Analysing and modelling spatial patterns to infer the influence of environmental heterogeneity using point pattern analysis, individual-based simulation modelling and landscape metrics

Dissertation

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Table of content

Index of figures

Index of Tables

Index of Examples

Abbreviations

$\lambda(x,y)$	intensity
c_i	competition value
cm	centimeter
CSR	complete spatial randomness
dbh	diameter at breast height
$G(r)$	Nearest neighbour distribution function
$g(r)$	pair-correlation function
ha	hectare
IBM	individual-based model
IV	importance value
$K(r)$	Ripley's K-function
$k_{mm}(r)$	Mark-correlation function
MRT	multivariate regression tree
nRMSE	normalised root-mean-square error
ODD	Overview, Design concepts, Details
POM	pattern-oriented modelling
S_i	Main effect
S_{Ti}	Total effect
SPPA	spatial point pattern analysis

Chapter 1 - Introduction

For many years, ecologists try to infer processes from patterns (Cale et al., 1989). In this context, the term pattern is used to describe structure visible in data extracted from nature (Grimm et al., 2005; Wiegand et al., 2003). Arguably, this is one of the main goals of ecology and probably science in general, as we try to explain what we see in the data (Brown et al., 2011; Levin, 1992; McIntire and Fajardo, 2009). Most ecological processes are spatially explicit and lead to identifiable spatial patterns in nature (Liebhold and Gurevitch, 2002; Wiegand et al., 2013). Consequently, non-random spatial patterns are more common than completely random ones (Perry et al., 2002; Szmyt, 2014). Because non-random spatial patterns can act as a memory of past processes (Law et al., 2009), analysing these non-random spatial patterns should allow to identify the underlying processes (Brown et al., 2016, 2011).

However, the pattern-process link might not always be straightforward (McIntire and Fajardo, 2009). Known issues include that different processes can lead to the same patterns (Barot et al., 1999; Wiegand et al., 2003), various processes can interact (Dovčiak et al., 2001; Wiegand et al., 2009) and lead to random patterns (Cale et al., 1989; Molofsky et al., 2002) or processes can be the result of patterns and not the other way around (Getzin et al., 2008). Nevertheless, a lot of these issues can be dealt with by meaningful ecological hypotheses, precise descriptions of the data, as well as appropriate usage of null models and simulation models (McIntire and Fajardo, 2009; Wiegand et al., 2003; Wiegand and Moloney, 2014).

Environmental heterogeneity can be defined as non-random or non-uniform spatial structure of environmental conditions (Ettema and Wardle, 2002; Stein et al., 2014) and can further complicate the pattern-process link. Environmental heterogeneity plays a role in many ecological processes. Examples include species diversity (Stein et al., 2014; Tamme et al., 2010), seed dispersal and regeneration processes (Jara-Guerrero et al., 2015; Ramon et al., 2018; Uriarte et al., 2017), demographic processes (Getzin et al., 2008) and the general spatial structure of plant populations (Du et al., 2017; Guo et al., 2016; Shen et al., 2013). Abiotic and biotic processes were shown to act simultaneously and to interact in many plant populations (e.g. Adler et al., 2007; Chase and Myers, 2011; Chisholm and Pacala, 2010;

1

Diniz-Filho et al., 2012; Furniss et al., 2017; Getzin et al., 2008; John et al., 2007; Legendre et al., 2009; Mitchell et al., 2017; Schouten and Houseman, 2019; Shen et al., 2013; van Waveren, 2016). Because both abiotic and biotic processes can result in similar spatial patterns of individuals, it can be challenging, yet not impossible, to study the relative importance of biotic and abiotic processes and disentangle possible interactions. This is further complicated by the scale dependence of ecological processes and environmental heterogeneity. This includes that processes and heterogeneity might be varying depending on the scale, but also that processes on one scale influence patterns on another scale and vice versa (Wu, 2004; Wu and Li, 2006). The importance of scale received considerable attention already decades ago (e.g. Levin, 1992; Wiens, 1989), but is still of scientific relevance until today (Chave, 2013; Estes et al., 2018).

Spatial point pattern analysis (SPPA) is a powerful scale-dependent approach to analyse spatial patterns and infer underlying processes (Law et al., 2009; Perry et al., 2002; Wiegand and Moloney, 2004). A point pattern includes the location of all individuals within a study region; normally simplified as points in a two-dimensional plane (Perry et al., 2006). By analysing and modelling the point pattern, possible underlying processes can be deduced (Brown et al., 2011; Law et al., 2009; McIntire and Fajardo, 2009). While the assumption of environmental homogeneity might be too simplistic for most study systems, many former point pattern analysis studies assumed just such conditions (Velázquez et al., 2016). However, SPPA provides tools to account for and explore the influence of environmental heterogeneity on spatial patterns (e.g. Harms et al., 2001; Shen et al., 2013).

Individual-based simulation models (IBMs) are another promising approach to study the role of environmental heterogeneity on emerging spatial patterns. IBMs are bottom-up simulation models in which populations are represented by discrete individuals that allow to link patterns to processes across scales (An et al., 2009). One fundamental feature of IBMs is that characteristics and behaviours differ across individuals (Grimm and Railsback, 2005). This gives the opportunity to explicitly include environmental heterogeneity and analyse its influence on the emerging patterns. However, despite increasing attention, spatially explicit environmental heterogeneity is often not a major consideration in

model design and analysis (Wallentin, 2017). This is even more striking since IBMs that include environmental heterogeneity showed its importance for the emerging patterns (e.g. Cabral and Kreft, 2012; Jeltsch et al., 1998; Liu and Ashton, 1998; Tietjen et al., 2010).

Environmental heterogeneity, patterns emerging from it and its influence on ecological processes have been discussed in the field of landscape ecology for many years (Turner, 1989). Landscape metrics are a common tool to quantify environmental heterogeneity for discrete land-cover maps (Kupfer, 2012; Uuemaa et al., 2013, 2009; With, 2019). Even though landscape metrics are criticised of being too simple to represent environmental heterogeneity and new approaches are suggested (e.g. surface metrics; Cushman et al., 2010; McGarigal et al., 2009), they allow to link patterns to processes in a straightforward way for many study systems (Lausch et al., 2015).

In this thesis, different methods are presented to study the role of environmental heterogeneity. All methods have in common that they use the power of spatial patterns to describe and model the data. Firstly, spatial point pattern analysis allowed to detect that abiotic processes had an influence on the spatial patterning of plants (chapter 2). Based on this basic understanding that abiotic processes were present, the next step was to link pattern to process. The pattern-process link could be modelled in more detail by an IBM, as it allowed to incorporate various biotic and abiotic processes and to discriminate between different hypotheses (chapter 3). Of course, to successfully study the role of abiotic processes, suitable tools to describe and quantify environmental heterogeneity were required and introduced (chapter 4).

Spatial point pattern analysis

Spatial point patterns include the discrete location of all so-called events within a usually two-dimensional study area represented as points (Fig. 1-1; Velázquez et al., 2016; Wiegand and Moloney, 2014). In addition to the location, further marks such as the size or status can be attached to the events (Grabarnik et al., 2011). One prominent example of spatial point patterns are the location of all tree individuals within a study area. Often, additional marks such as the diameter at breast height (dbh), the status (dead vs. alive) or the species (e.g. Du et al., 2017; Getzin et al., 2006; Lin et al., 2011; Wiegand

et al., 2007; Yang et al., 2016) are attached to the events. Because point patterns contain information about underlying processes (Law et al., 2009), analysing the patterns can allow to infer the processes (Perry et al., 2002; Wiegand and Moloney, 2004). SPPA typically includes i) the specification of a research question together with data gathering, ii) the selection of multiple appropriate summary statistics, iii) the selection of appropriate null models based on ecological hypotheses and iv) the comparison of data and null models (Wiegand and Moloney, 2014).

