Lindenmayer 2012). Apart from island biogeography theory, which is a precursor of neutral theory, the consideration of neutral assumptions in conservation studies seems to have been very limited. In general, considering neutral assumptions may be relevant whenever species show large niche overlap or are not very habitat-specific. We note that many species of conservation concern show high habitat-specificity (e.g. Goerck 1997), so that neutral theories cannot be applied to communities with these species. However, for the remaining communities, neutral theories could be valuable alternatives to niche theoretical approaches. Notably, together with the niche theory, the island biogeography theory has been considered more influential with respect to the development of conservation concepts than other tested theories (Schulte et al. 2006). Thus, niche theory and neutral theory both provide worthwhile (and potentially complementing) scopes for investigating the conservation implications of ecological theory.

Niche theory (MacArthur 1972; Tilman 1982; Gause 2003) explains the coexistence and co-occurrence of species with differences between species that are relevant for their survival under environmental conditions that vary in space and time. Each species has a specific ecological niche, i.e. a set of environmental conditions to which it is better adapted than its competitors. For conservation, this implies that species are not easily interchangeable or only with respect to a single or a few ecological functions. To a certain degree, this justifies the protection of every single species, challenges insurance effects, and calls for the combat of invasive species if they eliminate local species. However, since species can differ in many different traits, niche-based explanations of biodiversity often come with the disadvantage of increased complexity (Rosindell et al. 2011). This can make the implementation of niche theory into practice challenging.

Neutral theory (Hubbell 2001), in contrast, is very simple. It assumes that differences between species are irrelevant for demographic rates. Independent of species identity, individuals are equivalent in their fitness (Munoz & Huneman in press), e.g. with respect to birth and death rates or dispersal ability. The probability of a species to establish in an available habitat patch in a local community then depends solely on its frequency in the local community and not on how well it might be adapted to the environmental conditions in the gap (Purves & Pacala 2005). Additionally, in Hubbell (2001)'s neutral theory, there is a small probability that a species that is not present in the local community establishes in the gap by migration from the metacommunity or by speciation. Lacking differences in demographic rates, all species in a neutral community would be interchangeable at any time (Purves & Pacala 2005) without destabilizing the local community. Neutrality is related to the concept of functional redundancy of species. The functional overlap of species or communities reflects the potential domain of neutrality. However, species that differ in their function can still be ecologically equivalent, as it is required by neutral theory (Hubbell 2001). Here, functions denote capacities to provide a certain ecosystem service. If the applicability of neutral theories is established for a case study, e.g. by functional overlap or ecological equivalency of species, an additional value of actually applying neutral theories for conservation is their implementation of stochasticity and the high tractability of many neutral models (Rosindell et al. 2012). With respect to conservation management, protection of single species would only be necessary to the degree to which neutrality (and functional redundancy) can be rejected. Where there is evidence for neutrality (or functional redundancy), at most the protection of species numbers, not species identities or niches, can be derived from the neutrality assumption. Probably the most intuitive conservation targets for neutral communities would be the whole (meta-) community and its ecosystem processes.

The neutral theory has been strongly debated and criticized, not only for its disregard of niches and adaptation, but also for the weak speciation parts of the theory and the *de facto*-limitation to sessile species within the same trophic level (Ricklefs 2003). Hubbell (2006) argued that species can have differing characteristics in his theory. However, possible differences between species are not the focus of neutral theory, but rather what they have in common and makes them ecologically equivalent. For instance, tropical tree species are surrounded by many different species, which will lead to generalist strategies and thus quasi-equivalency on evolutionary time scales (Hubbell 2006). It has also been criticized that key parameters of the neutral theory are not clearly defined. Recent efforts have improved the definition of these key parameters, for instance with respect to ecological drift (Ricklefs 2006), size of the local community (Richardson, Barry J.; Arias-Bohart 2011), species age (Chisholm & O'Dwyer 2014), and spatial structure (Rosindell & Cornell 2013). Especially including spatial structure into neutral theory is important for discussions on metapopulations and habitat fragmentation, which are highly relevant in conservation biology.

Validation of biodiversity theories against real-world data and delineation of the applicability of niche versus neutral theories can be achieved with patterns such as rank-abundance distributions. Empirical rank-abundance distributions were successfully reproduced by the neutral theory for a range of ecosystems, such as tropical rainforests in Panama (Hubbell 2001), for prokaryotic communities (Sloan et al.

2006) and partly for microbial communities in waste water treatment plants (Ofiteru et al. 2010). Neutral theory was rejected and niche processes were shown for a coral reef community (Dornelas et al. 2006) and salt meadows (Anderson & Mouillot 2007). Purely neutral dynamics are especially rare on large scales where adaptation to environmental conditions can often be shown. In contrast, neutral dynamics do often occur at local scales where also most conservation efforts operate. In the following, we will first summarize conservation implications of the niche theory as a reference standard for comparisons. We will then compile cases studies based on neutral theories in two categories, i.e. (i) only implicit conclusions for conservation efforts can be drawn and (ii) explicit conservation conclusions are drawn in the study. Finally, we will synthesize our findings by evaluating the beneficial and detrimental consequences of neutral theory for conservation and highlighting the implications of current developments in biodiversity theory for conservation.

4.2 Methods

We searched the Web of Science for papers published between 2001 and June 2016 to obtain a sample of studies linking neutral theory and nature conservation (see Appendix S1 for a documentation of search terms). For a publication to be included in the review, it had to match one of the following criteria: i) It had to address a link between niche theory and conservation; ii) it had to introduce a new approach based on a neutral theory, which could theoretically be applied in conservation; or iii) it had to introduce an already established approach for the application of neutral theories in conservation. In the following, we consider neutral theories and neutral models that include (e.g. Hubbell 2001) or do not include speciation.

4.3 Results

Niche theory and conservation

The niche concept is firmly established as a basis for decision-making in modern nature conservation. A majority of nature conservation studies therefore implicitly or explicitly refer to the niche concept and its derivations. As explicit examples, ecological niche models have been used for the delineation of conservation areas (Eppink & van den Bergh 2007; Girardello et al. 2009; Cianfrani et al. 2013; Mateo et al. 2015), the assessment of habitat loss (Barrows et al. 2008, 2011), and invasive species management (Caplat et al. 2013; Vicente et al. 2013; Guisan et al. 2014; Thalmann et al. 2015). The following synthesis links the niche concept with nature conservation applications in the fields of ecological niche modeling, habitat loss and fragmentation, and invasive species management.

Ecological niche modeling

Ecological niche modeling is widely used to predict potential distributions of organisms in space (Giovanelli et al. 2008; Murray et al. 2011; Vasconcelos et al. 2012). This information provides guidelines for the selection of conservation areas and future strategies in conservation planning (Girardello et al. 2009; Knapp et al. 2009; Kleinbauer et al. 2010; Robinson et al. 2010; Vega Rivera et al. 2011; Tobler & Morehouse 2013). Beyond theoretical use, niche models are focused on explicit locations and landscapes (Girardello et al. 2009). This spatial context can help to evaluate the range in which species are protected by current conservation areas (Ochoa-Ochoa et al. 2009). Ortiz-Martínez et al. (2008) describe a modeling approach in which they discuss the use of projections by niche models for areas with no information about effective species distributions and the establishment of conservation areas based on this approach. Under the current impact of climate change, niche models improve the static network of nature reserves by providing predictions of responses of species to future environmental variation (Kleinbauer et al. 2010).

Habitat loss and habitat fragmentation

Habitat loss can only be critically assessed under the consideration of former geographical distribution of species - which can be estimated by niche models combined with abiotic variables that are independent of anthropogenic influence (Barrows et al. 2008). These historical distributions further can be used to locate suitable areas for restoration and reintroduction of species (Barrows et al. 2008). Habitat loss often leads to habitat fragmentation that can reduce population viability, and so a core objective of biological conservation is to maintain linkages between habitats (Barrows et al. 2011), e.g. in the form of habitat corridors. Again, niche models have been used to identify pertinent linkages, which can then be proposed as conversation areas (Barrows et al.

2011).

Invasive species

Most of the niche-related analyses that we found estimate the hypothetical distribution of non-native invasive species (Peterson & Robins 2003; Giovanelli et al. 2008; Kleinbauer et al. 2010; Murray et al. 2011). A common output is the determination of containment boundaries for ecological threats (Giovanelli et al. 2008; Murray et al. 2011). Furthermore, the results of niche-related analyses have been used to derive invasion potentials and to explain why species can invade new areas (Murray et al. 2011; Tobler & Morehouse 2013). While a majority of the analyses have dealt with spatial models, Batalha et al. (2013) used an ecological niche comparison to predict the potential threat on native species. A novel and creative approach has been promoted by Benito et al. (2009), in which they treated buildings (greenhouses in this case) like invasive species and built distribution models for them. To assess the extinction risks of an endangered native plant species, they identified overlaps in the predicted distributions of this species and the buildings.

Neutral theory with implicit conservation implications

Neutral theory has explicitly been addressed in only few studies with conservation concern (see next section). Implicitly, however, conservation conclusions can be drawn from many more applications of neutral theory as the following comprehensive, but probably not conclusive selection of studies demonstrates.

Neutral models, which are implementations of a neutral theory, have often been used to answer questions on species richness and extinction on different spatio-temporal scales (Adler & Muller-Landau 2005; Babak & He 2009; Dornelas 2010). Moreover, scenarios with different levels of ecological disturbance have been compared with the help of neutral models (Bell 2000; Kadmon & Benjamini 2006). Overall, the responses of the models to these scenarios were used to evaluate if these disturbances drive community assembly.

Metacommunity dynamics have recently found entrance to nature conservation studies (Gimona et al. 2012; Diaz et al. 2013). The knowledge gained about what drives metacommunities and which ecological impacts influence these species is fundamental for conservation. Neutral theory-derived models can be used for explorations of metacommunity theory, because of the appropriate representation of rare species in neutral theory (Driscoll & Lindenmayer 2009) and the recent advances in spatially-explicit implementations of neutral models (e.g. Rosindell & Cornell 2013). In particular, the progress made by Desjardins-Proulx & Gravel (2012) in the field of speciation within neutral theory improved the evolutionary parts of the neutral theory. The spatially-explicit version of the neutral theory has proven its ability to explain spatial patterns in several studies (Gardner & Engelhardt 2008; Seri et al. 2012; White & RAshleigh 2012; Yakimov et al. 2014). Predictions from a spatial neutral model can easily be applied to real landscapes, which provides a valuable simplification of conservation efforts. Such insights could be used to draw conclusions on the effects of disturbance on species loss, especially for rare species, or on the vulnerability of whole communities.

Neutral theory with explicit conservation implications

Explicit conservation implications are formulated only in a few studies that address neutral theories or neutral models. These studies aim to delineate protected areas, approximate species richness measures and predict extinction rates.

Habitat fragmentation and protected areas

A major concern of conservation is habitat fragmentation, since it is one of the primary causes of species loss (Tilman et al. 2001; Rands et al. 2010). To improve conservation management, it is crucial to develop tools that allow insights into the effects of habitat fragmentation on biodiversity. However, only few studies link habitat fragmentation and neutral theory. In one of these studies, Babak & He (2008) investigated habitat fragmentation impacts on species diversity with a neutral simulation model for species abundance dynamics in two local communities. These two local communities were connected to a regional metacommunity. In essence, this was similar to a source-sink metapopulation approach where the subpopulation dynamics are neutral. Scenarios with species extinctions and species monodominance were explored. In this neutral simulation model, migration between local communities leads to a homogenization of community composition, whereas immigration from the metacommunity into local communities causes community differentiation. Hence, the size of spatial habitat fragments mattered for biodiversity. With a similar approach, Economo & Keitt (2010) attempted to quantify the isolation of local communities in a network to assess the influence of spatial geographic structure on broad-scale biodiversity patterns. With a different spatially-explicit neutral model, Economo (2011) shifted the focus from the quantification of biodiversity to the identification of important habitat patches and suggests this shift as key to a longterm conservation of biodiversity. Using a neutral model, Borile et al. (2012) confirm the intuitive tenet that local sanctuaries for different competing species can result in an increase in species diversity at a given site and can thus contribute to species protection even under neutral assumptions.

Biodiversity and extinction

Biodiversity is a major concern for conservation efforts, first because it is considered a value in itself, second because it often is the basis for ecosystem functioning (Hooper et al. 2005). Tropical rain forests are hotspots of biodiversity with a distribution with a long tail of rare species, which can be described by the neutral theory (Hubbell 2001). Furthermore, (Hubbell 2013) identified the linkage between absolute abundance and geographic range of species as fundamental for conservation in these regions. By modelling species abundances and spatial distributions, neutral theory may inform strategies to combat species extinctions in these hotspots. Another modelling approach transferred an existing individual-based stochastic lattice model into a spatially-explicit neutral model to explore hypotheses of species richness and abundance patterns (Gardner & Engelhardt 2008). The results of the simulations showed that even small disturbances can cause increases, albeit small ones, in species diversity in plant communities. This could lead to strategic recommendations for the conservation of biodiversity such as considering already small disturbances in management schemes. Hubbell et al. (2008) were able to estimate stand characteristics such as number, relative abundance and range size for trees in an Amazonian metacommunity by implementing neutral assumptions. Based on this neutral model, they predicted the probability of extinction for a range of species under different scenarios. Furthermore, species vulnerability has been assessed for several global change scenarios by analyzing the degree of connectivity for estuarine communities along the Iberian coast (Chust et al. 2013). By combining these correlative analyses with neutral theory, a prioritization of the most vulnerable species and habitats for conservation plans was achieved. The recent work of Halley et al. (2014) provides a framework based on neutral theory linked to species area-relationships that can be used to evaluate results from extinction forecasts or simulated habitat contractions. Their work improves the distinction between imminent and delayed extinction debts by clarifying the relationship between extinction debt and species-area relationships and introducing refined species-area relationships. This in turn leads to more precise species-area relationships compared to those predicted by non-neutral models. This framework can highlight the driving forces of extinction processes and can be used to define area requirements of species and communities as a basis for planning protected areas.

Invasive species

Habitats that are more prone to species invasion are often created by stochastic disturbances (Daehler 2003; Davis et al. 2005). This calls for including stochasticity into ecological models of community dynamics. In their review of invasion of natural communities by alien species, Daleo et al. (2009) highlighted this need of including stochasticity in models of community structure. They emphasize that biological invasions and the ecological patterns that arise from invasions indicate that trait differences between species are not necessarily the only drivers of ecological patterns. Therefore, conservation research should consider random processes as they are provided by the neutral theory. Including stochasticity in invasion models has been shown to be justified: Herben (2009) observed broad agreement between the predictions of a simple neutral model with observations from field studies with respect to invasion patterns. Neutral theory, therefore, seems capable of elucidating invasion processes and provides tools for conservation purposes that do not require species-specific assumptions.

4.4 Discussion

Neutral and niche theories of biodiversity are complementary in their consequences for conservation, especially with respect to species conservation. Studies with a niche perspective focus on interactions of species with the environment and with other species. Neutral approaches ignore such interactions and highlight similarities between species and the influence of stochastic processes. Where niche theories apply, they can be used to justify protection of single species and niches as well as eradication of invasive species. As a contrast, a conservation strategy guided by neutrality assumptions would argue for the protection of communities, processes and areas instead of single species. Invasive species would be treated as any other species in a community, since all individuals, and thus all species, are ecologically equivalent in neutral theory (Hubbell 2001).

Neutral and niche theories have similar fields of application in conservation, but show great differences in their frequency of application. We found that niche theory still is the main theory driving conservation decisions. For instance, niche modelling is a very common technique and has been applied to plan protected areas, assess habitat fragmentation and derive invasion potential of exotic species. Contrastingly, our review shows that neutral theories have found much fewer explicit uses in conservation applications. Implicit applications of neutral assumptions can be found in several conservation contexts including stochastic disturbances or addressing metacommunities with many rare species. Explicit applications of neutral theory have dealt with species-abundance distributions, species-area relationships, habitat fragmentation, invasion patterns and extinction probabilities. Analogous to the heated debates that have accompanied the publication of the neutral theory (e.g. Ricklefs 2003, 2006), there are both reasons for and against considering neutral theories in the context of conservation.

As an argument in favor of neutral theories, they promote a more conscious consideration of stochasticity (Alonso et al. 2006) at the level of populations (reproduction, mortality) and communities (colonization, speciation; Fig. 1). This mirrors the awareness of conservation biology that stochasticity, e.g. in the form of demographic stochasticity (Lee et al. 2011), environmental stochasticity (Stacey & Taper 1992; Higgins et al. 2000), or random catastrophes (Lande 1993; Vélez-Espino & Koops 2012) can have huge impacts on species extinctions and community composition. The focus of neutral theory on individuals and abundances may at first glance differ from the traditional focus of conservation biology on species. However, it is single individuals that start an invasion, that make up the small populations of rare species, that are the level of natural selection or that use wildlife bridges and connect populations. Moreover, whenever knowledge about species traits is sparse, adopting a neutral approach that makes no assumptions on species differences might be more suitable than a niche approach (Rosindell et al. 2012; Fig. 1). Neutral theory, especially in its spatially-explicit versions, also highlights the importance of spatial processes such as dispersal and predicts reliable species-area relationships (Rosindell & Cornell 2007). In conservation, spatial relationships play an important role, for instance in the context of delineation of protected areas (Patiño et al. 2014), connectivity of (meta-)populations, and habitat fragmentation. It is thus not surprising that Holt (2006) declares the neutral theory crucial for understanding fundamental processes of community ecology and applying this understanding to conservation issues.