Depending on the research question and data type, point patterns can be classified into three fundamental classes (Velázquez et al., 2016; Wiegand and Moloney, 2014). Firstly, unmarked patterns include only the location of all events and, optionally, *a priori* types. For example, this includes different species because different processes are assumed to generate the patterns of the species (Goreaud and Pellissier, 2003). Secondly, qualitatively marked patterns include *a posteriori* generated marks. Here, the marks (e.g. dead vs. alive) are generated by the same process in the same set of events (Goreaud and Pellissier, 2003). Thirdly, also quantitative marked patterns include *a posteriori* marks, such as the size of the individuals.

Summary statistics are used to describe the spatial characteristics of a point pattern, and optionally its marks, briefly but as concisely as possible (Illian et al., 2008). This can be done in an exploratory context of the spatial structure as well as in a confirmatory context of hypotheses (Wiegand and Moloney, 2014). In the past, spatially explicit indices, such as the Clark-Evans index (Clark and Evans, 1954), were used (Szmyt, 2014). While many of these indices are straightforward in their application and interpretation (Illian et al., 2008), they aggregate the spatial characteristic of the whole pattern and thereby of many scales to a single number and hence lose important information (Dale et al., 2002; Szmyt, 2014). Today only the number or density of events per unit area, also called intensity $\lambda(x,y)$, is still commonly used (Velázquez et al., 2016). In contrast to indices, modern approaches use summary functions to describe the spatial characteristic of a pattern at several scales r (Fig. 1-1; Illian et al., 2008; Wiegand and Moloney, 2014). These second-order summary functions take all distances between pairs of events into account and are considered to be the most important tool of SPPA (Illian et al., 2008;

Velázquez et al., 2016). The pair-correlation function *g(r)* (equation 1-1; Stoyan and Stoyan, 1994) is assumed to be the most informative summary function by many authors (Illian et al., 2008; Wiegand et al., 2013; Wiegand and Moloney, 2014). It describes the event density at distance *r* from the typical event of the pattern (Velázquez et al., 2016). The pair-correlation function *g(r)* is defined as the derivate of Ripley's K-function *K(r)* (equation 1-2; Ripley, 1976) and has the advantage of describing the pattern at distance *r* and not cumulatively within distance *r* (as done in Ripley's K-function; Wiegand and Moloney, 2014). The pair-correlation function *g(r)* indicates complete spatial randomness (CSR) at distance *r* for a value of *g(r) = 1*, clustered patterns for a value of *g(r) > 1* and regular patterns for a value of *g(r) < 1* (Fig. 1-1).

$$g(r) = \frac{K'(r)}{2\pi r} \qquad (1\text{-}1)$$

$$K(r) = \int_{t=0}^{r} g(t)(2\pi t)dt \qquad (1\text{-}2)$$

Mark-correlation functions (equation 1-3; Stoyan and Stoyan, 1994) can be used to analyse quantitatively marked point patterns (Wälder and Wälder, 2008; Wiegand and Moloney, 2014). The mark-correlation function $k_{mm}(r)$ compares the means of two marks m_i and m_j separated by distance *r* to two randomly chosen marks (i.e. the overall mean). Hence, a positive correlation at distance *r* is present if the mean of events separated by distance *r* is larger than the overall mean. Correspondingly, a negative association is present if the mean of events separated by distance *r* is smaller than the overall mean (Wiegand and Moloney, 2014).

$$k_{mm}(r) = \frac{E_{ij}(m_i \times m_j)}{\bar{m}^2} \qquad (1\text{-}3)$$

In practice, the study area will always be restricted due to financial, temporal or logistical constraints. Therefore, events located close to the edge of the study area might be influenced by neighbouring events that were not sampled (Goreaud and Pélissier, 1999). This might happen for all distances *r* greater than the distance from an event *i* to the study area edge (Haase, 1995). To account for this, several edge correction methods exist, including buffer zone correction, toroidal edge correction or weighting edge

correction (Haase, 1995). Thereby, using the distance from event i to the edge as a weighting factor is the most practical approach for most situations (Haase, 1995; Yamada and Rogerson, 2003).

Point process models and null models are stochastic mechanisms that generate point patterns (Diggle, 2014). These models can be used to investigate if the data contains spatial structure, describe certain aspects of the spatial structure or test hypotheses of assumed generating processes (Law et al., 2009; Velázquez et al., 2016; Wiegand and Moloney, 2014). The selection of an appropriate null model is one of the most important steps of SPPA and can be challenging (Goreaud and Pélissier, 1999; Law et al., 2009; Wiegand and Moloney, 2004). Because it results in CSR, the homogenous Poisson process is the simplest null model and often used to determine whether the point pattern contains spatial characterises distinguishable from pure randomness (Wiegand and Moloney, 2014). This null model has two characteristic properties, namely a constant intensity λ throughout the study area and no interaction between events (Illian et al., 2008; Wiegand and Moloney, 2004). Of course, also more sophisticated null models exist, such as cluster processes (Thomas, 1949), inhibition processes (Matérn, 1986), independence and random labelling (Goreaud and Pellissier, 2003) or antecedent conditions (Wiegand and Moloney, 2004).

Because for many null models an analytical solution is not possible (Perry et al., 2006), Monte Carlo simulations are used to simulate random realisations of the null model and construct simulation envelopes (Fig. 1-1). For each random realisation, the same summary function as for the observed data is calculated and e.g. for an approximated significance of $\alpha \approx 0.05$ the 2.5th and 97.5th lowest and highest values of $n = 199$ simulations at each scale r (simulation envelope) compared to the summary function of the observed data. Scales r at which the observed value is not within the simulation envelope values suggest a deviation from the null model (Baddeley et al., 2014). However, as pointed out by Loosmore and Ford (2006) this approach has the problem of a Type I error inflation because it does not test only one particular scale r but all scales simultaneously (Loosmore and Ford, 2006). However, because hypothesis testing is not the major concern, for exploratory analysis simulation envelopes are still a powerful tool (Wiegand and Moloney, 2014). If hypothesis testing is required, Goodness-of-Fit tests