In disfavor of neutral theory, there are some communities, where its applicability was explicitly rejected (Bode et al. 2012), such as coral reefs (Dornelas et al. 2006) or salt meadows (Anderson & Mouillot 2007) or generally wherever species are strongly habitat-specific. Moreover, disregarding conspicuous differences in species has proven counterintuitive to many ecologists and conservationists. Here, niches are an appealing concept, because they explain community assembly based on the observable species differences. Hence, conclusions drawn on the basis of models based on neutral theory may be less acceptable to stakeholders and conservation funders than those based on niches. This should not be used as an argument against neutrality, but may be one reason for the fact that we found only few explicit neutral theory-related studies in the context of conservation biology. Another reason might be the *de facto* limited range of application of Hubbell's neutral theory to sessile organisms within trophic levels in homogeneous areas at local scales. Conclusively, in their compilation of the influential ecological theories with respect to forest biodiversity conservation, Schulte et al. (2006) list niche theory and island biogeography theory, but not neutral theory. Clark (2009) cautions against the loss of process knowledge should the process-free neutral theory be adopted in biodiversity science. Based on these arguments, there are claims to call the applicability of neutral theory to conservation contexts entirely into question (e.g. Clark 2009; Bode et al. 2012). We argue, however, that the fact that neutral theory applies only to some and not all cases does not call for a blanket ban of the theory. We rather advocate a conscious choice based on the assumptions that are fulfilled of the one or other theory. Further, this choice should account for the limitations of the different theories.

Theory in general may also be considered a source of confusion in normative conservation practice. This applies to both niche and neutral theories. According to Driscoll & Lindenmayer (2012), this confusion can be overcome if the predictive capacity of theory is better delineated, so that appropriate conservation applications can be identified. Here, both the simple assumptions and the limited, but clear set of possible predictions of neutral theory are advantageous. Thus, neutral theory can serve as a perfect null-model which can be accepted or rejected with the chance to "fail in informative ways" (Rosindell et al. 2011). Such an informative failure can lead to the successive addition of more assumptions, e.g. in the form of different degrees of niche structure, until realistic patterns are produced. More complex models can thus be inspired by neutral theory as a starting point (Fig. 1). Conservation can benefit indirectly (dAshed arrow in Fig. 1) from such applications of neutral theory if they lead to more accurate models for the projection of population and community dynamics. This approach also changes the point of view from an unquestioned niche perspective to a conscious and parsimonious choice of the amount of niche structure that is necessary to describe a given community. Thus, theory can be of great benefit to conservation if it is well defined and can flexibly be adapted to the case at hand.

Integrative biodiversity theories that accommodate both neutral and niche processes at variable proportions comply with Bode et al.'s (2012) call for new ecological theories that can better inform conservation (Fig. 1). Based on their study of species-area relationships as a basis of protected area design, Patiño et al. (2014) argue that rather than relying on a single framework that includes either niche or neutral parameters, the focus should shift further to integrative approaches that take advantage of both theories. Reconsidering the concept of functional redundancy (Wellnitz & Poff 2001; Rosenfeld 2002), niche-based approaches could be used to delineate functional overlaps, and neutral approaches could be applied to model species within the overlaps. Attempts to integrate niche and neutral processes into a single framework include stochastic niche theory (Tilman 2004), continuum theory (Gravel et al. 2006), a generalized neutral theory including environmental stochasticity (Bewick et al. 2015; Kalyuzhny et al. 2015) and a mathematical blend of both concepts (Noble & Fagan 2015), as well as the rising concept of emergent neutrality (e.g. Holt 2006). For instance, Noble & Fagan (2015) explicitly highlight the capacity of their blended model to quantify the impact of forces that stabilize or destabilize niches on population extinction times. Niche theory states that species need to be sufficiently different to coexist. Emergent neutrality additionally predicts that at evolutionary time scales, the opposing effects of habitat filtering and niche differentiation lead to the coexistence of ecologically similar species, ultimately resulting in neutral interactions (Scheffer & van Nes 2006). The progress in these hybrid models revealed the necessity of including further factors beyond those covered by niche or neutral theory alone (Kalyuzhny et al. 2014). This would advance the understanding of the dynamic properties of communities, which is of crucial importance for conservation decision-making.

In conclusion, models based on neutral theories have thus far been implicitly or explicitly used in only few conservation studies compared to the popularity of niche-based approaches. However, models based on the assumption of neutral theories could be an asset to many more conservation endeavors in the future if applications respect the limitations of the theory. We suggest to intensify the use of neutral models as null-models, especially whenever stochasticity is important or knowledge on species properties scarce. If a purely neutral null-model is rejected, the next step would be to use integrative hybrid models that add adjustable levels of niche structure. This shift of perspective towards approaches that unify niche and neutral views has been very much supported recently (Matthews & Whittaker 2014). Conservation could also use neutral theory and its derivations to attain a more scale-explicit understanding of communities as a basis for scale-explicit conservation decisions in the future. Since spatial and temporal scales can have a great influence on ecological processes and patterns (Meyer et al. 2010), they should be addressed in the corresponding conservation measures (Connolly et al. 2005). This can be achieved with neutral models that are inherently scale-explicit, e.g. more rare species at local than meta-community scales (Hubbell 2001). Overall, conservation practitioners and ecologists should thus work towards identifying and applying the suitable mix of neutrality and niche for their cases as a basis for successful future conservation.

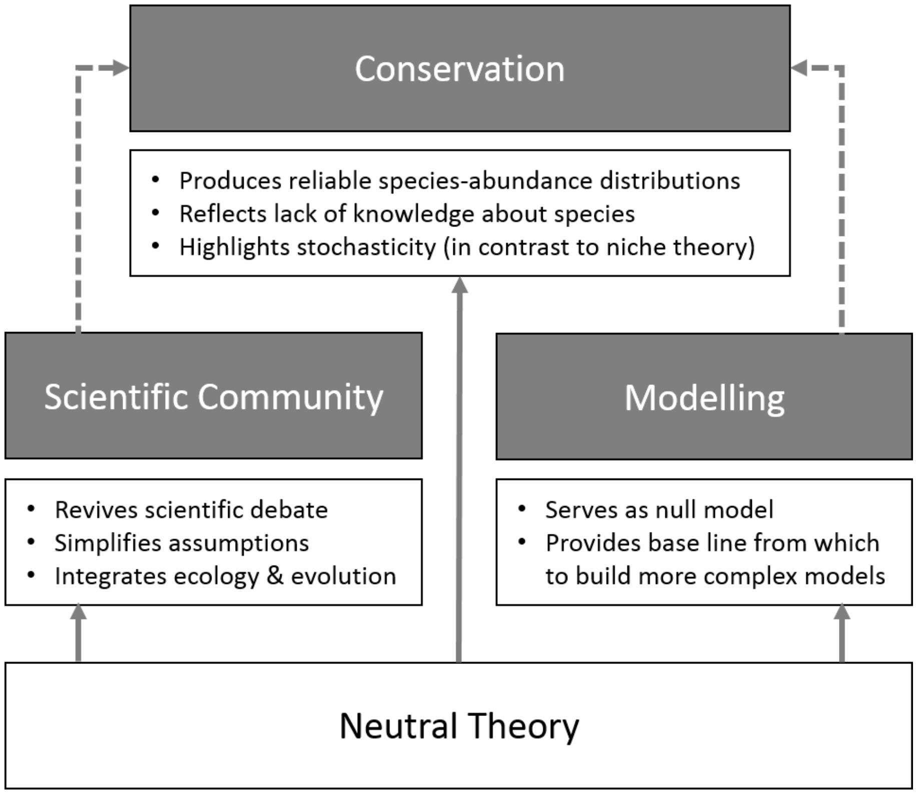

Figure 4-1: The neutral theory of biodiversity can affect conservation directly (solid arrows) and indirectly via its influence on the scientific community and on modelling practice (dAshed arrows).

4.5 Literature cited

Adler FR, Muller-Landau HC. 2005. When do localized natural enemies increase species richness? Ecology Letters **8**:438–447.

Alonso D, Etienne RS, McKane AJ. 2006. The merits of neutral theory. Trends in Ecology and Evolution **21**:451–457.

Anderson BJ, Mouillot D. 2007. Influence of scale and resolution on niche apportionment rules in saltmeadow vegetation. Aquatic Biology **1**:195–204.

Babak P, He F. 2008. Species abundance distribution and dynamics in two locally coupled communities. Journal of theoretical biology **253**:739–748.

Babak P, He F. 2009. A neutral model of edge effects. Theoretical population biology **75**:76–83.

Barrows CW, Fleming KD, Allen MF. 2011. Identifying habitat linkages to maintain connectivity for corridor dwellers in a fragmented landscape. The Journal of Wildlife Management **75**:682–691.

Barrows CW, Preston KL, Rotenberry JT, Allen MF. 2008. Using occurrence records to model historic distributions and estimate habitat losses for two psammophilic lizards. Biological Conservation **141**:1885–1893.

Batalha HR, Ramos J a., Cardoso GC. 2013. A successful avian invasion occupies a marginal ecological niche. Acta Oecologica **49**:92–98.

Bell G. 2000. The distribution of abundance in neutral communities. The American Naturalist **155**:606–617.

Benito BM, Martínez-Ortega MM, Muñoz LM, Lorite J, Peñas J. 2009. Assessing extinction-risk of endangered plants using species distribution models: a case study of habitat depletion caused by the spread of greenhouses. Biodiversity and Conservation **18**:2509–2520.

Bewick S, Chisholm RA, Akçay E, Godsoe W. 2015. A stochastic biodiversity model with overlapping niche structure. Theoretical ecology **8**:81–109.

Bode M, Connolly SR, Pandolfi JM. 2012. Species Differences Drive Nonneutral Structure in Pleistocene Coral Communities. The American Naturalist **180**:577–588.

Borile C, Muñoz M a., Azaele S, Banavar JR, Maritan a. 2012. Spontaneously broken neutral symmetry in an ecological system. Physical Review Letters **109**:1–5.

Caplat P et al. 2013. Movement, impacts and management of plant distributions in response to climate change: insights from invasions. Oikos **122**:1265–1274. Wiley

Online Library.

Chisholm R a, O'Dwyer JP. 2014. Species ages in neutral biodiversity models. Theoretical Population Biology **93**:85–94.

Chust G et al. 2013. Connectivity, neutral theories and the assessment of species vulnerability to global change in temperate estuaries. Estuarine, Coastal and Shelf Science **131**:52–63.

Cianfrani C, Maiorano L, Loy A, Kranz A, Lehmann A, Maggini R, Guisan A. 2013. There and back again? Combining habitat suitability modelling and connectivity analyses to assess a potential return of the otter to Switzerland. Animal Conservation **16**:584–594.

Clark JS. 2009. Beyond neutral science. Trends in Ecology and Evolution **24**:8–15.

Connolly SR, Hughes TP, Bellwood DR, Karlson RH. 2005. Community structure of corals and reef fishes at multiple scales. Science **309**:1363–1365.

Daehler CC. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annual Review of Ecology, Evolution, and Systematics:183–211.

Daleo P, Alberti J, Iribarne O. 2009. Biological invasions and the neutral theory. Diversity and Distributions **15**:547–553.

Davis MA, Thompson K, Philip Grime J. 2005. Invasibility: the local mechanism driving community assembly and species diversity. Ecography **28**:696–704.

Desjardins-Proulx P, Gravel D. 2012. How likely is speciation in neutral ecology? The American naturalist **179**:137–144.

Diaz A, Keith S a., Bullock JM, Hooftman D a P, Newton AC. 2013. Conservation implications of long-term changes detected in a lowland heath plant metacommunity. Biological Conservation **167**:325–333.

Dornelas M. 2010. Disturbance and change in biodiversity. Philosophical transactions of the Royal Society of London. Series B, Biological sciences **365**:3719–3727.

Dornelas M, Connolly SR, Hughes TP. 2006. Coral reef diversity refutes the neutral theory of biodiversity. Nature **440**:80–82. Nature Publishing Group.

Driscoll DA, Lindenmayer DB. 2009. Empirical tests of metacommunity theory using an isolation gradient. Ecological Monographs **79**:485–501.

Driscoll DA, Lindenmayer DB. 2012. Framework to improve the application of theory in ecology and conservation. Ecological Monographs **82**:129–147.

Economo EP. 2011. Biodiversity Conservation in Metacommunity Networks: Linking Pattern and Persistence. The American Naturalist **177**:E167–E180.

Economo EP, Keitt TH. 2010. Network isolation and local diversity in neutral metacommunities. Oikos **119**:1355–1363.

Eppink F V., van den Bergh JCJM. 2007. Ecological theories and indicators in economic models of biodiversity loss and conservation: A critical review. Ecological Economics **61**:284–293.

Gardner RH, Engelhardt K a M. 2008. Spatial processes that maintain biodiversity in plant communities. Perspectives in Plant Ecology, Evolution and Systematics **9**:211–228.

Gause GF. 2003. The struggle for existence. Courier Corporation.

Gimona A, Poggio L, Brown I, Castellazzi M. 2012. Woodland networks in a changing climate: Threats from land use change. Biological Conservation **149**:93–102.

Giovanelli JGR, Haddad CFB, Alexandrino J. 2008. Predicting the potential distribution of the alien invasive American bullfrog (Lithobates catesbeianus) in Brazil. Biological Invasions **10**:585–590.

Girardello M, Griggio M, Whittingham MJ, Rushton SP. 2009. Identifying important areas for butterfly conservation in Italy. Animal Conservation **12**:20–28.

Goerck JM. 1997. Patterns of rarity in the birds of the Atlantic Forest of Brazil. Conservation Biology **11**:112–118.

Gravel D, Canham CD, Beaudet M, Messier C. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology letters **9**:399–409.

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C. 2014. Unifying niche shift studies: insights from biological invasions. Trends in ecology & evolution **29**:260–269.

Gunderson LH. 2000. Ecological resilience - in theory and application. Annual review of ecology and systematics **31**:425–439.

Halley JM, Sgardeli V, Triantis K a. 2014. Extinction debt and the species-area relationship: A neutral perspective. Global Ecology and Biogeography **23**:113–123.

Hanski I, Gilpin M. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological journal of the Linnean Society **42**:3–16.

Herben T. 2009. Invasibility of neutral communities. Basic and Applied Ecology **10**:197–207.

Higgins SI, Pickett STA, Bond WJ. 2000. Predicting extinction risks for plants: environmental stochasticity can save declining populations. Trends in Ecology & Evolution **15**:516–520. Elsevier.

Holt RD. 2006. Emergent neutrality. Trends in ecology & evolution **21**:531–533.

Hooper DU, Chapin III FS, Ewel JJ. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75**:3–35.

Hubbell SP. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.

Hubbell SP. 2006. Neutral theory and the evolution of ecological equivalence. Ecology **87**:1387–1398.

Hubbell SP. 2013. Tropical rain forest conservation and the twin challenges of diversity and rarity. Ecology and evolution **3**:3263–3274.

Hubbell SP, He F, Condit R, Borda-de-Agua L, Kellner J, ter Steege H. 2008. How many tree species are there in the Amazon and how many of them will go extinct? Proceedings of the National Academy of Sciences **105**:11498–11504.

Kadmon R, Benjamini Y. 2006. Effects of productivity and disturbance on species richness: a neutral model. The American Naturalist **167**:939–946.

Kalyuzhny M, Kadmon R, Shnerb NM. 2015. A neutral theory with environmental stochasticity explains static and dynamic properties of ecological communities. Ecology Letters **18**:572–580.

Kalyuzhny M, Seri E, Chocron R, Flather CH, Kadmon R, Shnerb NM. 2014. Niche versus neutrality: a dynamical analysis. The American naturalist **184**:439–446.

Kleinbauer I, Dullinger S, Peterseil J, Essl F. 2010. Climate change might drive the invasive tree Robinia pseudacacia into nature reserves and endangered habitats. Biological Conservation **143**:382–390.

Knapp S, Kühn I, Bakker JP, Kleyer M, Klotz S, Ozinga W a., Poschlod P, Thompson K, Thuiller W, Römermann C. 2009. How species traits and affinity to urban land use control large-scale species frequency. Diversity and Distributions **15**:533–546.

Lande R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist:911–927.