can be used to deal with the Type I error inflation (Baddeley et al., 2014; Loosmore and Ford, 2006; Wiegand and Moloney, 2014).
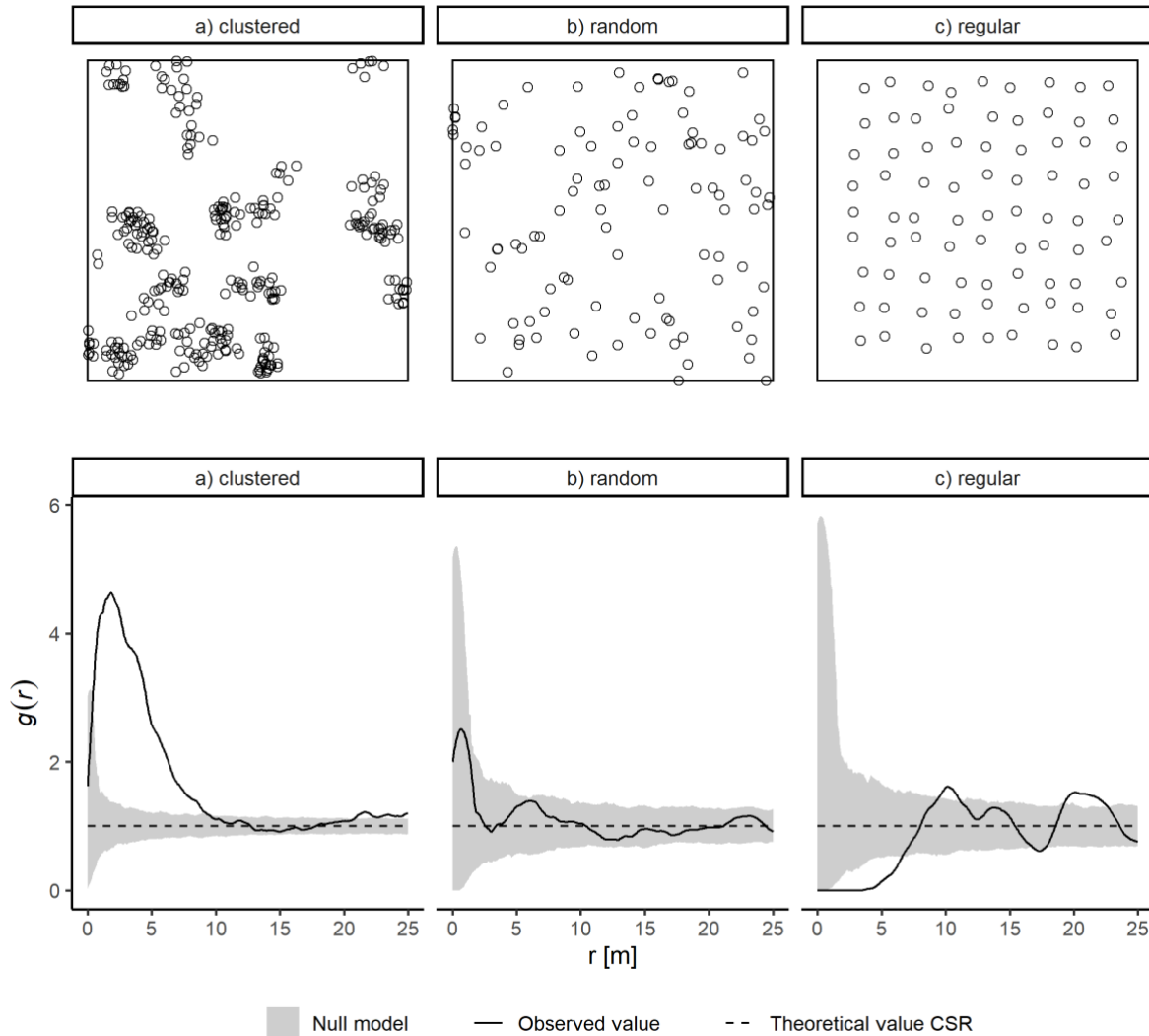
Figure 1-1: *Example representation of three types of spatial point patterns with a) clustered, b) random and c) regular spatial characteristics. The corresponding pair-correlation functions g(r) and simulation envelopes based on 1999 simulations of the null model of complete spatial randomness (CSR) are shown.*

Individual-based simulation models

Individual-based simulation models (IBMs) are a bottom-up approach, in which not the whole population, but discrete individuals are simulated (DeAngelis and Grimm, 2014; Pommerening and Grabarnik, 2019). Because the emerging characteristics of the whole population result from the characteristics and behaviours of the individuals, the modelling approach is bottom-up (Grimm and

Railsback, 2005). Uchmanski and Grimm (1996) suggested four main criteria to classify a simulation model as individual-based. Firstly, IBMs must consider different size, age or life cycle stages of individuals and a development of individuals (e.g. growth). Secondly, individuals need to explicitly use resources depending on their own state. Thirdly, because individuals are discretely represented, the overall population size must be quantified by an integer value. Fourthly, there needs to be variability between individuals of the same size, age or life cycle stage (Grimm and Railsback, 2005; Uchmanski and Grimm, 1996). Another feature of IBMs are local interactions between individuals in contrast to often global interactions between all individuals of e.g. mathematical models (Grimm, 2008). This feature is of great importance especially in plant populations, because interactions between immobile plant individuals are local (Berger et al., 2008). Lastly, because of their individual-based characteristics, explicitly considering space is often natural in IBMs (An et al., 2009; Wallentin, 2017). Even though sometimes criticised of being too complex or not contributing to the understanding of the study system (O'Sullivan et al., 2016, 2012), IBMs can be a powerful tool to study populations and carry out "virtual" experiments. Consequently, IBMs can be helpful especially for study systems that are too complex or with spatial and temporal scales too large to study experimentally (Grimm, 2008; Grimm and Railsback, 2012; Stillman et al., 2015). Additionally, IBMs are a suitable tool for research questions that include variability between individuals, local interactions among individuals or individual adaptive behaviour (DeAngelis and Grimm, 2014).

Even the simplest IBMs include at least two entities, namely the individuals and their environment. Individuals can all belong to the same type or different types can be considered (e.g. different species). Likewise, the environment can be homogeneous or heterogeneous (Grimm, 2008). Individuals are described by so-called state variables, such as the location or size. These variables describe the individuals at the lowest level of the model and cannot be aggregated from other variables (Grimm et al., 2006). When aggregating the state variables, information about higher levels and finally about the whole population can be gained, for example the overall population size. This is also referred to as emergent behaviour (An et al., 2009). Of course, the selection of appropriate entities and state variables depends on the specific research question (Grimm and Railsback, 2005).

Once all entities and state variables are defined, the included processes described by submodels modify them (Fig. 1-2; Grimm, 2008). Common examples include growth, dispersal or mortality of individuals. Submodels normally describe ecological processes using mathematical functions and rules based on the current state variables (Grimm, 2008; Grimm et al., 2006). Thereby, it is important to consider the scheduling, i.e. how and in which ordering submodels are executed in the IBM because it can heavily affect the model outcome (Grimm and Railsback, 2005). As an example, in a mortality submodel in which the mortality probability depends on the resource acquisition of each time step, naturally, the mortality probability will differ depending on if it is calculated before or after the resource acquisition. Related to this, also the spatial and temporal extent and grain are important characteristics of an IBM. While the extent refers to the total area of the environment and to the total time period, the grain refers to the resolution of the environmental data and to the length of the time steps (Grimm, 2008). Of course, appropriate choices highly depend on the research question (Grimm, 2008).
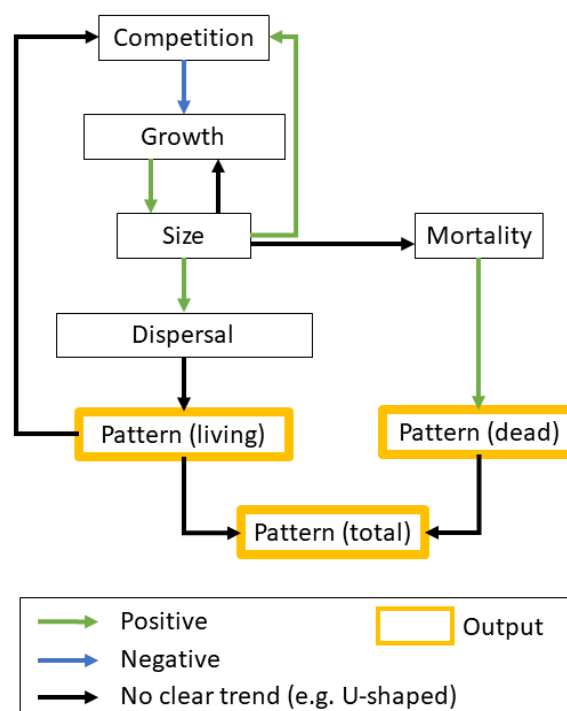
Figure 1-2: Exemplary model concept of an individual-based simulation model including several ecological processes (competition, growth, dispersal, mortality). The relationship between processes is indicated by the colour of the arrow. As example, competition slows the growth, while growth increases the size. Because mortality is described by a U-shaped probability depending on the size, there is a relationship between the two, but no "clear" trend.