Lee AM, Sæther B-E, Engen S. 2011. Demographic stochasticity, Allee effects, and extinction: the influence of mating system and sex ratio. The American Naturalist **177**:301–313.

MacArthur RH. 1972. Geographical ecology: patterns in the distribution of species. Princeton University Press.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton University Press.

Mateo RG, Broennimann O, Petitpierre B, Muñoz J, van Rooy J, Laenen B, Guisan A, Vanderpoorten A. 2015. What is the potential of spread in invasive bryophytes? Ecography **38**:480–487.

Matthews TJ, Whittaker RJ. 2014. Neutral theory and the species abundance distribution: recent developments and prospects for unifying niche and neutral perspectives. Ecology and evolution **4**:2263–2277.

Meyer KM et al. 2010. Predicting population and community dynamics: The type of aggregation matters. Basic and Applied Ecology **11**:563–571. Elsevier.

Munoz F, Huneman P. 2016. From the neutral theory to a comprehensive and multiscale theory of ecological equivalence. The Quarterly Review of Biology **in press**.

Murray K a., Retallick RWR, Puschendorf R, Skerratt LF, Rosauer D, McCallum HI, Berger L, Speare R, VanDerWal J. 2011. Assessing spatial patterns of disease risk to biodiversity: implications for the management of the amphibian pathogen, Batrachochytrium dendrobatidis. Journal of Applied Ecology **48**:163–173.

Nee S. 2005. The neutral theory of biodiversity: do the numbers add up? Functional Ecology **19**:173–176.

Noble AE, Fagan WF. 2015. A niche remedy for the dynamical problems of neutral theory. Theoretical ecology **8**:149–161.

Ochoa-Ochoa L, Urbina-Cardona JN, Vázquez L-B, Flores-Villela O, Bezaury-Creel J. 2009. The effects of governmental protected areas and social initiatives for land protection on the conservation of Mexican amphibians. PloS one **4**:e6878.

Ofiteru ID, Lunn M, Curtis TP, Wells GF, Criddle CS, Francis CA, Sloan WT. 2010. Combined niche and neutral effects in a microbial wastewater treatment community. Proceedings of the National Academy of Sciences **107**:15345–15350.

Ortiz-Martínez T, Rico-Gray V, Martínez-Meyer E. 2008. Predicted and verified distributions of Ateles geoffroyi and Alouatta palliata in Oaxaca, Mexico. Primates; journal of primatology **49**:186–194.

Patiño J, Weigelt P, Guilhaumon F, Kreft H, Triantis K a., Naranjo-Cigala A, Sólymos P, Vanderpoorten A. 2014. Differences in species-area relationships among the major lineages of land plants: a macroecological perspective. Global Ecology and Biogeography **23**:1275–1283.

Peterson a. T, Robins CR. 2003. Using Ecological-Niche Modeling to Predict Barred Owl Invasions with Implications for Spotted Owl Conservation. Conservation Biology **17**:1161–1165.

Purves DW, Pacala SW. 2005. Ecological drift in niche-structured communities: neutral pattern does not imply neutral process. Pages 107–138 in D. Burslem, M. Pinard, and S. Hartley, editors. Biotic Interactions in the Tropics. Cambridge University Press.

Rands MRW et al. 2010. Biodiversity conservation: challenges beyond 2010. Science **329**:1298–1303.

Richardson, Barry J.; Arias-Bohart ET. 2011. From genetic neighbourhood to local community: Estimating a key parameter of the Unified Neutral Theory of Biodiversity. Revista chilena de historia … **84**:501–507.

Ricklefs RE. 2003. A comment on Hubbell's zero-sum ecological drift model. Oikos **100**:185–192.

Ricklefs RE. 2006. THE UNIFIED NEUTRAL THEORY OF BIODIVERSITY: DO THE NUMBERS ADD UP? Ecology **87**:1424–1431.

Robinson TP, van Klinken RD, Metternicht G. 2010. Comparison of alternative strategies for invasive species distribution modeling. Ecological Modelling **221**:2261–2269.

Rosenfeld JS. 2002. Functional redundancy in ecology and conservation. Oikos **98**:156–162.

Rosindell J, Cornell SJ. 2007. Species--area relationships from a spatially explicit neutral model in an infinite landscape. Ecology Letters **10**:586–595.

Rosindell J, Cornell SJ. 2013. Universal scaling of species-abundance distributions across multiple scales. Oikos **122**:1101–1111.

Rosindell J, Hubbell SP, Etienne RS. 2011. The unified neutral theory of biodiversity and biogeography at age ten. Trends in Ecology & Evolution **26**:340–8.

Rosindell J, Hubbell SP, He F, Harmon LJ, Etienne RS. 2012. The case for ecological neutral theory. Trends in Ecology and Evolution **27**:203–208. Elsevier Ltd.

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. Nature **413**:591–596.

Scheffer M, van Nes EH. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. Proceedings of the National Academy of Sciences **103**:6230–6235.

Schulte LA, Mitchell RJ, Hunter ML, Franklin JF, McIntyre RK, Palik BJ. 2006. Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the US. Forest Ecology and Management **232**:1–11.

Seri E, Maruvka YE, Shnerb NM. 2012. Neutral Dynamics and Cluster Statistics in a Tropical Forest. The American Naturalist **180**:000–000.

Sloan WT, Lunn M, Woodcock S, Head IM, Nee S, Curtis TP. 2006. Quantifying the roles of immigration and chance in shaping prokaryote community structure. Environmental microbiology **8**:732–740.

Stacey PB, Taper M. 1992. Environmental variation and the persistence of small populations. Ecological Applications **2**:18–29.

Thalmann DJK, Kikodze D, Khutsishvili M, Kharazishvili D, Guisan A, Broennimann O, Müller-Schärer H. 2015. Areas of high conservation value in Georgia: present and future threats by invasive alien plants. Biological Invasions **17**:1041–1054.

Tilman D. 1982. Resource Competition and Community Structure, 17th edition. Princeton University Press.

Tilman D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences of the United States of America **101**:10854–10861.

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D. 2001. Forecasting agriculturally driven global environmental change. Science **292**:281–284.

Tobler M, Morehouse RL. 2013. Invasion of rusty crayfish, Orconectes rusticus, in the United States: niche shifts and potential future distribution. Journal of Crustacean Biology **33**:293–300.

Vasconcelos R, Brito JC, Carvalho SB, Carranza S, James Harris D. 2012. Identifying priority areas for island endemics using genetic versus specific diversity - The case of terrestrial reptiles of the Cape Verde Islands. Biological Conservation **153**:276–286.

Vega Rivera JH, Ortega-Huerta M a., Sarkar S, Rappole JH. 2011. Modelling the potential winter distribution of the endangered Black-capped Vireo (Vireo atricapilla). Bird

Conservation International **21**:92–106.

Vélez-Espino LA, Koops MA. 2012. Capacity for increase, compensatory reserves, and catastrophes as determinants of minimum viable population in freshwater fishes. Ecological modelling **247**:319–326.

Vicente JR, Pinto AT, Araújo MB, Verburg PH, Lomba A, Randin CF, Guisan A, Honrado JP. 2013. Using Life Strategies to Explore the Vulnerability of Ecosystem Services to Invasion by Alien Plants. Ecosystems **16**:678–693.

Walker BH. 1992. Biodiversity and Ecological Redundancy.

Wellnitz T, Poff NL. 2001. Functional redundancy in heterogeneous environments: implications for conservation. Ecology Letters **4**:177–179.

White D, RAshleigh B. 2012. Effects of stream topology on ecological community results from neutral models. Ecological Modelling **231**:20–24.

Wiegand T, Huth A, Getzin S, Wang X, Hao Z, Gunatilleke CVS, Gunatilleke IAUN. 2012. Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. Proceedings of the Royal Society of London B: Biological Sciences:rspb20120376. The Royal Society.

Yakimov BN, Iudin DI, Solntsev L a., GelAshvili DB. 2014. Multifractal analysis of neutral community spatial structure. Journal of Theoretical Biology **343**:44–53.

5 Concluding discussion

This thesis had the aims to identify possible coexistence mechanisms of six co-occurring tree species in near-natural temperate forests with known abiotic heterogeneity. Our study is one of the few taken (Zhang et al. 2011, Uria-Diez et al. 2013) that combines spatial analyses with field data and links the tree-environment interaction to the distribution process of trees. We achieved this by taking the following steps: 1) characterise the spatial pattern with regard to niche patterns (Chapter 1), 2a) compile abiotic habitat information of the study plot (Chapter 2), 2b) build abiotic species-specific habitat suitability model to infer on the impact of abiotic heterogeneity for niche processes and spatial occurrence (Chapter 2), and 3) for all six species, build species-specific distribution models that combine abiotic and biotic information (density and nearest neighbour distances) to infer on the scales of the tree-tree and tree-environment interactions (Chapter 3).

Heterogeneity was expressed in various forms throughout our study. This included spatial variability in tree density (e.g. beech, ash, and hornbeam), heterogeneous distribution of abiotic resources in time and three-dimensional space (e.g. contained water in soil for beech), and endogenous heterogeneity caused by strong intraspecific interactions due to a small niche breadth (e.g. sycamore) or a narrow dispersal kernel (e.g. beech).

The spatial tree pattern of the forest as a whole was affected by the density of beech trees. More specifically, the three most abundant species beech, ash, and hornbeam were spatially segregated with respect to their large trees (Chapter 1). However, we did find an influence of the frequency per species on the spatial pattern, where all three applied summary functions (pair-correlation function, nearest-neighbour distribution function, and empty-space function) revealed increasing clumping with increasing frequency.

The analysis of the abiotic basis of niche separation showed that species differed in their dependence on the abiotic habitat. We used tree size as an indicator for habitat suitability. This assumption allowed us to infer an the interaction strength between abiotic environment and tree size distribution in space: Species that were better predicted by large-tree density in general than by species-specific density experienced a weaker impact of the abiotic environment (Chapter 2, beech, hornbeam, elm). In contrast to this, if tree size distribution was better predicted by the distribution of conspecific large trees only, the abiotic habitat had more influence on the habitat suitability for a species, (Chapter 1, Ash, Sycamore, and Norway Maple).

Species also differed in the identity of the abiotic components that were useful to model habitat suitability (Chapter 2). More specifically, niche separation occurred with respect to resource type (e.g. gap space between beech and hornbeam and soil water content between beech and ash), seasonal patterns of abiotic components (sensitivity towards spring conditions in beech vs. sensitivity to summer conditions in ash) and small-scale distribution of abiotic components (e.g. soil water content between seasons and soil layers). A key finding of our study is that abiotic factors that have a negative impact on the species in question (Chapter 2, 3, and (Saefken et al. 2013)) seem to be those that separate the abiotic niche factors of the species. The inclusion of adverse factors (e.g. slope for beech and high soil acidity for Hornbeam) is therefore useful to identify available niche space because these adverse factors can imply a competitive inferiority compared to the other species. The importance of biotic interactions was also visible in the spatial distribution (point) processes of the species (Chapter 3). We were able to underline the importance of intraspecific competition for coexistence schemes. While interspecific interactions significantly influenced the distribution of elm, sycamore, and small beech, intraspecific competition influenced the spatial distributions of all species. For sycamore and beech, this impact of intraspecific interactions prevailed over several spatial scales from very local (< 1 m) to the scale of large tree interactions (20-30 m).

Our results suggest that most of the spatial dynamics in this forest communities is driven by beech. Beech is known to push other species to the margins of their potential niche (Pignatti et al. 1996, Leuschner and Ellenberg 2010a), making their realised niche much smaller than the potential niche. This was also tangible in our study, where beech seemed to define the available niche space for the other species which leads to the distinct segregated patterns between the tree most abundant species (beech, ash, and hornbeam) and repulsion patterns in late point of competitive thinning (Chapter 1).

It is long known that there are typical plant associations or types of forest communities that occur due to a certain set of abiotic conditions. These typical formations can be interpreted as arising from habitat filtering which selects for similar species at different locations within a similar set of abiotic conditions (Baldeck et al. 2013). The stability of these communities may be explained by our results that niche differentiation happens at fine scales (see also (John et al. 2007). This encourages the conclusion that the level of niche differentiation is – within the limits of habitat filtering and phylogeny - the individual. This is a conclusive result of the individual being the units of competition and evolution. Therefore, the outcome of interaction between species on the level of individuals can be considered the link towards both, niche differentiation and *de facto* neutral interactions.

There is growing evidence that *de facto* neutrality can result from ecological similarity. This was (implicitly) included in the neutral theory by Hubbel (2001) and explicitly stated as such by Holt (2006) and Scheffer and van Nes (2006b) in the concept of emergent neutrality. This concept includes niche separation as the result of competitive exclusion (Abrams 1986), but also assumes that coexistence comes into being by species being sufficiently similar, so that the outcome of the competitive exclusion is stochastic between the competing species. Bar-Massada (2014) refined these argument in observing that the importance of neutrality (along the gradient between niche and neutrality) is affected by dispersal mode (in our study: beech), and the distribution of resources (in our study: sycamore, ash, Norway maple) and individuals (in our study: beech, hornbeam, elm). We thus present evidence for the influence of all these factors, showing that the spatial pattern is formed by combined neutral drivers (frequency and dispersal mode) and niche dynamics (resource and space partitioning). This is in line with our findings that species segregate in space (Chapter 1) and differ in their abiotic niches (Chapter 2), but within these habitats the distribution of the individuals is only marginally affected by the presence of other species (Chapter 3).

Especially for modelling spatial distributions, the species identity of the heterospecific neighbours did not need to be explicitly included. The only exception to this was the very strong negative link between hornbeam and beech in spatial patterns where the two species showed full-scale repulsion (Chapter 1). This is in line with Ratcliffe et al. (2015) who found that neighbourhood interactions where largely irrelevant for the productivity of the stand, but highly negative between beech and hornbeam.

Our results suggest that theoretically the forest community found in the Hainich could coexist without extinctions over ecological time scales. This possibility, however, is thwarted by the severe lack of rejuvenation in all other species than beech. Several studies (Huss and Butler-Manning 2006) found that browsing is highly asymmetric: Beech is much less browsed than other species, especially *Acer sp.* and Ash. This effect is particularly dramatic because even small differences in browsing damage can put other species into such a disadvantage that can lead over time to species exclusion (Heinrichs et al. 2012, Ammer and Vor 2013b). Therefore, we argue that, despite the chances of coexistence revealed by this dissertation, over time the study area in the Hainich National Park can be assumed to turn into an almost pure beech stand which was also argued before (Butler-Manning 2008). In a mainly neutral setting, this would be of little concern. However, in our study area, as known for other temperate forest (Gilbert and Lechowicz 2004, Zhang et al. 2013) we found evidence for dominating niche processes. Forest structure changes rapidly if the environmental conditions change (Wohlgemuth et al. 2006). Therefore, the conscious application of niche properties should be considered under conservation concern (Chapter 4) in the National Park area.

Our study found that under heterogeneity, niche and neutral processes influence the spatial forest pattern simultaneously, stabilising the coexistence of species due to spatial and temporal resource partitioning, and spatial segregation at the level of the individual.

6 Literature

Abràmoff, M. D. et al. 2004. Image processing with ImageJ. - Biophotonics Int. 11: 36–42.

Abrams, P. 1975. Limiting similarity and the form of the competition coefficient. - Theor. Popul. Biol. 8: 356–375.

Abrams, P. A. 1976. Niche overlap and environmental variability. - Math. Biosci. 28: 357–372.

Abrams, P. A. 1986. The competitive exclusion principle: Other views and a reply. - Trends Ecol. Evol. 1: 131–132.

Adler, P. B. et al. 2010. Coexistence of perennial plants: an embarrassment of niches. - Ecol. Lett.: no-no.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. - Ecol. Lett. 6: 1109–1122.

Ammer, C. and Vor, T. 2013a. Verlust von Mischbaumarten durch Wildverbiss in Buchenwäldern. - AFZ Wald in press.

Ammer, C. and Vor, T. 2013b. Verlust von Mischbaumarten durch Wildverbiss in Buchenwäldern. - AFZ Wald in press.

Baddeley, A. and Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. - J. Stat. Softw. 12: 1–42.

Baddeley, A. J. et al. 2000. Non-and semi-parametric estimation of interaction in inhomogeneous point patterns. - Stat. Neerlandica 54: 329–350.

Baddeley, A. et al. 2015. Spatial Point Patterns: Methodology and Applications With R. - Chapman & Hall.

Bagchi, S. 2007. Relationship between size hierarchy and density of trees in a tropical dry deciduous forest of western India. - J. Veg. Sci. 18: 389–394.

Bagchi, R. et al. 2011. Spatial patterns reveal negative density dependence and habitat associations in tropical trees. - Ecology 92: 1723–1729.

Bailey, D. and Gilligan, C. 2004. Modeling and analysis of disease-induced host growth in the epidemiology of take-all. - Phytopathology 94: 535–540.

Baldeck, C. A. et al. 2013. Habitat filtering across tree life stages in tropical forest communities. - Proc. R. Soc. B Biol. Sci. 280: 20130548–20130548.

Barkman, J. J. et al. 1964. Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. - Acta Bot. Neerlandica 13: 394–419.

Bar-Massada, A. et al. 2014. Environmental heterogeneity affects the location of modelled communities along the niche-neutrality continuum. - Proc. R. Soc. B Biol. Sci. 281: 20133249–20133249.

Bartsch, J. and Bartsch, M. 2013. Der Schluchtwald und der Bach-Eschenwald. - Springer-Verlag.

Beckage, B. and Clark, J. S. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. - Ecology 84: 1849–1861.

Begon, M. et al. 2006. Ecology: From Individuals to Ecosystems. - Blackwell Publishing Ltd.

Bengtsson, J. et al. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. - For. Ecol. Manag. 132: 39–50.

Berman, M. and Diggle, P. 1989. Estimating weighted integrals of the second-order intensity of a spatial point process. - J. R. Stat. Soc. Ser. B Methodol.: 81–92.

Bewick, S. et al. 2015. A stochastic biodiversity model with overlapping niche structure. - Theor. Ecol. 8: 81–109.

Biau, G. 2012. Analysis of a random forests model. - J. Mach. Learn. Res. 13: 1063–1095.

Blanco, J. M. 1993. Relationship between the logistic equation and the Lotka-Volterra models. - Ecol. Model. 66: 301–303.

Boyden, S. et al. 2012. Seeing the forest for the heterogeneous trees: stand-scale resource distributions emerge from tree-scale structure. - Ecol. Appl. Publ. Ecol. Soc. Am. 22: 1578–1588.

Breiman, L. 2001. Random forests. - Mach. Learn. 45: 5–32.

Büsgen, M. 1897. Bau und Leben unserer Waldbäume. - Fischer.

Butler-Manning, D. 2008. Stand structure, gap dynamics and regeneration of a semi-natural mixed Beech forest on limestone in central Europe: a case study. - Universität Freiburg, Forstwissenschaftliche Fakultät.

Callaway, R. M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. - Oecologia 112: 143–149.

Ceballos, G. et al. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. - Sci. Adv. 1: e1400253.

Ceyhan 2013. New Tests of Spatial Segregation Based on Nearest Neighbor Contingency Tables. - arXiv in press.

Chacón-Labella, J. et al. 2016. Individual species affect plant traits structure in their surroundings: evidence of functional mechanisms of assembly. - Oecologia 180: 975–987.

Chapin, F. S. et al. 2011. Principles of terrestrial ecosystem ecology. - Springer Science & Business Media.

Chave, J. 2004. Neutral theory and community ecology. - Ecol. Lett. 7: 241.

Chesson, P. 2000a. Mechanisms of maintenance of species diversity. - Annu. Rev. Ecol. Syst.: 343–366.

Chesson, P. 2000b. Mechanisms of maintenance of species diversity. - Annu. Rev. Ecol. Syst.: 343–366.

Chesson, P. L. and Warner, R. R. 1981. Environmental variability promotes coexistence in lottery competitive systems. - Am. Nat. 117: 923–943.

Cimmery, V. 2010. User Guide for SAGA (version 2.0. 5). Vol. 1 and 2.

Clark, D. A. and Clark, D. B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connel model. - Am. Nat. 124: 769–788.

Clark, J. S. et al. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. - Ecology 80: 1475–1494.

Commarmot, B. et al. 2005. Structures of virgin and managed Beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. - For. Snow Landsc. Res. 79: 45–56.

Condit, R. 2006. The importance of demographic niches to tree diversity. - Science 313: 98–101.

Condit, R. et al. 2000. Spatial patterns in the distribution of tropical tree species. - Science 288: 1414–1418.

Connell, J. H. 1971. On the role of natural enemies in preventing exclusion in some marine animals and in rain forest trees. - In: Den Boer, P. J. and Gradwell, G. R. (eds), Dynamics of Populations. PUDOC, pp. 298–312.

Connell, J. H. 1980. Diversity and the Coevolution of Competitors, or the Ghost of Competition Past. - Oikos 35: 131.

Conrad, O. et al. 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. - Geosci. Model Dev. 8: 1991–2007.

Coomes, D. A. and Grubb, P. J. 1998. Responses of juvenile trees to above- and belowground competition in nutrient-starved Amazonian rain forest. - Ecology 79: 768–782.

Coomes, D. A. and Grubb, P. J. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. - Ecol. Monogr. 70: 171–207.

Cornulier, T. and Bretagnolle, V. 2006. Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors. - Ecography 29: 240–250.

Cosner, C. and Lazer, A. C. 1984. Stable Coexistence States in the Volterra–Lotka Competition Model with Diffusion. - SIAM J. Appl. Math. 44: 1112–1132.

Cressie, N. A. 1993. Statistics for spatial data. - John Wiley & Sons, INC.

Dale, M. R. T. 1999. Spatial pattern analysis in plant ecology. - Cambridge University Press.

Dale, M. R. T. et al. 2002. Conceptual and mathematical relationships among methods for sopatial nalysis. - Ecography 25: 558–577.

Day, K. et al. 2003. The effects of spatial pattern of nutrient supply on the early stages of growth in plant populations. - J. Ecol. 91: 305–315.

Diggle, P. J. 1983. The statistical analysis of spatial point patterns. - Academic Press.

Diggle, P. J. 1985. A kernel method for smoothing point process data. 34: 138–147.

Diggle, P. J. 2001. Statistical analysis of spatial point patterns. - Academic Press..

Diggle, P. J. and Ribeiro Jr, P. J. 2007. Model Based Geostatistics. - Springer.

Dixon, P. 1994. Testing spatial segregation using a nearest-neighbor contingency table. - Ecology 75: 1940–1948.

Dixon, P. M. 2002. Nearest neighbor methods. - Encycl. Environmetrics in press.

Dobrowolska, D. et al. 2011. A review of European Ash (Fraxinus excelsior L.): implications for silviculture. - Forestry 84: 133–148.

Duarte, L. C. et al. 1998. Scaling phenomena and ecological interactions in space: cutting to the core. - Trends Ecol. Evol. 13: 176–177.

DWD 2011. DWD Rückblick Sommer 2011.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. - Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

Ellenberg, H. et al. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. - Verlag Erich Goltze.

Fauth, J. et al. 1996. Simplifying the jargon of community ecology: a conceptual approach. - Am. Nat.: 282–286.

Frech, A. et al. 2003. Nachbarschaftsbezogene Analyse der Kronenraumbesetzung von Esche, Hainbuche und Winterlinde in einem artenreichen Laubmischwald (Nationalpark Hainich, Thüringen). - Forstwiss. Cent. Ver. Mit Tharandter Forstl. Jahrb. 122: 22–35.

Gause, G. 1934. The Struggle fbr Existence. - N. Y. Hafner in press.

Genet, A. et al. 2014. Incorporating the mechanisms underlying inter-tree competition into a random point process model to improve spatial tree pattern analysis in forestry. - Ecol. Model. 288: 143–154.

Getzin, S. et al. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. - Ecography 29: 671–682.

Getzin, S. et al. 2008. Heterogeneity influences spatial patterns and demographics in forest stands. - J. Ecol. 96: 807–820.

Getzin, S. et al. 2012. Assessing biodiversity in forests using very high-resolution images and unmanned aerial vehicles. - Methods Ecol. Evol. 3: 397–404.

Gilbert, B. and Lechowicz, M. J. 2004. Neutrality, niches, and dispersal in a temperate forest understory. - Proc. Natl. Acad. Sci. U. S. A. 101: 7651–7656.

Glatthorn, J. and Beckschäfer, P. 2014. Standardizing the Protocol for Hemispherical Photographs: Accuracy Assessment of Binarization Algorithms (D Rocchini, Ed.). - PLoS ONE 9: e111924.

Gotelli, N. J. 2000. Null-Model analysis of species co-occurrence patterns. - Ecology 81: 2606–2621.

Gotelli, N. J. and Graves, G. R. 1996. Null-Models in ecology. in press.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. - Ecology 84: 2809–2815.

Gravel, D. et al. 2006. Reconciling niche and neutrality: the continuum hypothesis. - Ecol. Lett. 9: 399–409.

Gremer, J. R. et al. 2013. Water-use efficiency and relative growth rate mediate competitive interactions in Sonoran Desert winter annual plants. - Am. J. Bot. 100: 2009–2015.

Grimm, V. et al. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. - science 310: 987–991.

Großmann, M. 2001. Auf dem Weg zum Buchen-Urwald. - Sonderdr. Aus Z. Natl. 113: 2001.

Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. - Ecol. Model. 135: 147–186.

Hanisch, K. H. 1984. Some remarks on estimators of the distribution function of nearest neighbour distance in stationary spatial point processes. - Ser. Stat. 15: 409–412.

Hardin, G. and others 1960. The competitive exclusion principle. - science 131: 1292–1297.

Hardy, O. J. and Sonké, B. 2004. Spatial pattern analysis of tree species distribution in a tropical rain forest of Cameroon: assessing the role of limited dispersal and niche differentiation. - For. Ecol. Manag. 197: 191–202.

Harms, K. E. et al. 2001. Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. - J. Ecol. 89: 947–959.

Hein, S. et al. 2009. A review of growth and stand dynamics of Acer pseudoplatanus L. in Europe: implications for silviculture. - Forestry 82: 361–385.

Heinrichs, S. et al. 2012. Vegetation dynamics of Beech forests on limestone in central Germany over half a century – effects of climate change, forest management, eutrophication or game browsing? - Biodivers. Ecol. 4: 49–61.

Hirzel, A. H. and Le Lay, G. 2008. Habitat suitability modelling and niche theory. - J. Appl. Ecol. 45: 1372–1381.

Hofmann, G. 1965. Die Vegetation im Waldschutzgebiet „Hainich “(Westthüringen). - Landschaftspflege U Naturschutz Thür 2: 1–12.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. - Am. Nat.: 377–406.

Holt, R. 2006. Emergent neutrality. - Trends Ecol. Evol. 21: 531–533.

Holt, R. D. and Gaines, M. S. 1992. Analysis of adaptation in heterogeneous landscapes: Implications for the evolution of fundamental niches. - Evol. Ecol. 6: 433–447.

Holzwarth, F. et al. 2013. Many ways to die–partitioning tree mortality dynamics in a near-natural mixed deciduous forest. - J. Ecol. 101: 220–230.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. - Princeton University Press.

Hubbell, S. P. 2006. Neutral Theory and the evolution of ecological equivalence. - Ecology 87: 1387–1398.

Huss, J. and Butler-Manning, D. 2006. Entwicklungsdynamik eines buchendominierten „Naturwald “-Dauerbeobachtungsbestands auf Kalk im Nationalpark Hainich/Thüringen. - Waldökologie Online 3: 67–81.

Huston, M. 1979. A general hypothesis of species diversity. - Am. Nat.: 81–101.

Huston, M. A. and DeAngelis, D. L. 1994. Competition and coexistence: the effects of resource transport and supply rates. - Am. Nat. 144: 954–977.

Hutchinson, G. E. 1957. Concluding remarks. - Cold Spring Harb. Symp. Quant. Biol. 22: 415–427.

Hutchinson, G. E. 1961. The paradox of the plankton. - Am. Nat.: 137–145.

Illian, J. et al. 2008. Statistical Analysis and Modelling of Spatial Point Patterns (S Senn and M Scott, Eds.). - Wiley.

Itoh, A. et al. 2003. Importance of topography and soil texture in the spatial distribution of two sympatric dipterocarp trees in a Bornean rainforest. - Ecol. Res. 18: 307–320.

Jacob, M. et al. 2010. Productivity of temperate broad-leaved forest stands differing in tree species diversity. - Ann. For. Sci. 67: 503.

Janík, D. et al. 2016. Breaking through Beech: A three-decade rise of Sycamore in old-growth European forest. - For. Ecol. Manag. 366: 106–117.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. - Am. Nat. 104: 501–528.

John, R. et al. 2007. Soil nutrients influence spatial distributions of tropical tree species. - Proc. Natl. Acad. Sci. 104: 864–869.

Johnson, J. B. and Omland, K. S. 2004. Model selection in ecology and evolution. - Trends Ecol. Evol. 19: 101–108.

Jonckheere, I. et al. 2004. Review of methods for in situ leaf area index determination: Part I. Theories, sensors and hemispherical photography. - Agric. For. Meteorol. 121: 19–35.

Jonckheere, I. et al. 2005. Assessment of automatic gap fraction estimation of forests from digital hemispherical photography. - Agric. For. Meteorol. 132: 96–114.

Jongman, R. H. G. et al. 2002. Data analysis in community and landscape ecology. - Cambridge University Press.

Jump, A. S. et al. 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. - Glob. Change Biol. 12: 2163–2174.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. - J. Veg. Sci. 3: 157–164.

Kenkel, N. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. - Ecology 69: 1017–1024.

Kimmins, J. 2009. Forest Ecology. - In: Ecology. Encycolpedia of Life Support Systems. EOLSS UNESCO, in press.

Klaus, S. and Reisinger, E. 1995. Der Hainich – ein Weltnaturerbe.: 32.

Kobe, R. K. et al. 1995. Juvenile tree survivorship as a component of shade tolerance. - Ecol. Appl. 5: 517–532.

Kohyama, T. 1993. Size-Structured Tree Populations in Gap-Dynamic Forest--The Forest Architecture Hypothesis for the Stable Coexistence of Species. - J. Ecol. 81: 131.

Kopecky, M. and Cizkova, S. 2010. Using topographic wetness index in vegetation ecology: does the algorithm matter? - Appl. Veg. Sci. 13: 450–459.

Kraft, N. J. B. et al. 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. - Science 322: 580–582.

Law, R. et al. 2009. Ecological information from spatial patterns of plants: insights from point process theory. - J. Ecol. 97: 616–628.

Le Roux, X. et al. 1995. Spatial partitioning of the soil-water resource between grass and shrub components in a West-African humid savanna. - Oecologia 104: 147–155.

Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. - Ecology 76: 1371–1382.

Leuschner, C. and Ellenberg, H. 2010. Vegetation Mitteleuropas mit den Alpen. - UTB Ulm. in press.

Leuschner, C. et al. 2009. Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. - Basic Appl. Ecol. 10: 1–9.

Levin, S. A. 1992a. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. - Ecology 73: 1943–1967.

Levin, S. A. 1992b. The problem of pattern and scale in ecology. - Ecology 73: 1943–1967.

Levin, S. A. and Paine, R. T. 1974. Disturbance, patch formation, and community structure (spatial heterogeneity / intertidal zone). 71: 2744–2747.

Levine, J. M. and HilleRisLambers, J. 2009. The importance of niches for the maintenance of species diversity. - Nature 461: 254–257.

Liaw, A. and Wiener, M. 2002. Classification and Regression by randomForest. - R News 2: 18–22.

Lieshout, M. van and Baddeley, A. 1996. A nonparametric measure of spatial interaction in point patterns. - Stat. Neerlandica 50: 344–361.

Lin, Y.-C. et al. 2011. Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation. - Oecologia 165: 175–184.

Lindner, M. et al. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. - For. Ecol. Manag. 259: 698–709.

Lockow, K.-W. and Lockow, J. 2009. Die Hainbuche im nordostdeutschen Tiefland: Wuchsverhalten und Bewirtschaftungshinweise. - MLUV, Referat Presse-und Öffentlichkeitsarbeit.

Londo, G. 1976. The decimal scale for releves of permanent quadrats. - Vegetatio 33: 61–64.

Loosmore, N. B. and Ford, E. D. 2006. Statistical inference using the G or K point pattern spatial statistics. - Ecology 87: 1925–1931.

Lotka, A. J. 1907. Studies on the mode of growth of material aggregates. - Am.J.Sci. 24: 199–216.

Mart’ınez, I. et al. 2013. Spatial patterns of seedling-adult associations in a temperate forest community. - For. Ecol. Manag. 296: 74–80.

McGill, B. J. et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. - Ecol. Lett. 10: 995–1015.

McIntire, E. J. B. and Fajardo, A. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. - Ecology 90: 46–56.

McKane, R. B. et al. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. - Nature 415: 68–71.

Metz, J. et al. 2016. Site-adapted admixed tree species reduce drought susceptibility of mature European Beech. - Glob. Change Biol. 22: 903–920.

Meyer, K. and Leveau, J. J. 2012. Microbiology of the phyllosphere: a playground for testing ecological concepts. - Oecologia 168: 621–629.

Mi, X. et al. 2014. Point process models, the dimensions of biodiversity and the importance of small-scale biotic interactions. - J. Plant Ecol. 7: 126–133.

Mø ller, J. and Waagepetersen, R. P. 2003. Statistical inference and simulation for spatial point processes. - Chapman & Hall/ CRC.

Molofsky, J. and Bever, J. D. 2002. A novel theory to explain species diversity in landscapes: positive frequency dependence and habitat suitability. - Proc. R. Soc. Lond. B 269: 2389–2393.