9

Pattern-oriented modelling (POM; Grimm et al., 1996) is a strategy to make use of patterns in the data to construct, optimise and parameterise IBMs as well as to contrast hypotheses (Grimm et al., 2005; Wiegand et al., 2003). As mentioned in the section on point pattern analysis, patterns indicate underlying processes that generated them (Janssen et al., 2009; Wiegand et al., 2003). The essence of POM is an iterative processes of constantly comparing patterns of the IBM output and the field data during model development, parameterisation and analysis (Wiegand et al., 2003). Because it might be relatively simple to reproduce only one pattern at a time, it is recommend to use several patterns simultaneously and to use patterns on individual- and population-level (Grimm et al., 2005; Janssen et al., 2009; Wiegand et al., 2003). Using several patterns also allows to exclude unrealistic processes and parameterisations of the model (Wiegand et al., 2003). While this strategy is not a new concept but rather one of the main concepts of ecology and sciences in general (Grimm et al., 2005; Levin, 1992), internalising POM during the modelling progress can improve the IBM and thus increase possible insights into the research question (Grimm and Railsback, 2005).

Landscape metrics

Linking patterns of environmental heterogeneity to ecological processes is one of the central goals of landscape ecology (Kupfer, 2012; Turner, 2005, 1989). There are several definitions of the term landscape, but generally a landscape is defined as a spatially heterogeneous area (Turner, 1989). In order to link spatial heterogeneity to ecological processes, one of the main challenges is how to describe and quantify the heterogeneity (With, 2019). Thus, different approaches and methods were developed in the past and new ideas are still being put forward (Frazier and Kedron, 2017; Gustafson, 2019; Lausch et al., 2015; Nowosad and Stepinski, 2019).

One of the most used approaches describes landscapes as patches of discrete land-cover classes in a raster context (Fig. 1-3; Forman, 1995; Forman and Godron, 1986; Wiens, 1995). Landscape metrics are commonly used to quantify the composition (number and abundance) and configuration (spatial arrangement) of the land-cover classes (Frazier and Kedron, 2017; Kupfer, 2012). Traditionally, landscape metrics describe landscapes on patch level, class level and landscape level. A patch is defined

as neighbouring cells belonging to the same land-cover class. Class level metrics describe all patches belonging to the same class and lastly, landscape level metrics describe the whole landscape composed of all patches (McGarigal, 2015). Regardless of the level, landscape metrics can be classified additionally depending on the characteristic of the landscape they describe, such as area and edge metrics, shape metrics, core area metrics, aggregation metrics or diversity metrics (McGarigal, 2015; Šímová and Gdulová, 2012). However, since landscape metrics do not have an informative value on their own, results must be connected to ecological information and processes (e.g. biodiversity data).
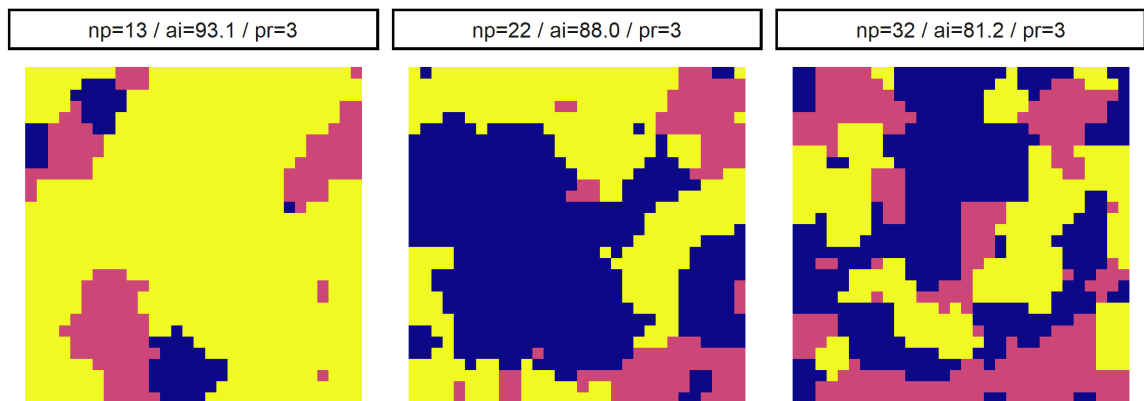
Figure 1-3: *Different landscapes represented by discrete patches of land-cover classes indicated by colours. The landscapes are described by three exemplary landscape metrics (np = number of patches; ai = aggregation index; pr = patch richness). All landscapes have the same diversity (pr), however, a different composition (np) and configuration (ai).*

While often criticised for being too simplifying, landscape metrics also have the advantage of straightforward application, interpretation and communication (Lausch et al., 2015) and are still widely used (Kupfer, 2012; Uuemaa et al., 2013, 2009; With, 2019). Recent examples of studies using landscape metrics include biodiversity studies in agricultural landscapes (Decaëns et al., 2018), studies of bird biodiversity (Herrera et al., 2018) or natural disturbance studies in temperate forests (Senf and Seidl, 2018).

Study area

For the first two chapters of this thesis, field data from the Hainich National Park (Thuringia, Germany) was used. The national park (51°06′ N, 10°31′ E) is located in the Hainich-Dün region which

is close to the cities of Eisenach in the south-west, Bad Langensalza in the east and Mühlhausen in the north east (Fig. 1-4). The region is characterised by two low mountain ranges with similar climate and growing conditions (the Hainich and the Dün) separated by the Unstrut valley (Mund, 2004) and is hosting one of the largest continuous broadleaved forests in Germany (Butler-Manning, 2007; Holzwarth et al., 2013).

The climate is suboceanic to subcontinental and long-term mean annual temperature and precipitation are 7.5 - 8.0 °C and 750 - 800 mm, respectively (Holzwarth et al., 2013; Knohl et al., 2003; van Waveren, 2016). The predominant parent material is limestone and soil conditions can be mainly classified as brown soils or Cambisols to Luvisols covered by a loess layer (Holzwarth et al., 2013; Mund, 2004). Elevation varied between 430 - 460 m a.s.l. with a gentle slope (Huss and Butler-Manning, 2006; van Waveren, 2016).

Figure 1-4: *Location of the Hainich National Park (Modified after: © User:Lencer / Wikimedia Commons / CC-BY-SA-3.0).*

The 28.5 ha forest dynamics plot is located in the former district "Weberstedter Holz" in the core zone I of the Hainich National Park, which was founded in 1997 (Mund, 2004; van Waveren, 2016). In the core zone I, no silviculture or other human management is realised (Butler-Manning, 2007). When establishing the forest dynamics plot, awareness was raised to select a forest with an already high

similarity to natural forest structures and dynamics (Huss and Butler-Manning, 2006). This was possible because already previous to the founding of the national park, the area was used as a military training ground by the national army of the former German Democratic Republic since 1965 (Butler-Manning, 2007). The forest mainly served as a buffer between the shooting ranges and the surrounding villages and hence human access and management was restricted (van Waveren, 2016). Before that, the forest was most likely managed as coppice-with-standards and was subsequently developed into a selection forest during the 18th and 19th centuries (Huss and Butler-Manning, 2006; van Waveren, 2016). Because the forest has not been managed for several decades now (Butler-Manning, 2007), it already developed towards an old-growth uneven-aged forest representative for the region (Huss and Butler-Manning, 2006).

The forest association is *Hordelymo-Fagetum* and the forest is dominated by *Fagus sylvatica L.* (European beech) making up to about 90% of all tree individuals (Butler-Manning, 2007; Huss and Butler-Manning, 2006). This is not surprising since *F. sylvatica* is the most dominant tree species in central Europe (Leuschner and Ellenberg, 2017). Other present tree species include *Fraxinus excelsior L.* (European ash), *Carpinus betulus L.* (hornbeam) and *Acer pseudoplatanus L.* (sycamore) as well as some less abundant species (Butler-Manning, 2007). The relatively high proportion of admixed species, especially of the rather light demanding species such as *F. excelsior* and *A. pseudoplatanus*, is most likely still a remnant of former management (Butler-Manning, 2007). Nevertheless, the forest can be classified as an old-growth forest with largely natural characteristics (Butler-Manning, 2007; Huss and Butler-Manning, 2006).