Muller-Dombois, D. and Ellenberg, H. 1974. Aims and methods of vegetation ecology. - John Wiley & Sons.

Mund, M. 2004. Carbon pools of European Beech forests (Fagus sylvatica) under different silvicultural management. - FZW.

NakAshizuka, T. 2001. Species coexistence in temperate, mixed deciduous forests. - Trends Ecol. Evol. 16: 205–210.

Olaya, V. 2004. A gentle introduction to SAGA GIS. - SAGA User Group EV Gottingen Ger. in press.

Oliver, C. D. and Larson, B. C. 1996. Forest stand dynamics. - John Wiley & Sons.

Ostling, A. et al. 2000. Self-similarity and clustering in the spatial distribution of species. - Science 290: 671–671.

Otto, H.-J. 1994. Waldökologie. - Ulmer.

Pacala, S. W. and Deutschman, D. H. 1995. Details that matter: the spatial distribution of individual trees maintains forest ecosystem function. - Oikos 74: 357–365.

Pacala, S. W. and Levin, S. A. 1997. Biologically generated spatial pattern and the coexistence of competing species. - In: Tilman, D. and Kareiva, P. (eds), Spatial ecology: The role of space in population dynamics and interspecific interactions. Princeton University Press, pp. 204–232.

Pacala, S. W. et al. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. - Ecol. Monogr. 66: 1–43.

Parviainen, J. 2005. Virgin and natural forests in the temperate zone of Europe. - Snow Landsc Res 79: 9–18.

Pearman, P. B. et al. 2008. Niche dynamics in space and time. - Trends Ecol. Evol. 23: 149–158.

Pelissier, R. 1998. Tree spatial patterns in three contrasting plots of a southern Indian tropical moist evergreen forest. - J. Trop. Ecol. 14: 1–16.

Pélissier, R. and Goreaud, F. 2001. A practical approach to the study of spatial structure in simple cases of heterogeneous vegetation. - J. Veg. Sci. 12: 99–108.

Penttinen, A. et al. 1992. Marked point processes in forest statistics. - For. Sci. 38: 806–824.

Peterken, G. F. 1996. Natural woodland: ecology and conservation in northern temperate regions. - Cambridge University Press.

Peterson, A. T. 1999. Conservatism of Ecological Niches in Evolutionary Time. - Science 285: 1265–1267.

Pignatti, S. and others 1996. Ecograms for phytosociological tables based on Ellenberg's Zeigerwerte. - Ann BotRoma 54: 5–14.

Plotnick, R. E. and Gardner, R. H. 2002. A general model for simulating the effects of landscape heterogeneity and disturbance on community patterns. - Ecol. Model. 147: 171–197.

Potts, M. et al. 2004. Habitat heterogeneity and niche structure of trees in two tropical rain forests. - Oecologia 139: 446–453.

Pulliam, H. R. 2000. On the relationship between niche and distribution. - Ecol. Lett. 3: 349–361.

Punchi-Manage, R. et al. 2013. Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest (P Zuidema, Ed.). - J. Ecol. 101: 149–160.

R Core Team 2015. R: A Language and Environment for Statistical Computing. - R Foundation for Statistical Computing.

Rahbek, C. 2004. The role of spatial scale and the perception of large-scale species-richness patterns: Scale and species-richness patterns. - Ecol. Lett. 8: 224–239.

Ratcliffe, S. et al. 2015. Tree neighbourhood matters – Tree species composition drives diversity–productivity patterns in a near-natural Beech forest. - For. Ecol. Manag. 335: 225–234.

Rathbun, S. L. and Cressie, N. 1994. A Space-Time Survival Point Process for a Longleaf Pine Forest in Southern Georgia. - J. Am. Stat. Assoc. 89: 1164–1174.

Reichelt, G. and Wilmanns, O. 1973. Vegetationsgeographie. - Westermann.

Ripley, B. D. 1976. The second-order analysis of stationary point processes. - J. Appl. Probab. 13: 255–266.

Ripley, B. D. 1977. Modelling spatial patterns. - J. R. Stat. Soc. Ser. B Methodol. 41: 368–374.

Roloff, A. 2009. Berg-Ahorn: Baum des Jahres 2009. - AFZ- Wald 8: 409–411.

Rust, S. and Savill, P. 2000. The root systems of Fraxinus excelsior and Fagus sylvatica and their competitive relationships. - Forestry 73: 499–508.

Saefken, B. et al. 2013. A Unifying Approach to the Estimation of the Conditional Akaike Information in Generalized Linear Mixed Models. - Electron. J. Stat. in press.

Scheffer, M. and van Nes, E. H. 2006a. Self-organized similarity, the evolutionary emergence of groups of similar species. - Proc. Natl. Acad. Sci. 103: 6230–6235.

Scheffer, M. and van Nes, E. H. 2006b. Self-organized similarity, the evolutionary emergence of groups of similar species. - Proc. Natl. Acad. Sci. 103: 6230–6235.

Schmid, I. and Kazda, M. 2001. Vertical distribution and radial growth of coarse roots in pure and mixed stands of Fagus sylvatica and Picea abies. - Can. J. For. Res. 31: 539–548.

Schmidt, M. et al. 2011. Waldartenlisten der Farn-und Blütenpflanzen, Moose und Flechten Deutschlands. - BfN.

Schoener, T. W. 1974. Resource partitioning in ecological communities. - Science 185: 27–39.

Seidel, D. 2011. Terrestrial laser scanning. in press.

Shen, G. et al. 2009. Species-area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. - Ecology 90: 3033–3041.

Shen, G. et al. 2013. Quantifying spatial phylogenetic structures of fully stem-mapped plant communities (RB O'Hara, Ed.). - Methods Ecol. Evol. 4: 1132–1141.

Simberloff, D. and Dayan, T. 1991. The guild concept and the structure of ecological communities. - Annu. Rev. Ecol. Syst.: 115–143.

Snyder, R. E. and Chesson, P. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. - Ecol. Lett. 6: 301–309.

Snyder, R. E. and Chesson, P. 2004. How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. - Am. Nat. 164: 633–650.

Stoll, P. and Bergius, E. 2005. Pattern and process: competition causes regular spacing of individuals within plant populations. - J. Ecol. 93: 395–403.

Stoyan, D. and Ohser, J. 1982. Correlations between planar random structures, with an ecological application. - Biom. J. 24: 631–647.

Stoyan, D. and Stoyan, H. 1994a. Fraktals, random shapes, and point fields: Methods of geometrical statistics. - John Wiley & Sons.

Stoyan, D. and Stoyan, H. 1994b. Fractals, random shapes and point fields: Methods of geometrical statistics. - John Wiley & Sons.

Stoyan, D. and Penttinen, A. 2000a. Recent applications of point process methods in forestry statistics. - Stat. Sci. 15: 61–78.

Stoyan, D. and Penttinen, A. 2000b. Recent applications of point process methods in forestry statistics. - Stat. Sci.: 61–78.

Stoyan, D. et al. 1995. Stochastic geometry and its applications. - Wiley New York.

Sutherland, W. J. et al. 2013. Identification of 100 fundamental ecological questions. - J. Ecol. 101: 58–67.

Tabaku, V. 2000. Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und-Wirtschaftswäldern. - Cuvillier Verlag.

Tilman, D. 1980. Resources: A graphical-mechanistic approach to competition and predation. - Am. Nat. 116: 362–393.

Tilman, D. 1982. Resource competition and community structure. - Princeton University Press.

Trotsiuk, V. et al. 2012. Age structure and disturbance dynamics of the relic virgin Beech forest Uholka (Ukrainian Carpathians). - For. Ecol. Manag. 265: 181–190.

Turner, P. E. et al. 1996. Tests of ecological mechanisms promoting the stable coexistence of two bacterial genotypes. - Ecology: 2119–2129.

Uria-Diez, J. et al. 2013. Importance of habitat heterogeneity and biotic processes in the spatial distribution of a riparian herb (Carex remota L.): a point process approach. -

Stoch. Environ. Res. Risk Assess. 27: 59–76.

Velázquez, E. et al. 2015. An evaluation of the state of spatial point pattern analysis in ecology. - Ecography in press.

Velázquez, E. et al. 2016. An evaluation of the state of spatial point pattern analysis in ecology. - Ecography: n/a-n/a.

Vergnon, R. et al. 2012. Emergent neutrality leads to multimodal species abundance distributions. - Nat Commun 3: 663.

Wang, X. et al. 2010. Species associations in an old-growth temperate forest in north-eastern China. - J. Ecol. 98: 674–686.

Wang, X. et al. 2011. Spatial patterns of tree species richness in two temperate forests: Detecting underlying mechanisms controlling species-area relationships. - J. Ecol. 99: 1382–1393.

Wang, X. et al. 2012. Local-Scale Drivers of Tree Survival in a Temperate Forest (KO Reinhart, Ed.). - PLoS ONE 7: e29469.

Webb, C. O. et al. 2002. Phylogenies and Community Ecology. - Annu. Rev. Ecol. Syst. 33: 475–505.

Weltzin, J. F. and McPherson, G. R. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. - Oecologia 112: 156–164.

Whitmore, T. C. 1989. Canopy Gaps and the Two Major Groups of Forest Trees. - Ecology 70: 536–538.

Whittaker, R. H. 1965. Dominance and Diversity in Land Plant Communities: Numerical relations of species express the importance of competition in community function and evolution. - Science 147: 250–260.

Wiegand, T. and A Moloney, K. 2004. Rings, circles, and null-models for point pattern analysis in ecology. - Oikos 104: 209–229.

Wiegand, T. and Moloney, K. A. 2014. Handbook of spatial point-pattern analysis (R Smith, Ed.). - CRC Press.

Wiegand, K. et al. 2000. Do spatial effects play a role in the spatial distribution of desert-dwelling Acacia raddiana? - J. Veg. Sci. 11: 473–484.

Wiegand, T. et al. 2012. A systematic comparison of summary characteristics for quantifying point patterns in ecology. - Ecography in press.

Wiegand, T. et al. 2013. A systematic comparison of summary characteristics for quantifying point patterns in ecology. - Ecography 36: 92–103.

Wilmanns, O. 1989. Ökologische Pflanzensoziologie. - Quelle & Meyer.

Wilson, W. G. et al. 2003. Biodiversity and species interactions: extending Lotka-Volterra community theory. - Ecol. Lett. 6: 944–952.

Wohlgemuth, T. et al. 2006. Wie rasch ändert sich die Waldvegetation als Folge von raschen Klimaveränderungen. - Forum Für Wissen 2006: 7–16.

Wood, S. N. 2006. Low-Rank Scale-Invariant Tensor Product Smooths for Generalized Additive Mixed Models. - Biometrics 62: 1025–1036.

Wood, S. N. and Augustin, N. H. 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. - Ecol. Model. 157: 157–177.

Wright, J. S. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. - Oecologia 130: 1–14.

Yenni, G. et al. 2012. Strong self-limitation promotes the persistence of rare species. - Ecology 93: 456–461.

Zevenbergen, L. W. and Thorne, C. R. 1987. Quantitative analysis of land surface topography. - Earth Surf. Process. Landf. 12: 47–56.

Zhang, Y. et al. 2005. Determining digital hemispherical photograph exposure for leaf area index estimation. - Agric. For. Meteorol. 133: 166–181.

Zhang, L. et al. 2011. Strong plant-soil associations in a heterogeneous subtropical broad-leaved forest. - Plant Soil 347: 211–220.

Zhang, C. et al. 2013. Spatial Characteristics of Tree Diameter Distributions in a Temperate Old-Growth Forest. - PloS One 8: e58983.

Zhang, C. et al. 2014. Scale dependent structuring of spatial diversity in two temperate forest communities. - For. Ecol. Manag. 316: 110–116.

7 Appendix 1: Supplementary material for Chapter 1

7.1 Homogeneity

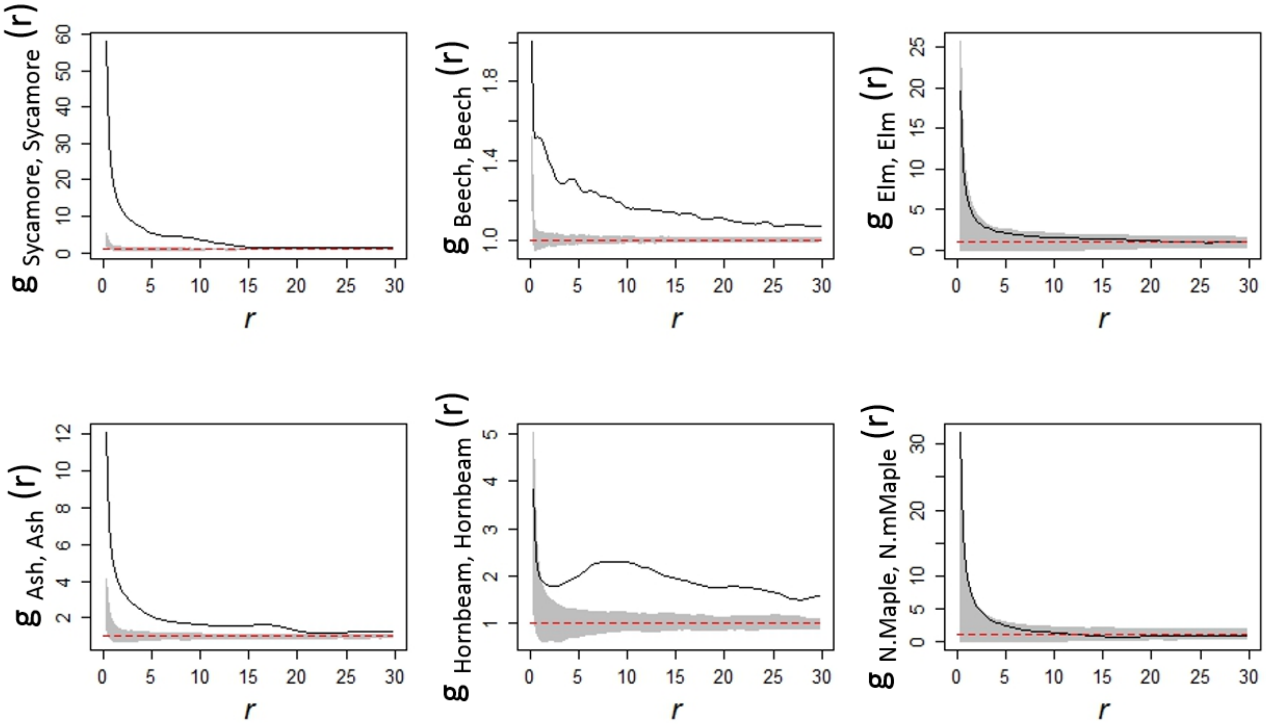

__Figure A 7-1 Complete spatial randomness and exclusion of homogeneity__ Univariate pair-correlation function. Confidence envelopes result from 199 simulations of a homogeneous Poisson process as a null-model. Black line: data, red dashed line: expectation under CSR, grey area: 95% confidence envelope derived from simulating the CSR null-model. Large scale deviations from the envelope indicate heterogeneity. Here, this is the case for beech, ash, hornbeam and sycamore. For N. maple and elm, observed pattern is very close to the upper border of the envelope. Thus we allow for heterogeneity in all six species in our spatial analyses.

7.2 Nearest neighbour contingency tables

We applied nearest neighbour contingency tables (Dixon 1994) that contain the observed mean nearest neighbour distances and applied a Dixon test to compare the nearest neighbour distances to the expected distances (Dixon 1994).

Nearest neighbour contingency tables can provide information whether competition is roughly symmetric (Dixon 1994) and thus cam imply stability properties of coexistence. The intra-specific combinations ranged from 2 m to 48 m. Interspecific distances ranged from 15 to 55 m. The intraspecific distances were distinctly shorter than the interspecific distances, except for elm, where both the distances were roughly equal. Deviations from expectation under random distributions were observed in combinations that involved the three main species, beech, ash, and hornbeam. However, combinations with ash showed distances smaller than expected, whereas distances in combinations with Beech and Hornbeam were larger than expected (Tab. A1).

Table A 7-1 Nearest neighbour contingency table *of observed mean nearest neighbour distances between target species (rows) and neighbour species (columns). Asterisks indicate significant deviations from expectation (* p < 0.05, ** p<0.01) according to Dixon-test.. Significant deviations towards clumping are indicated by* ***+****, deviations to repulsion by* ***-****.*

	beech	ash	hornbeam	sycamore	elm
beech	2	15	- 22**	52	55
ash	-15**	+10**	22	-52**	53
hornbeam	22	22	12	52	-43*
sycamore	-16**	16	15	+17*	52
elm	55	-53*	43	45	48

7.3 Spatial summary functions

Table A 7-2 Summary of spatial statistics*. To reduce the pair-correlation function to one value, it is transformed to Ripley's K(r=30).*

$$K = 2\pi \int_{r=0}^{r} g(r)$$

The empty space and nearest neighbour distribution are characterised by the proportion of locations or, respectively, trees that have their nearest tree within the distances r [m]. In cases where the function values differ, the proportions are characterised by the benchmarks of 10 %, 50%, or 90 % of trees falling within this distance Example: Beech: Empty-space function 90%: Around a Beech tree, in 90% of the cases, the empty space will be 8.28, i.e. between Beech trees, the gaps are usually not larger than roughly 8 m.

	Ripley's K	empty-space-function			nearest-neighbour-function		
species	(r=30)	10%	50%	90%	10%	50%	90%
beech	29784.63	1.77	4.55	8.28	1.15	3.19	6.17
ash	37755.60		44.42		14.49	41.81	44.42
hornbeam	32976.22		53.67			53.67	
sycamore	32786.90		54.90		10.08	32.17	54.90
maple	18898.71		161.22			161.22	
elm	9422.55		163.28			163.28	

8 Appendix 2: Supplementary material for Chapter 2

Table A 8-1 Measured and calculated abiotic covariates and the variance explained by the best predicting model *. a= few data points. b = not interpolated, derived from DEM. An abbreviation code is included in Chapter 2, Table 1.*

Abiotic variable	**mean**	**min**	**max**	**var**	**R^2**
Area.max1	298994.742	26183	2485885	215413424600.359	0.26
Area.max2	284400.097	25768	2426017	211052409231.368	0.26
Area.max3	213441.258	23003	2288468	127500838371.047	0.18
cont.water_1	30.833	11.060	54.480	63.727	0.26
cont.water_2	35.970	12.000	131.380	421.080	0.21
cont.water_3	33.174	18.580	53.130	65.081	0.21
diff.soil1_1	3.720	-27.830	23.610	26.813	0.04
diff.soil1_2	5.922	1.120	14.110	6.106	0.12
diff.soil1_3	5.933	1.180	11.040	5.952	0.20
diff.soil1_4	7.935	2.190	36.480	25.102	0.17
diff.soil1_5	8.653	1.750	38.270	28.505	0.21
diff.soil2_1	5.239	-0.050	58.700	58.357	0.06
diff.soil2_2	6.265	0.630	25.070	15.659	0.14
diff.soil2_3	6.136	1.680	20.900	9.190	0.05
diff.soil2_4	7.383	1.590	31.330	18.910	0.08
diff.soil2_5	8.936	2.800	57.350	56.340	0.18
diff.soil3_1	6.544	0.460	11.000	3.948	0.22
diff.soil3_2	6.867	1.480	12.380	5.052	0.17
diff.soil3_3	7.034	1.300	14.570	9.009	0.06
diff.soil3_4	6.551	2.410	11.110	4.591	0.06
DUS2_1	5.930	2.000	75.000	118.257	0.06
DW1_1_1	13.520	4.260	52.410	73.839	0.09
DW1_1_2	19.376	5.870	33.130	47.943	0.08
DW1_1_3	20.082	5.850	44.680	62.852	0.15
DW1_1_4	25.533	8.030	55.910	127.416	0.35
DW1_1_5	31.037	6.120	56.730	187.468	0.40
DW1_1_6	34.634	11.360	61.980	195.972	0.16
DW1_1_7	47.588	16.880	65.680	165.392	0.30
DW1_1_8	42.824	4.890	61.910	419.158	0.81
DW1_1_9	57.163	47.680	66.830	61.138	a

Continued

Table A 8-1

Abiotic variable	**mean**	**min**	**max**	**var**	**R^2**
DW2_1_2	21.568	3.110	71.810	95.761	0.20
DW2_1_3	22.638	7.500	55.160	85.483	0.01
DW2_1_4	27.371	7.510	61.200	143.093	0.05
DW2_1_5	32.873	5.450	67.560	239.228	0.14
DW2_1_6	39.861	18.490	68.480	182.273	0.16
DW2_1_7	49.916	24.620	71.760	156.482	0.20
DW2_1_8	44.420	13.750	80.180	402.986	0.40
DW2_1_9	41.223	19.170	54.900	220.615	a
DW3_1_1	14.907	2.530	30.270	17.317	0.20
DW3_1_2	18.630	6.750	31.180	29.086	0.20
DW3_1_3	20.748	7.380	39.630	58.748	0.06
DW3_1_4	20.158	7.110	38.170	35.806	0.06
DW3_1_5	20.861	3.440	40.490	58.139	0.27
DW3_1_6	26.876	3.610	227.260	861.515	0.08
DW3_1_7	26.659	3.330	42.680	101.204	0.38
DW3_1_8	22.744	5.870	46.330	144.311	0.29
DW3_1_9	23.554	7.920	38.910	122.243	0.55
DW3_1_10	12.305	7.170	17.440	52.736	a
DWUS1_1	47.323	7.710	171.080	901.470	0.20
DWUS2_1	56.718	12.420	115.590	488.702	0.38
FW1_1_1	17.398	5.310	76.020	109.376	0.19
FW1_1_2	25.580	6.990	42.750	83.018	0.17
FW1_1_3	26.041	7.030	55.410	100.863	0.13
FW1_1_4	33.497	10.290	68.480	210.492	0.24
FW1_1_5	39.871	7.870	71.600	287.778	0.37
FW1_1_6	43.429	12.980	78.500	278.612	0.13
FW1_1_7	58.661	20.350	81.220	234.864	0.01
FW1_1_8	52.298	5.220	79.690	725.949	0.69
FW1_1_9	69.520	55.810	78.450	93.659	a
FW2_1_1	18.767	4.920	82.170	163.275	0.06
FW2_1_2	27.525	3.740	96.880	170.920	0.17
FW2_1_3	28.436	9.500	66.440	122.399	0.10
FW2_1_4	34.319	9.100	73.790	197.897	0.04
FW2_1_5	42.263	12.640	79.830	308.555	0.34
FW2_1_6	48.857	24.330	83.240	260.245	0.17
FW2_1_7	60.602	27.430	114.400	333.415	0.19
FW2_1_8	62.542	27.280	88.210	379.838	0.65

Continued
Table A 8-1

Abiotic variable	**mean**	**min**	**max**	**var**	**R²**
FW3_1_2	25.535	8.230	43.560	55.562	0.18
FW3_1_3	27.608	9.150	52.490	110.762	0.05
FW3_1_4	26.572	9.520	48.740	63.574	0.19
FW3_1_5	27.111	4.090	52.230	103.528	0.32
FW3_1_6	29.766	4.640	57.380	125.862	0.18
FW3_1_7	33.825	4.090	58.180	169.062	0.09
FW3_1_8	28.857	6.900	56.830	224.432	0.39
FW3_1_9	27.065	5.360	47.840	220.101	0.16
FW3_1_10	14.565	8.800	20.330	66.470	a
FWUS1_1	66.262	12.290	237.850	1687.624	0.20
FWUS2_1	83.286	15.900	156.720	1248.663	0.54
GSCI.max2	7.669	3.869	16.409	6.679	0.21
GSCI.max3	6.957	2.727	12.466	5.125	0.17
GSCIplot.median	7.647	3.072	16.507	6.783	0.19
logArea.max1	12.000	10.173	14.726	1.018	0.42
logArea.max2	11.873	10.157	14.702	1.177	0.05
logArea.max3	11.597	10.043	14.643	1.141	0.09
MD1_1	59.210	26.000	90.000	190.627	0.56
MD2_1	59.008	25.000	86.000	199.869	0.51
MD3_1	69.393	30.000	94.000	178.743	0.38
mean_depth	62.742	43.667	86.333	88.888	0.53
nFK	95.355	60.200	221.975	401.388	0.32
Perim.max1	13715.663	2636.664	60087.427	152428194.257	0.31
Perim.max2	13162.109	3183.480	57011.784	149300183.144	0.29
Perim.max3	10502.428	1571.741	61711.751	98652927.757	0.31
pF1_8	121.925	87.260	155.230	186.373	0.18
sd_depth	12.341	1.155	25.865	34.081	0.26
var_depth	185.824	1.333	669.000	25913.768	0.25
Analytical.Hillshading	42.120	0.087	117.376	196.535	b
Aspect	2.694	0.000	6.283	5.825	b
Catchment_Area	761.718	1.000	981133.313	136765160.851	b
Cross.Sectional_Curvature	0.000	-0.276	0.311	0.000	b
dtmHuss	433.869	365.760	475.585	652.265	b
Slope	0.087	0.000	0.836	0.004	b

***Table A 8-2 Interpolated abiotic covariate with best spline type and explained variance** by best model.*

interpolated abiotic variable	Smoothing spline /kernel type	R2 of best interpolation model
Area1	s.aniostropic	0.52
Area2	s.aniostropic	0.51
Area3	s.aniostropic	0.2
cont.water	s.aniostropic	0.24
diff.soil1	s.aniostropic	0.3
diff.soil2	s.aniostropic	0.33
diff.soil3	s.aniostropic	0.16
diff.soil4	s.aniostropic	0.03
diff.soil5	s.aniostropic	0.18
DUS2_1	s.aniostropic	0.07
FWUS2_1	s.aniostropic	0.48
GCSI1	s.aniostropic	0.19
GCSI2	s.aniostropic	0.21
GCSI3	s.aniostropic	0.19
GCSIplot.median	s.aniostropic	0.19
logArea	isotropic	0.44
MD1_1	s.aniostropic	0.56
MD2_1	s.aniostropic	0.51
MD3_1	anisotropic	0.51
mean_depth	s.aniostropic	0.53
nFK	anisotropic	0.24
pF1_8	s.aniostropic	0.18
sd_depth	s.aniostropic	0.26
var_depth	s.aniostropic	0.24
wF	s.aniostropic	0.25
wK	s.aniostropic	0.05
wL	isotropic	0.35
wN	anisotropic	0.17
wT	s.aniostropic	0.27
wR	s.aniostropic	0.24

***Table A 8-3 available on CD: Results of vegetation relevés at all 62 sample plots**. Information include Plot name, Gauss-Krueger coordinates, date of relevé, Species name (Latin and German), vegetation type, total cover per plot (in per cent and on ordinal Braun-Blanquet scale)*

Table A 8-4 Summary table of species identified in relevés *and the according indicator values used for weighing with cover. Lay= Layer (T=Tree, H= Herbacious, S=Shrub) Abbreviations according to German Ellenberg indicator values (L=Light, T=Temperature, K=Continentality, F-Wetness, R=Soil acidity, N=Nitrogen/ soil productivity)*

Species Latin	**Species German**	**Lay**	**L**	**T**	**K**	**F**	**R**	**N**
Acer platanoides	Spitz-Ahorn	T	4	x	4	6	x	7
Acer pseudoplatanus	Berg-Ahorn	T	4	x	4	6	x	7
Aegopodium podagraria	Giersch	H	5	5	3	6	7	8
Ajuga reptans	Kriechender Günsel	H	6	x	2	6	6	6
Alliaria petiolata	Knoblauchsraute	H	5	6	3	5	7	9
Allium ursinum	Bärlauch	H	2	x	2	6	7	8
Anemone nemorosa	Busch-Windröschen	H	x	x	3	5	x	x
Anemone ranunculoides	Gelbes Windröschen	H	3	6	4	6	8	8
Arctium lappa	Große Klette	H	3	3	4	2	4	5
Arum maculatum	Gefleckter Aronstab	H	2	4	2	3	4	3
Asarum europaeum	Europäische Haselwurz	H	2	4	2	3	4	3
Athyrium filix-femina	Gewöhnlicher Frauenfarn	H	2	3	2	3	2	3
Brachypodium sylvaticum	Wald-Zwenke	H	3	3	3	3	3	3
Cardamine bulbifera	Zwiebel-Schaumkraut	H	3	5	4	5	7	6
Cardamine heptaphylla	Fiederblättrige Zahnwurz	H	2	3	2	3	4	4
Cardamine pentaphyllos	Fingerblättrige Zahnwurz	H	3	5	2	5	7	6
Carex remota	Lockerährige Segge	H	3	5	3	8	x	x
Carex sylvatica	Wald-Segge	H	2	5	3	5	6	5
Carpinus betulus	Hainbuche	T	4	6	4	x	x	x
Convallaria majalis	Maiglöckchen	H	5	x	3	4	x	4
Corydalis cava	Hohlknolliger Lerchensporn	H	3	6	4	6	8	8
Crataegus laevigata	Zweigriffeliger Weissdorn	H	6	6	4	5	7	5
Crataegus monogyna	Eingriffeliger Weissdorn	H	7	5	3	4	8	4
Crataegus sp.	Zweigriffeliger Weissdorn	H	6	6	4	5	7	5
Deschampsia cespitosa	Rasen-Schmiele	H	6	x	x	7	x	3
Dryopteris carthusiana	Dorniger Wurmfarn	H	5	x	3	x	4	3
Dryopteris dilatata	Breiter Wurmfarn	H	4	x	3	6	x	7

Species Latin	**Species German**	**Lay**	**L**	**T**	**K**	**F**	**R**	**N**
Dryopteris filix-mas	Echter Wurmfarn	H	3	x	3	5	5	6
Euonymus europaeus	Gemeines Pfaffenhütchen	H	3	3	3	3	4	3
Fagus sylvatica	Rot-Buche	T	3	5	2	5	x	x
Fraxinus excelsior	Gemeine Esche	T	4	5	3	x	7	7
Geum urbanum	Echte Nelkenwurz	H	4	5	5	5	x	7
Hedera helix	Efeu	H	4	5	2	5	x	x
Hordelymus europaeus	Waldgerste	H	4	5	4	5	7	6
Hypericum perforatum	Echtes Johanniskraut	H	7	6	5	4	6	4
Juncus effusus	Flatter-Binse	H	8	5	3	7	3	4
Lamium maculatum	Gefleckte Taubnessel	H	5	x	4	6	7	8
Lamium purpureum	Rote Taubnessel	H	7	5	3	5	7	7
Lathyrus vernus	Gewöhnliche Frühlings-Platterbse	H	4	6	4	5	8	4
Lilium martagon	Türkenbund-Lilie	H	4	x	5	5	7	5
Melica nutans	Nickendes Perlgras	H	4	x	3	4	x	3
Mercurialis perennis	Wald-Bingelkraut	H	2	x	3	x	8	7
Milium effusum	Waldhirse	H	4	x	3	5	5	5
Oxalis acetosella	Wald-Sauerklee	H	1	x	3	5	4	6
Paris quadrifolia	Vierblättrige Einbeere	H	3	x	4	6	7	7
Polygonatum multiflorum	Vielblütiges Salomonssiegel	H	2	x	5	5	6	5
Polygonatum odoratum	Echtes Salomonssiegel	H	7	5	5	3	7	3
Polygonatum verticillatum	Quirlblättriges Salomonssiegel	H	4	4	2	5	4	5
Primula elatior	Hohe Schlüsselblume	H	6	x	4	6	7	7
Prunus avium	Süsskirsche	T	4	5	4	5	7	5
Ranunculus auricomus	Gold-Hahnenfuss	H	5	6	3	x	7	x
Ranunculus lanuginosus	Wolliger Hahnenfuss	H	3	6	4	6	7	7
Rubus fruticosus agg.	Brombeere	H	3	6	4	6	7	7
Rumex sanguineus	Blut-Ampfer	H	4	6	2	8	7	7
Sanicula europaea	Sanikel	H	4	5	3	5	8	6
Scrophularia nodosa	Knotige Braunwurz	H	4	5	3	6	6	7
Senecio ovatus	Fuchs' Greiskraut	H	7	x	4	5	x	8
Stachys sylvatica	Wald-Ziest	H	4	x	3	7	7	7
Stellaria holostea	Grossblütige Sternmiere	H	5	6	3	5	6	5
Ulmus glabra	Berg-Ulme	T	4	5	3	6	7	7
Urtica dioica	Grosse Brennnessel	H	x	x	x	6	7	9
Viola reichenbachiana	Wald-Veilchen	H	4	x	4	5	7	6

Table A 8-5 Species-specific tree-size model results when not including topography, *aligned with species number in both census years*

Species	**Number of individuals**		**R^2 no topography**	**Most influential covariate**
	1999	2007		
beech *(Fagus sylvatica)*	13307	12191	0.05	no niche
ash *(Fraxinus excelsior)*	550	527	0.10	Light
hornbeam *(Carpinus betulus)*	389	361	0.16	plant-avail. water
sycamore *(Acer pseudoplatanus)*	321	345	0.44	plant-avail. water
Norway maple *(Acer platanoides)*	44	40	0.34	plant-avail. water
elm *(Ulmus glabra)*	69	39	0.08	continentality