The coordinates of all individual trees with a diameter at breast height (dbh) larger than 1 cm were mapped in 1999. All trees were tagged with an aluminium tag that allowed to re-measure all trees in 2007 (Holzwarth et al., 2013) and 2013. Additionally to the coordinates, also the species of each tree, the dbh and the social class were recorded (Butler-Manning, 2007). The resulting point pattern data set allowed to study the spatial patterning of individuals (van Waveren, 2016), tree productivity (Ratcliffe

et al., 2015) or tree mortality (Holzwarth et al., 2013). In this thesis, the point pattern data set will be used to study the importance and interactions of biotic and abiotic processes for the tree population.

Outlook of this thesis

The aim of this thesis was to demonstrate how patterns can be used to infer underlying ecological processes. To this end, different methods that focus especially on spatial patterns were used. Advantages of this focus on spatial patterns and the usage of various methods were demonstrated by analysing the importance and interactions of biotic and abiotic processes on the spatial pattern of forest trees, which is an ongoing discussion (e.g. Getzin et al., 2008; Jara-Guerrero et al., 2015; Lin et al., 2017; Shibata et al., 2010; Yang et al., 2016). Many former similar studies were located in tropical forest and only few studies exist for temperate forests (but see e.g. Gilbert and Lechowicz, 2004; van Waveren, 2016; Wang et al., 2010a). Additionally, to the bias towards tropical forests, most former studies are based on only one descriptive or inferential approach, not always allowing to fully conclude underlying processes. This might be one reason why even for the same forest type, the assumed underlying processes and their importance and interactions differ (e.g. Harms et al., 2001; Lan et al., 2012; Plotkin et al., 2000; Yamada et al., 2006). Thus, in this thesis the importance and interactions of biotic and abiotic processes were analysed using different, but related approaches to reveal a pattern-process link.

In chapter 2, point pattern analysis was used to study species-habitat associations in a temperate old-growth forest dominated by *F. sylvatica*. This was motivated by the idea that species-habitat associations identifiable in the spatial pattern of individuals are strong evidence for the importance of abiotic processes.

In chapter 3, an individual-based simulation model was developed with two model versions, one including only biotic processes, one combining both biotic and abiotic processes. The model was used to further explore acting processes in a temperate old-growth forest using not only rather descriptive and inferential point pattern analysis, but a dynamic simulation model that allowed to model the link between patterns and processes in more detail.

Lastly, in chapter 4, an open-source software tool was introduced to quantify environmental heterogeneity on landscape level using landscape metrics. The software was designed to overcome constraints and shortcomings of existing software tools and hopefully improves the integration of heterogeneity measures into ecological research.

Chapter 2 - Species-habitat associations of forest trees: A virtual ecologist approach comparing common methods and application in a temperate old-growth beech forest

This chapter is a manuscript to be submitted as a research article: Hesselbarth, M.H.K., Wiegand, K. In prep. Species-habitat associations of forest trees: A virtual ecologist approach comparing common methods and application in a temperate, old-growth beech forest.

Abstract

1. Species-specific habitat associations are one process leading to a clustered spatial pattern of trees, a trend observable in tropical and temperate forests. Two contrasting methods are commonly used to analyse species-habitat associations, namely the *gamma*-test and the torus-translation test. However, the strengths and weaknesses of both methods were never analysed in detail. Additionally, regardless of the method, there is little knowledge on species-habitat associations in temperate forests, albeit environmental heterogeneity was shown to play an important role in these forests.

2. We conducted a simulation study to analyse the strengths and weaknesses of four methods that seem suitable to study species-habitat associations: the *gamma*-test, the torus-translation test, the randomised-habitats procedure and pattern reconstruction. The simulation study included the simulation of neutral landscapes representing habitat patches and point patterns with known positive and negative habitat associations with increasing association strength. In addition, we applied all methods to a real-world data set of a temperate old-growth forest dominated by *Fagus sylvatica*. Applying multivariate regression trees to soil variables, we identified discrete habitat patches and analysed species-habitat associations of living and dead trees as well as of different life-history stages.

3. Overall, all methods were able to detect species-habitat associations similarly well. Only pattern reconstruction slightly outperformed all other methods. However, pattern reconstruction was also related to the highest computational demands. The soil variables of the real-world data were classified to four discrete habitats. Two out of five species showed species-habitat associations to at least one habitat, whereby, *Fraxinus excelsior* showed contrasting species-habitat associations to *Fagus sylvatica*.

16

There was no clear trend for different size classes and dead trees did not show contrasting species-habitat associations to living trees.

4. Although computationally intensive, pattern reconstruction has many advantages over all other methods, such as the applicability to non-quadratic study plots and complex point patterns. The presence of species-habitat associations in a temperate old-growth forest showed the importance of abiotic processes shaping the spatial pattern.

1. Introduction

Worldwide, tree populations show a trend towards spatial clustering (Condit et al., 2000; Getzin et al., 2006; Jia et al., 2016). This can be caused by either biotic or abiotic processes or a combination of both acting simultaneously on the population (Cottenie, 2005; Legendre et al., 2009). An example for biotic processes leading to clustered patterns of trees is spatially limited seed dispersal (Condit et al., 2000). Contrastingly, also species-habitat associations, as an example of abiotic processes, can lead to clustered patterns of trees (Shen et al., 2013). Species-habitat associations reflect the idea that species are specialised to certain environmental conditions (Tilman and Pacala, 1993) and are clustered at suitable habitats (Comita et al., 2007; Harms et al., 2001). Thus, studying small-scale species-habitat associations can give insights into the importance of environmental heterogeneity for shaping the spatial pattern of a tree population (Garzon-Lopez et al., 2014).

Analyses of species-habitat associations can be found mainly in tropical forests (Chuyong et al., 2011; Comita et al., 2007; Gunatilleke et al., 2006), but also in sub-tropical forests (Lai et al., 2009; Wang et al., 2009). In temperate forests, similar studies are rather rare (but see Furniss et al., 2017; Ye et al., 2011). However, environmental heterogeneity was shown to be an important driver of the spatial pattern of trees in temperate forests (Gilbert and Lechowicz, 2004; van Waveren, 2016; Zhang et al., 2014). Thus, we analysed species-habitat associations in a temperate old-growth forest to investigate possible influences of environmental heterogeneity on the spatial plant pattern (Garzon-Lopez et al., 2014).

Most studies analysing small-scale species-habitat associations use one of two contrasting methods, either the *gamma*-test (Plotkin et al., 2000) or the torus-translation test (Harms et al., 2001). Both methods have in common that they require data on the location of all individuals in the study area (a point pattern, whereby individual points are referred to as events) and on small-scale environmental conditions, such as topography or soil conditions, classified into discrete habitat patches (Fig. 2-1). To test the null hypothesis that the point pattern is independent of the distribution of the habitat patches, possible spatial dependencies between the two must be broken and this is how the two methods differ. Whereas the *gamma*-test randomises the point pattern, the torus-translation test randomises the habitat patches.