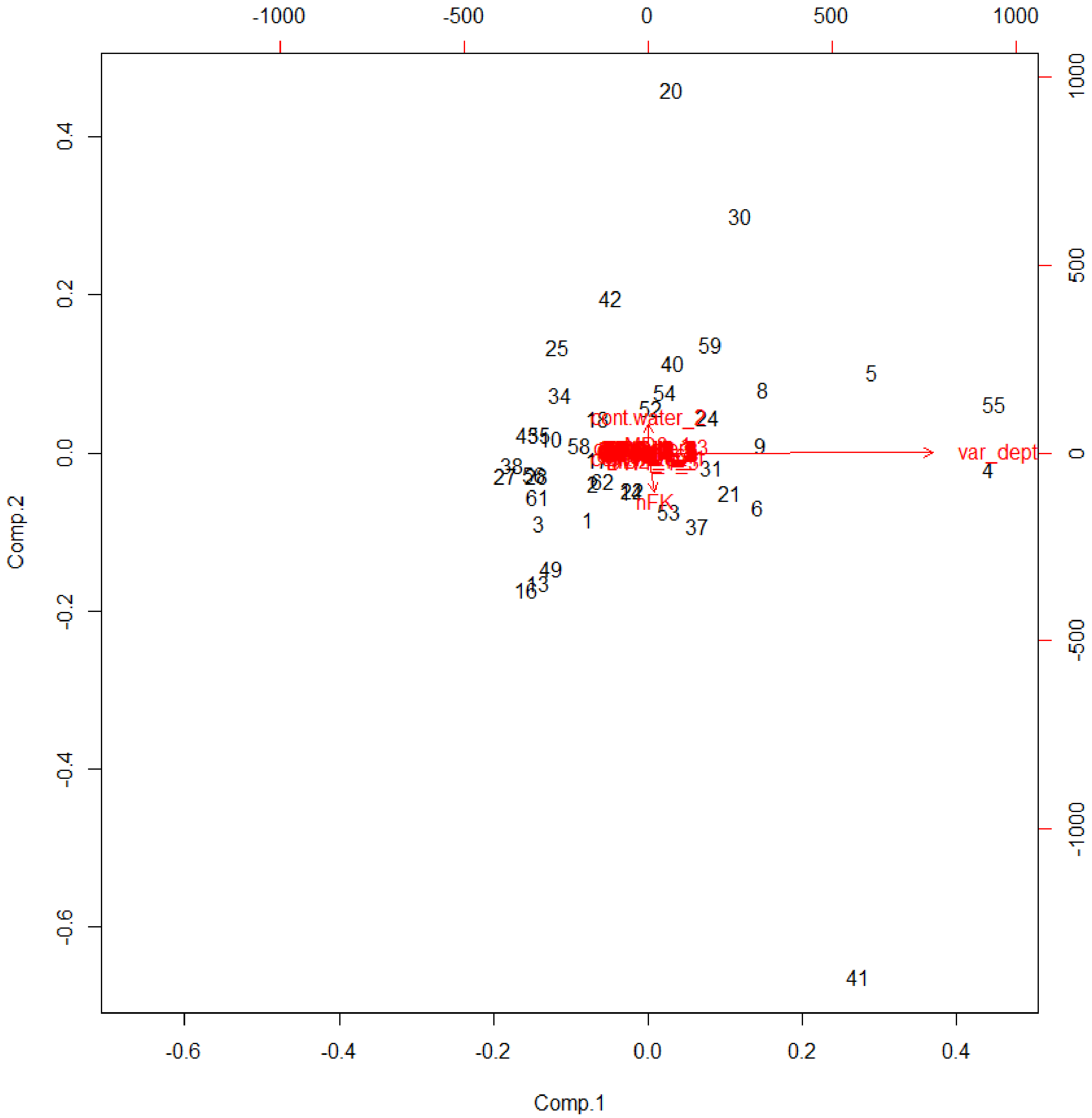

Figure A 8-1- PCA analyses of soil sample results*. Variation in soil depth over time was by far the most pronounced variables, followed by plant-available water and contained water in summer.*

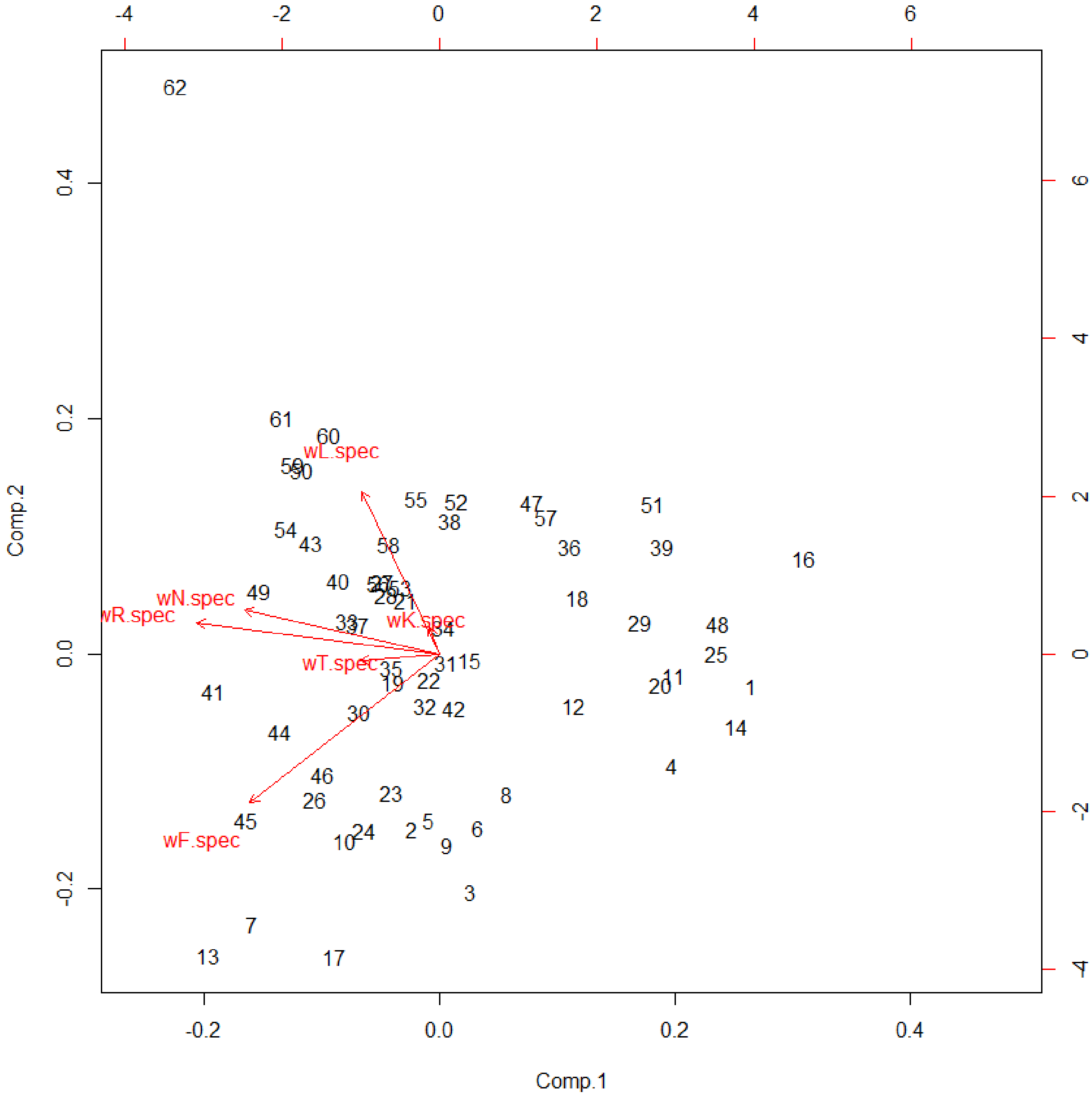

Figure A 8-2PCA of Ellenberg's indicator values from vegetation releves*, weighted by coverage. Numbers are numbers of plot, showing an ordering from south-east to north-west plots in left to right direction. This is also discernible in spatial distribution of indicator values.*

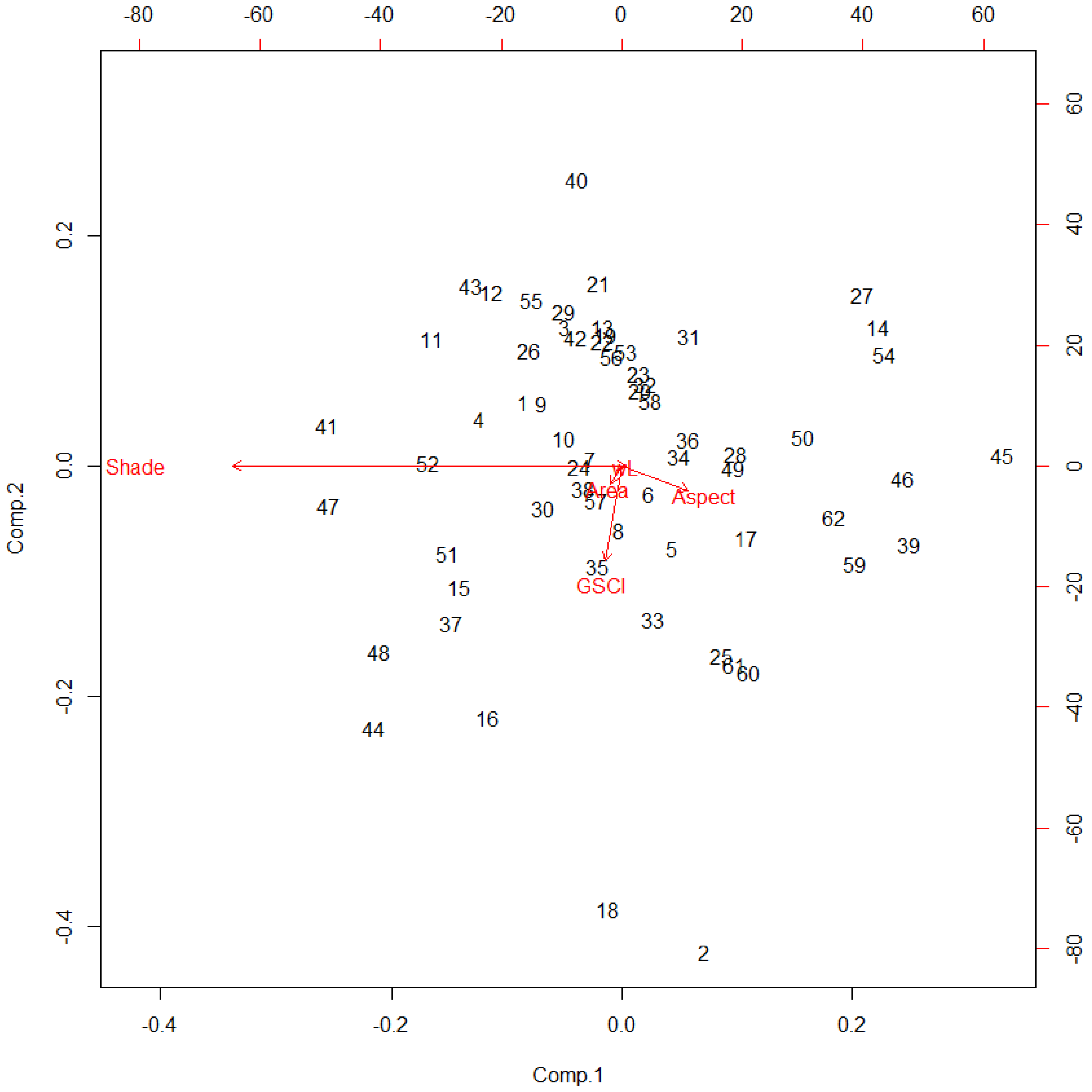

Figure A 8-3 PCA of light-related variables*, calculated from hemispherical photos and topography*

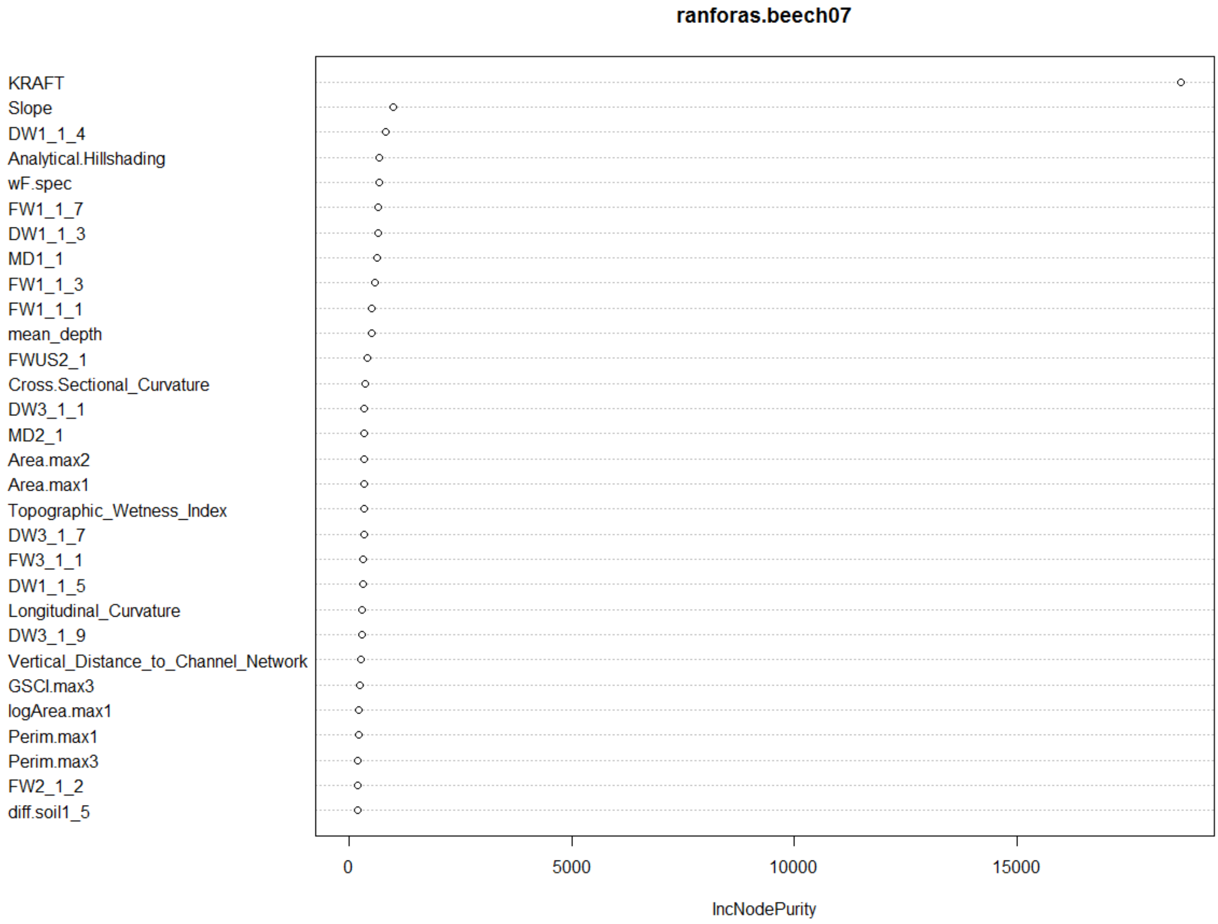

Figure A 8- 4 Result of RandomForest variable selection for beech *(tree size distribution explained by abiotic covariates). The Kraft class (dominance in canopy) as the covariate of best explaining growth was also found in (Saefken et al. 2013). We did not include this a) because it is not abiotic and b) to avoid tautology (large trees are, where large trees are). An abbreviation key to the covariates is included in Chapter2, Table 1.*

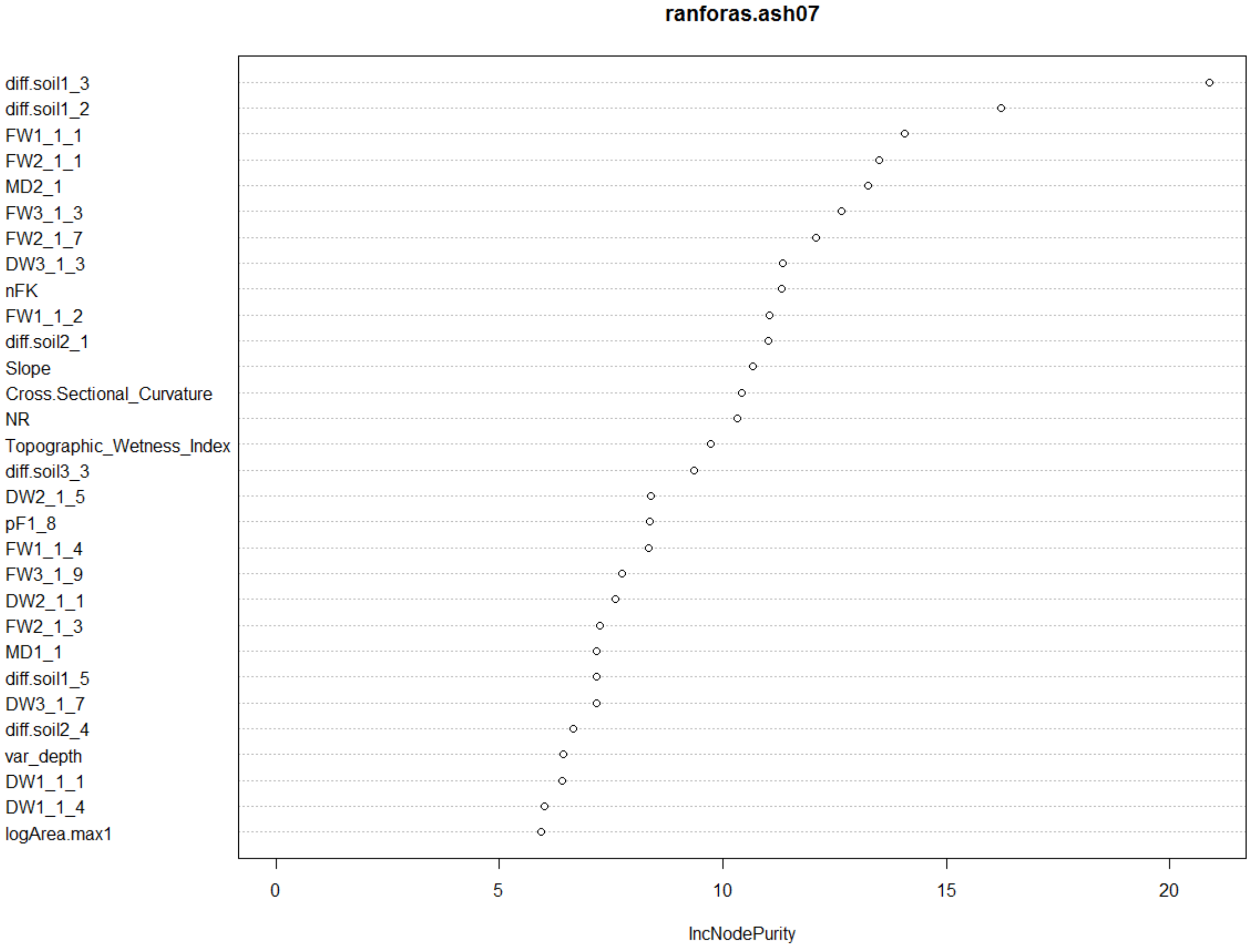

Figure A 8-5 Result of RandomForest variable selection for ash *(tree size distribution explained by abiotic covariates). Note the majority of water content related covariates and fresh weight (FW) compared to dry weight (DW).*

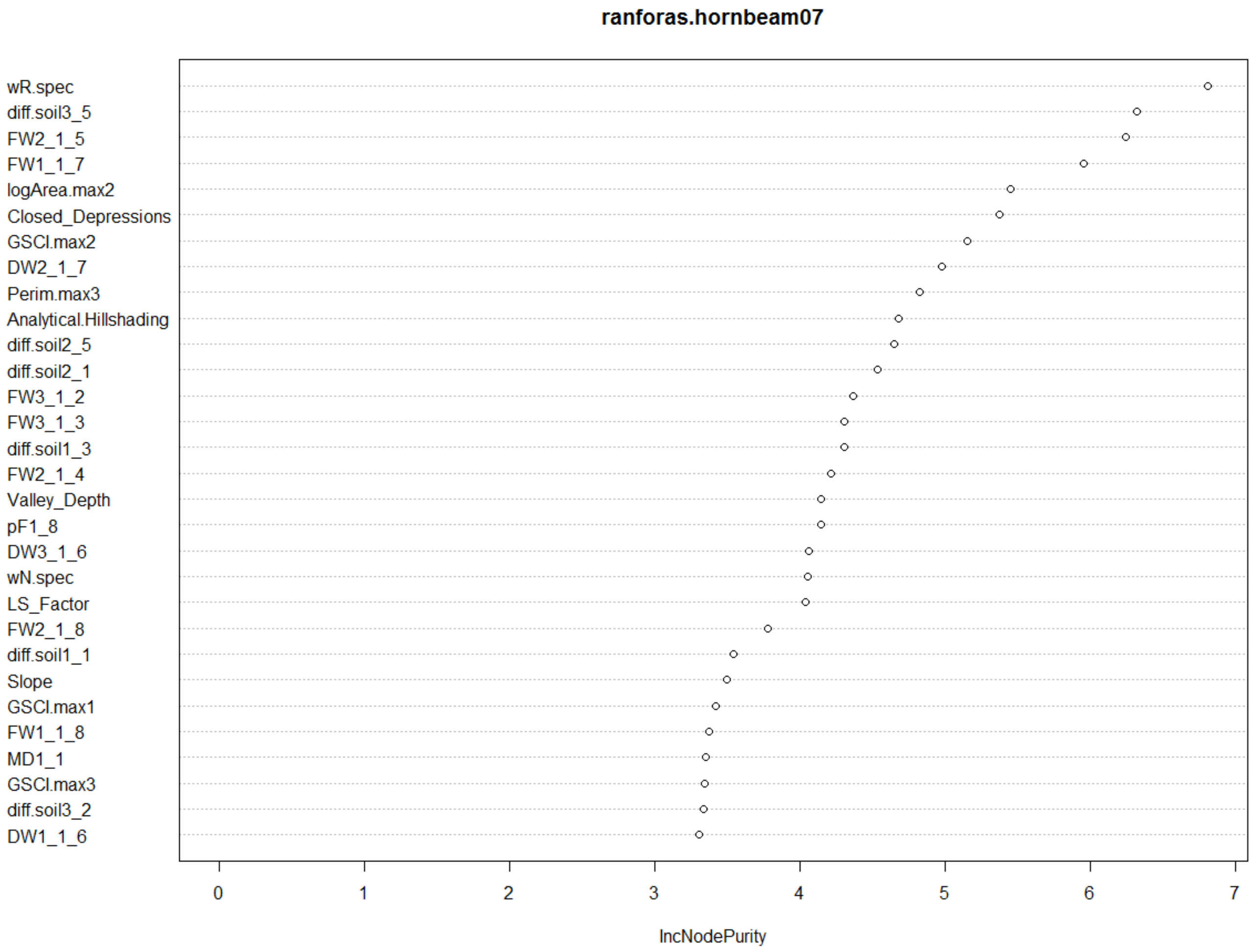

***Figure A 8-6 Result of RandomForests for hornbeam** (tree size distribution explained by covariates) Note that soil acidity is selected as most influential and light related covariates occur amongst the most important covariates.*

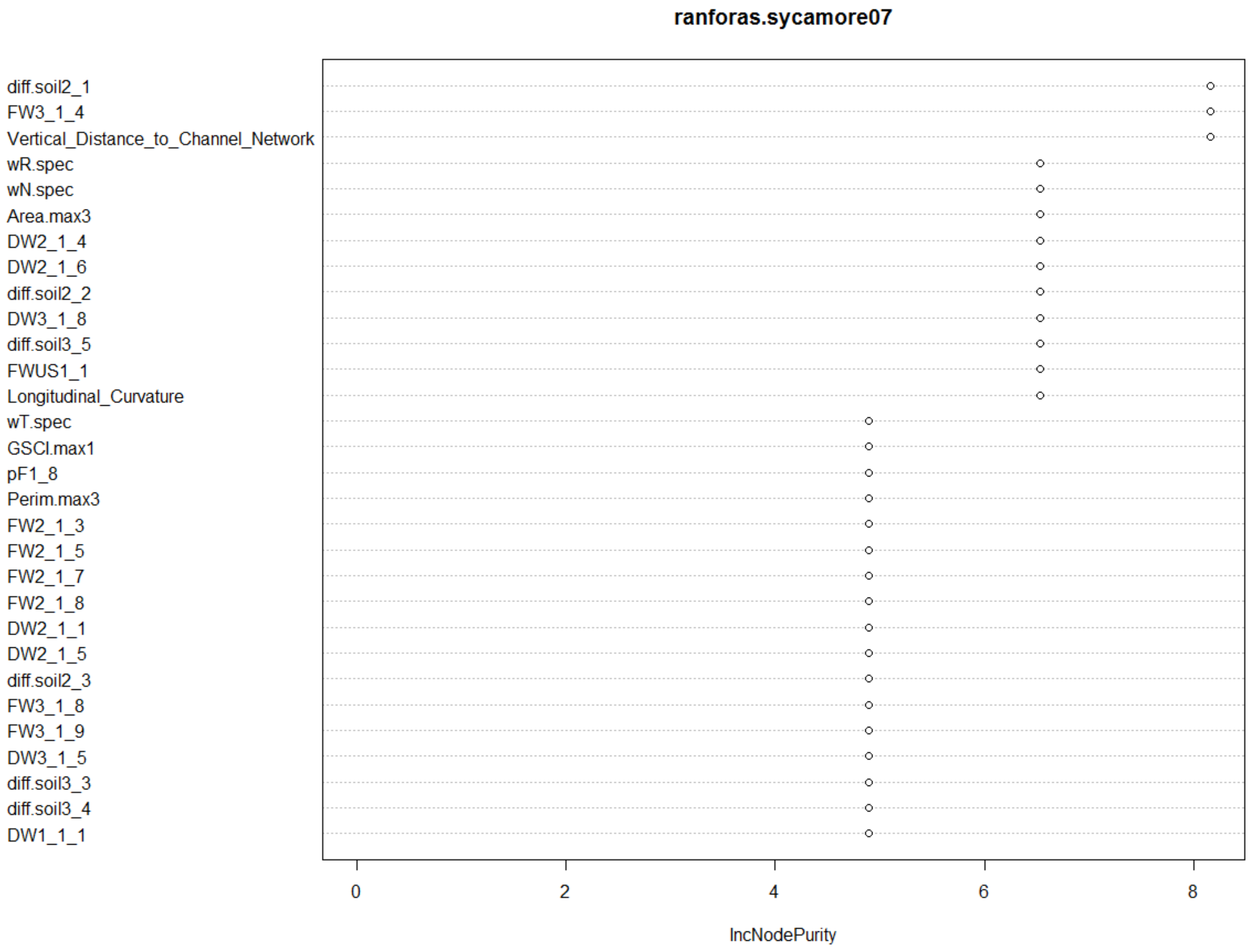

Figure A 8-7 Results of Random Forest variable selection for sycamore. *Note the increased importance of indicator values.*

9 Appendix 3: Supplementary material for Chapter 3

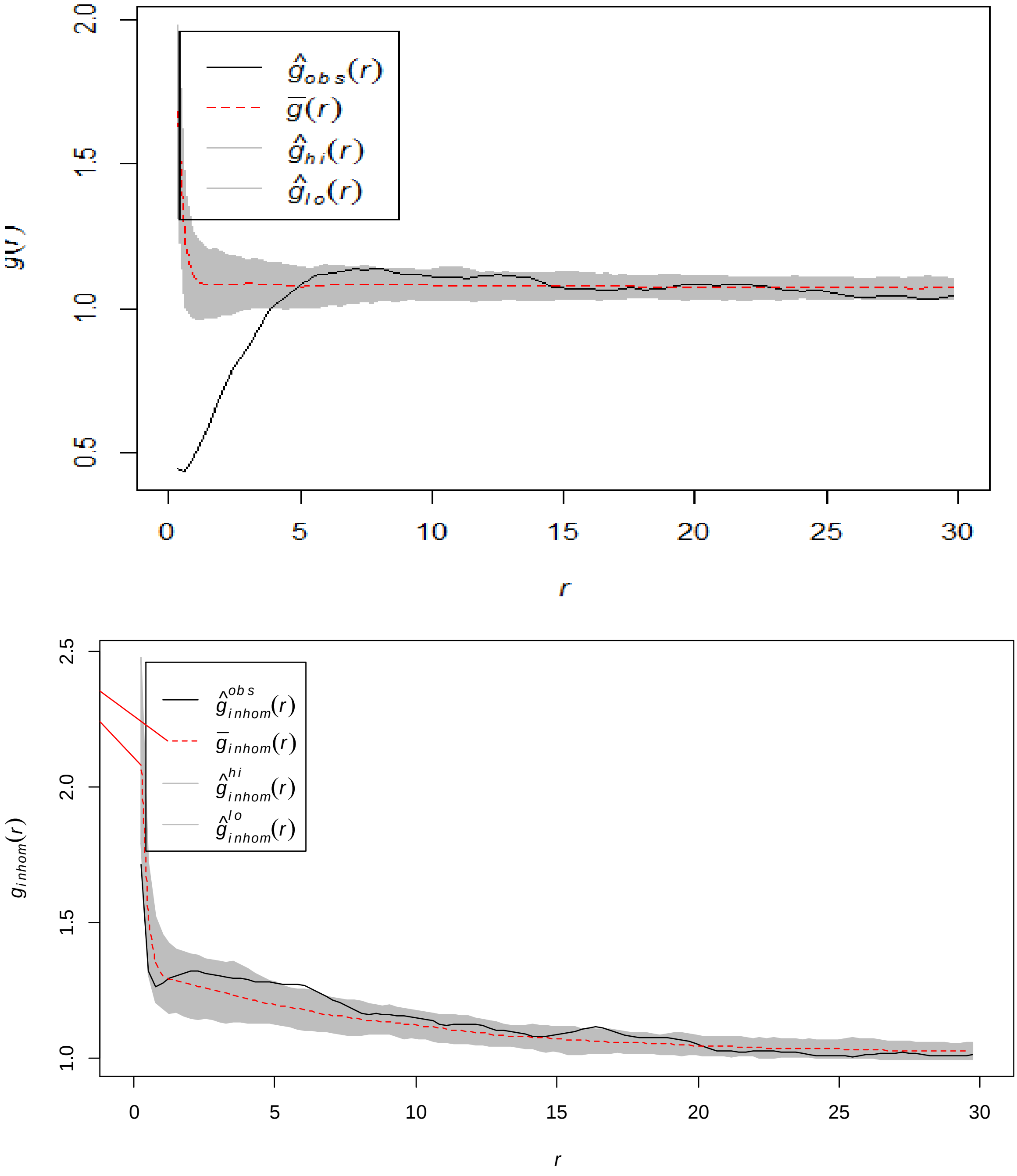

***Figure A 9-1 Results of LogGaussian Cluster Process** including biotic and abiotic covariates for Beech with DBH 10-30 cm (top) and > 30 cm (bottom). Black line = observed pattern evaluated with inhomogenous pair-correlation function, red = mean model assumption, grey envelope: created from 199 random realisation of the point process.*

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I am so happy and proud to know you all - every single day.

11 Curriculum Vitae

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12 Promovierenden-Erklärung der Georg-August-Universität Göttingen

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Ich beabsichtige, eine Dissertation zum Thema *„The role of heterogeity in spatial plant population dynamics“*.

an der Georg-August-Universität Göttingen anzufertigen. Dabei werde ich von Frau

Prof. Kerstin Wiegand betreut.

Ich gebe folgende Erklärung ab:
1. Die Gelegenheit zum vorliegenden Promotionsvorhaben ist mir nicht kommerziell vermittelt worden. Insbesondere habe ich keine Organisation eingeschaltet, die gegen Entgelt Betreuerinnen und Betreuer für die Anfertigung von Dissertationen sucht oder die mir obliegenden Pflichten hinsichtlich der Prüfungsleistungen für mich ganz oder teilweise erledigt.

2. Hilfe Dritter wurde bis jetzt und wird auch künftig nur in wissenschaftlich vertretbarem und prüfungsrechtlich zulässigem Ausmaß in Anspruch genommen. Insbesondere werden alle Teile der Dissertation selbst angefertigt; unzulässige fremde Hilfe habe ich dazu weder unentgeltlich noch entgeltlich entgegengenommen und werde dies auch zukünftig so halten.

Die Kapitel 1-3 sind für eine baldige Einreichung bei wissenschaftlichen Zeitschriften vorgesehen. Das 4. Kapitel basiert auf einem Manuskript, das bereits bei einer wissenschaftlichen Zeitschrift eingereicht ist. Hierfür war ich Mitautorin und habe im wissenschaftlich üblichen Rahmen mit Katrin Meyer und Marco Sciani zusammengearbeitet. Ich bin ausdrücklich <u>nicht</u> Erstautor. Anteile der Arbeit sind entsprechend nicht von mir, sondern von den beiden Erstautoren verfasst worden.

3. Die Richtlinien zur Sicherung der guten wissenschaftlichen Praxis an der Universität Göttingen werden von mir beachtet.

4. Eine entsprechende Promotion wurde an keiner anderen Hochschule im In- oder Ausland beantragt; die eingereichte Dissertation oder Teile von ihr wurden nicht für ein anderes Promotionsvorhaben verwendet.

Mir ist bekannt, dass unrichtige Angaben die Zulassung zur Promotion ausschließen bzw. später zum Verfahrensabbruch oder zur Rücknahme des erlangten Grades führen.

(Ort)…………………………….., den ………………………….

(Unterschrift)