While the torus-translation test (e.g. Du et al., 2017; Furniss et al., 2017; Guo et al., 2016) is more commonly used than the *gamma*-test (e.g. Garzon-Lopez et al., 2014; John et al., 2007; Yang et al., 2016), this preference is not based on published knowledge on the strengths and weaknesses of the methods. We found just a single study analysing the power of one method (Comita et al., 2007) and only very few studies comparing several methods to each other (Furniss et al., 2017; Harms et al., 2001). Comita et al. (2007) calculated expected false positive detections for the torus-translation test only to determine an appropriate significance level. Furniss et al. (2017) and Harms et al. (2001) did not discuss differences in detail, but only compared which method is more conservative (Harms et al., 2001), or used more than one method to ensure that results are not sensitive to the used method (Furniss et al., 2017). Following, a simulation study analysing the power of the methods is missing to this day. Besides species characteristics and local environmental conditions, differences in the used methods may be another reason why results differ between studies for similar forest types. For tropical forest, the percentage of species with habitat associations varies strongly, e.g. 29.5% (Plotkin et al., 2000), 64% (Harms et al., 2001), 70% (Lan et al., 2012) to 80% (Yamada et al., 2006). Adapting the virtual ecologist approach (Zurell et al., 2010), we compared the ability of both the *gamma*-test and the torus-translation test to detect species-habitat associations. Also, we propose to use pattern reconstruction (Tscheschel

and Stoyan, 2006; Wiegand and Moloney, 2014) as a modification of the *gamma*-test (Plotkin et al., 2000) for tree populations with complex spatial patterns.

To demonstrate the compared methods using field data, we analysed point pattern data from the Hainich National Park (Thuringia, Germany). With the help of spatial point process models, van Waveren (2016) showed that environmental heterogeneity is important for the spatial pattern of trees in a 28.5 ha forest dynamics plot. To study the role of abiotic processes in this system further, we analysed species-habitat associations of the most common tree species in the forest dynamics plot based on four hypotheses. Because *Fagus sylvatica L.* (European beech) is the most dominant and competitive vigorous species in the forest dynamics plot (Bolte et al., 2007; Butler-Manning, 2007; Huss and Butler-Manning, 2006; Leuschner et al., 2006; Leuschner and Ellenberg, 2017), we hypothesise that *(H1)* abiotic processes are the least important for *F. sylvatica* and the species shows less species-habitat associations than all other species. Contrastingly, to avoid competition, *(H2)* all other species show species-habitat associations opposite to *F. sylvatica* (Dobrowolska et al., 2011). Species-habitat associations (Comita et al., 2007; Kanagaraj et al., 2011; Lai et al., 2009) and environmental measures explaining the spatial pattern of trees differ for different life-history stages (van Waveren, 2016). Therefore, we hypothesise that because seedlings and saplings in unsuitable habitats have a higher mortality probability, *(H3)* species-habitat associations will become more prominent for later life-history stages. This should be supported by *(H4)* contrasting species-habitat associations between living and dead trees.

2. Methods

The two dominant methods to analyse species-habitat associations in the literature, namely the *gamma*-test (Plotkin et al., 2000) and the torus-translation test (Harms et al., 2001) break possible dependencies between the point pattern and the discrete habitat patches by randomising the data (Fig. 2-1). However, because independence between events or between habitat patches is most likely not fulfilled, the spatial structures of the point pattern and the habitat patches must be preserved (Plotkin et al., 2000; Wiegand and Moloney, 2014). Dependence between events can be caused by e.g. limited seed

dispersal and following spatial clustering of tree populations (Lutz et al., 2014; Nguyen et al., 2016) or competition between trees resulting in regular spatial patterns (Kenkel, 1988; Pielou, 1962). Similarly, according to Tobler's fist law of geography (Tobler, 1970), spatial autocorrelation between the habitat patches will most likely be present that leads to neighbouring patches being more similar than distant ones.
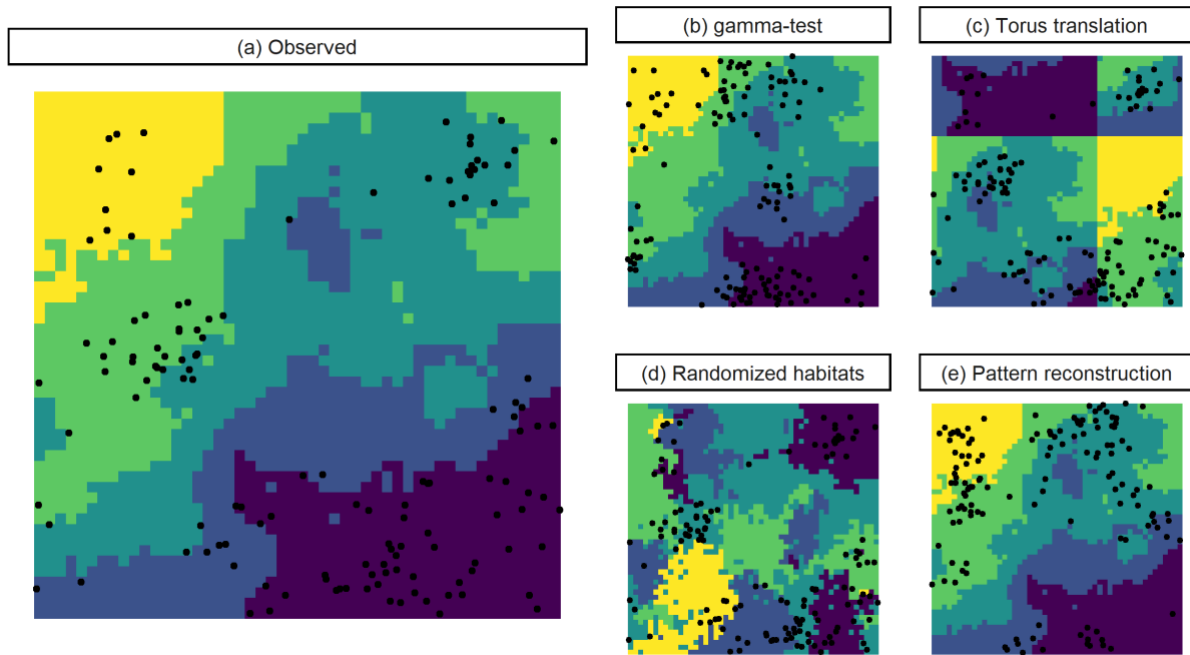
Figure 2-1: Illustration of methods to analyse species-habitat associations. While the (b) gamma test and (e) pattern reconstruction randomise the point pattern, (c) torus translation and (d) randomised-habitats procedures randomise the habitat patches. Common to all methods is that either the point pattern (black points) or habitat patches (coloured raster cells) of the (a) observed data is kept identical.

Species-habitat associations can be tested for by comparing, within each habitat type, the stem density of the observed data with the stem density of randomised null model data (Harms et al., 2001; Plotkin et al., 2000). Species-habitat associations are supported with an approximated significance of $\rho \approx 0.05$ for a two-tailed test if the observed stem density is above the 97.5th percentile or below the 2.5th percentile of n times simulated null model data for positive or negative associations, respectively (Harms et al., 2001).

2.1 The *gamma*-test

The *gamma*-test (Plotkin et al., 2000) randomises the point pattern. Firstly, a suitable point process model is fitted to the observed data (Fig. 2-2). Secondly, point patterns are simulated using the fitted point process model. Lastly, the simulated point patterns are superimposed on the observed habitat patches and the stem density within each habitat type compared between the observed data and the null model data (Fig. 2-1b; Plotkin et al., 2000). The *gamma*-test, however, should only be applied if the observed point pattern can be described by a suitable point process model (Wiegand et al., 2009, 2007).

2.2 Torus-translation test

The torus-translation test (Harms et al., 2001) randomises the habitat patches. This is done by shifting the patches about a 2D-torus in all four cardinal directions. Whenever patches reach the border of the study plot, they are replaced to the opposite side of the plot. Additionally, also rotating and mirroring the shifted habitat patches is possible to simulate further null model data. Finally, the observed point pattern is superimposed on the simulated habitat patches and the stem densities for each habitat type compared between the observed data and the null model data (Fig. 2-1c; Harms et al., 2001). However, this test is only possible for rectangular study plots (Harms et al., 2001) and if no strong gradients are present in the environmental data.

2.3 Randomised-habitats procedure

Harms et al. (2001) also proposed a "randomised-habitats procedure" that randomises the habitat patches and works for irregular study plots. At the beginning, all cells of the null model data are "empty" and a random cell is assigned to the rarest habitat type. Random, but neighbouring cells are subsequently assigned to the same habitat. This is repeated until the same number of cells as in the observed data are assigned to the habitat. Afterwards, the assignment is redone with the second rarest habitat. To prevent too large patches of cells for one habitat, we modified the procedure slightly: if $\frac{\sum Cells_{patch}}{\sum Cells_{plot}} < r; 0 < r \leq 1$ the procedure jumps to a random, non-neighbouring starting cell. The procedure stops when all cells are assigned to a habitat. Lastly, the observed point pattern is superimposed on the simulated habitat

patches and for each habitat the stem densities between the observed data and the null model data are compared (Fig. 2-1d; Harms et al., 2001).

2.4 Pattern reconstruction

Pattern reconstruction (Tscheschel and Stoyan, 2006) randomises the point pattern using an optimisation algorithm comparable to simulated annealing (Kirkpatrick et al., 1983). The method does not depend on specific point process models (Fig. 2-2). Firstly, a random pattern ψ is created with the same number of events as the observed pattern φ. Secondly, both the reconstructed pattern ψ and the observed pattern φ are described by summary functions $f_i(r, \psi)$ and $f_i(r, \varphi)$, respectively, to describe the spatial characteristics of the point patterns at several scales r (Velázquez et al., 2016). The spatial characteristics of the point patterns can be described best if several summary functions are used (Wiegand et al., 2013). However, since pattern reconstruction is computational demanding (Tscheschel and Stoyan, 2006), we recommend using the most powerful combination of two summary functions (Wiegand et al., 2013), namely the pair-correlation function $g(r)$ (Stoyan and Stoyan, 1994) and the nearest-neighbour-distribution function $G(r)$ (Diggle, 2014; Illian et al., 2008). While the pair-correlation function estimates the number of events at distance r for an arbitrary event of the pattern, the nearest-neighbour-distribution function estimates the cumulative probability of finding the nearest neighbour within a certain distance r for an arbitrate event of the pattern (Wiegand and Moloney, 2014). Thirdly, the difference between the patterns is described by the energy $E^{\varphi}_{total}(\psi_t) = \frac{1}{n_i}\sqrt{\sum_{r=1}^{n_i}\left[f_i^{\varphi}(r) - f_i^{\psi_t}(r)\right]^2}$. Fourthly, an event of the reconstructed pattern ψ is relocated to a new location and it is kept only if $E_{\varphi total}(\psi_t)$ decreases. If the energy does not decrease, the event is moved back to its original location. To avoid optimising towards a local minimum, with a small probability the new locations is kept even if $E_{\varphi total}(\psi_t)$ increases. The procedure is reiterated until the stopping criterion is met, i.e. a pre-set threshold of $E_{\varphi total}(\psi_t)$ or a maximum number of iterations (Tscheschel and Stoyan, 2006). Lastly, the simulated point pattern is superimposed on the observed habitat patches and for each habitat the stem densities are compared between the observed data and the null model data (Fig. 2-1e).
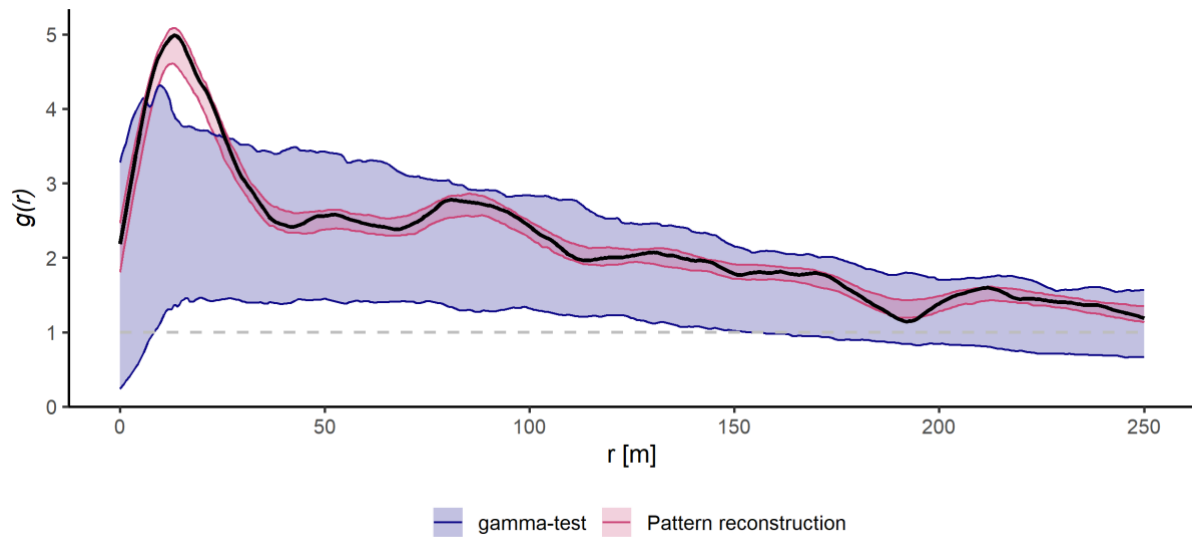
Figure 2-2: *Comparison between the randomised null model data using the gamma-test and pattern reconstruction for an exemplary species of the simulation study. The pair correlation function g(r) of the observed pattern (solid black line) is better described by the 2.5% and 97.5% quantiles of 199 simulated patterns using and pattern reconstruction (red envelop) than point process fitting (gamma-test; blue envelope). For a complete spatial random pattern (CSR), the pair correlation function would equal g(r) = 1 (dashed gray line).*

2.5 Simulation study

In order to analyse all methods described, we conducted a simulation study inspired by the virtual ecologist approach (Zurell et al., 2010). The virtual ecologist includes four major steps: *i)* using a virtual ecological model to simulate data, *ii)* an virtual observation process (e.g. sampling), *iii)* drawing inferences from the data and *iv)* evaluation against the simulated data (Zurell et al., 2010).

Firstly, we created landscapes using the two-dimensional fractional Brownian motion neutral landscape model of the *NLMR* R package (Sciaini et al., 2018). The landscapes had an extent of 50×50 cells and a resolution of 20 m. The continuous values between 0 - 1 were classified into five discrete habitats using natural breaks (Fisher, 1958; Jenks and Caspall, 1971). Secondly, we created point patterns with known habitat associations (Table 2-1) and increasing association strength α. We increased the association strength from $0.05 \leq \alpha \leq 1$ by 0.05 increment steps. The habitats to which the patterns showed a positive or negative association were chosen randomly. To simulate the starting patterns, we used a Poisson process (complete spatial randomness; CSR) and a Thomas (cluster) process (Thomas, 1949) with 100 events for each pattern. In case of positive associations, we subsequently

added additional events $events_{add} = events_{pattern} * \alpha$ to the habitat. In case of negative associations, we subsequently thinned events from the habitat with a probability of $\rho_{thin} = 1 - \alpha$ for each event to remain. Accordingly, this resulted in a higher number of events for positive associations and in a lower number of events for negative associations.

Table 2-1: Characteristics of simulated patterns including type of association and point process.

Patterns	Association	Point process
Pattern 1	Positive association	Poisson process (CSR)
Pattern 2	Positive association	Thomas (cluster) process
Pattern 3	Negative association	Poisson process (CSR)
Pattern 4	Negative associations	Thomas (cluster) process

For all methods, with exception of the torus translation test, we simulated 199 null model data sets. The number of null model data sets for the torus translation test is determined automatically by the grain and the extent of the study plot resulting in 2597 translated raster. The detection of the correct habitat association (positive or negative) to the respective habitat was considered as the "correct" result. Since a positive association to a habitat can lead to a negative association to another habitat (and vice versa; Yamada et al., 2006), we defined a "false" detection as *i)* whenever the opposite associations was detected for the habitat, *ii)* whenever no significance association was detected for the habitat, *iii)* whenever the "correct" association was detected for a wrong habitat. All simulations were repeated 50 times for each association strength α using the same observed data, but new simulated null mode data each time. However, with a probability of $\rho = 25\%$ each repetition, also the observed data was simulated again. All results present the mean of correct and false detections for all repetitions (i.e. the rate of correct and false detections).

2.6 Real-word data set

We analysed a real-word data set from the Hainich National Park (Thuringia, Germany). The national park is located in the Hainich-Dün region, in which one of the largest continuous beech forests in

Germany can be found (Butler-Manning, 2007; Huss and Butler-Manning, 2006). A 28.5 ha forest dynamics plot (Lat: 51°4'44" Long: 10°26'31") was located within an old-growth *F. sylvatica* forest at an altitude of 425 - 455 m. The area was used as buffer zone for a military training area since 1965 and no major silviculture activities were carried out since then. In 1997, the study plot became part of the national park (Butler-Manning, 2007; Mund, 2004). Therefore, the forest partly reached, and is further developing, a natural old-growth character (Butler-Manning, 2007; Huss and Butler-Manning, 2006). The mean annual temperature was 6.5 °C and the mean annual precipitation 720 mm (Butler-Manning, 2007). The soils were mainly calcareous rendzina or brown rendzina covered by a loess layer on shell limestone (Mund, 2004; van Waveren, 2016). The point pattern of all trees (diameter at breast height dbh > 1 cm) was mapped and identified to species level. For a detailed description of the plot and the stand mapping see Butler-Manning (2007). The most common species was *F. sylvatica* with a relative abundance of 90.0% (Appendix Fig. A2-1). Other occurring species included *Fraxinus excelsior L.* (European ash; relative abundance 3.9%), *Carpinus betulus L.* (hornbeam, relative abundance 2.6%) and *Acer pseudoplatanus L.* (sycamore; relative abundance 2.6%). All other species were summarised as "others" (relative abundance 0.9%). Additionally to the point pattern, van Waveren (2016) sampled environmental data using soil samples and vegetation relevés for Ellenberg's indicator values (Ellenberg and Leuschner, 2010). The measurements were interpolated to the whole study plot using generalised additive models (Saefken et al., 2014; van Waveren, 2016). For a detailed description of the environmental data sampling and interpolation see van Waveren (2016).

To classify the cells into discrete habitat patches, we divided the plot into 846 20×20 m cells and used multivariate regression trees (MRT; De'ath, 2002). MRT classifies cells into similar clusters using the species assemblages as response variable and the environmental data as explanatory variables (De'ath, 2002). We used the importance value (*IV*) defined as $IV = abundance_{relative} + basal\ area_{relative}$ as response variable. As explanatory variables, we used seven environmental measures (Table 2-2) that were identified as being important for the spatial pattern of the occurring tree species (van Waveren, 2016). At the edges of the study plot, we added one row and column, respectively, with the value that

was the most common in all neighbouring cells. This was done to ensure that every tree can be assigned to a habitat even though the study plot is not rectangular. The simulation study showed a similar performance of all methods (section 3.1). Therefore, to achieve the most robust results for possible species-habitat associations, we used all previously described methods, with exception of the torus translation test (because of the irregular plot shape, Fig. 2-4).

Table 2-2: Environmental measures used to classify habitat patches.

Environmental measures	
Soil water content (spring)	Soil water content (summer)
Ellenberg's indicator value soil acidity	Ellenber's indicator value soil nitrogen
Ellenberg's indicator value light	Plant available water
Soil depth	

For the *gamma*-test, we used a Thomas process to simulated 4999 null model patterns for each input pattern because all point patterns were clustered (Appendix Fig. A2-3). Also, for the randomised-habitats procedure, 4999 null model habitat raster were simulated. To decrease the computational demand for pattern reconstruction, we did not start with a completely random pattern, but firstly fitted a cluster process to the data. Therefore, our approach is closely related to Plotkin (2000), but by reconstructing the spatial structure a higher similarity between the null model and the observed data was achieved. Due to the high computational demand, we only reconstructed 199 patterns for each input pattern with a stopping criterion of either $E_{\varphi total}(\psi_t) \leq 0.01$ or $iterations_{max} = 20000$.

Additionally, for hypothesis 3 we used the dbh in cm as a proxy for the life-history stage and classified trees as "small" (dbh ≤ 2.5), "medium" (2.5 < dbh ≤ 10) and "large" (dbh > 10) and analysed species-habitat associations separately for life-history stages.

All analyses and simulations were performed using R v3.5 (R Core Team, 2019). All used methods are implemented in the open-source R package *shar* (Hesselbarth and Sciaini, 2019) and analysis scripts are available online at <https://zenodo.org/record/3541690>.

3. Results

3. 1 Simulation study

Positive associations generated with CSR starting patterns were detected the best by all methods. In case of 10% additional events within the habitat (i.e. $\alpha = 0.1$), all methods detected positive associations correctly in about 50% of all repetitions. Starting from 30% additional events within the habitat, all methods detected positive associations correctly in all repetitions (Fig. 2-3a). For starting patterns simulated using a cluster process and positive associations, the correct detections rate was slightly worse. A correct detection of positive associations in 50% of all repetitions was present starting from about 20 - 25% of additional events. Not until 50% of additional events, all methods detected positive associations correctly in all repetitions. Pattern reconstruction slightly outperformed all other methods, showing a higher correct detection rate, especially for lower positive association strengths α (Fig. 2-3b).

Compared to positive habitat associations, negative associations were detected less reliable. For starting patterns simulated with CSR, all methods detected negative association in about 50% of all repetitions only if 50% of events were removed from the habitat (i.e. $\alpha = 0.5$). Negative associations were not detected in all repetitions for any association strength α and only approximated if all event were removed from the habitat (i.e. $\alpha = 1$; Fig. 2-3c). Clustered starting patterns with negative associations were detected in 50% of all repetitions for a relatively high associations strength of approximated $0.75 < \alpha < 0.8$ (i.e. removing 75 - 80% of all events from the corresponding habitat). Even if no events were present in the corresponding habitat (i.e. $\alpha = 1$), the detection rate of negative associations did not reach 100% (Fig. 2-3d). Again, pattern reconstruction showed a slightly higher correct detection rate for almost all association strengths α compared to all other methods.

For false detections (i.e. opposite association, no significant association, or "correct" association to a wrong habitat) the overall trend was similar (Fig. 2-3). Firstly, starting patterns simulated using CSR had lower false detection rates than starting patterns simulated using a cluster process. Secondly, positive habitat associations had a lower false detection rate than negative associations. Following, the lowest false detection rates were present for positive associations and CSR starting patterns (Fig. 2-3a),

27

whereas the highest false detection rates were present for negative associations and clustered starting patterns (Fig. 2-3d). Generally, for negative habitat associations and lower associations strengths α, pattern reconstruction had lower false detection rates than all other methods (Fig. 2-3c,d). Contrastingly, for positive associations, the false detection rate was slightly higher for pattern reconstruction compared to all other methods (Fig. 2-3a,b).
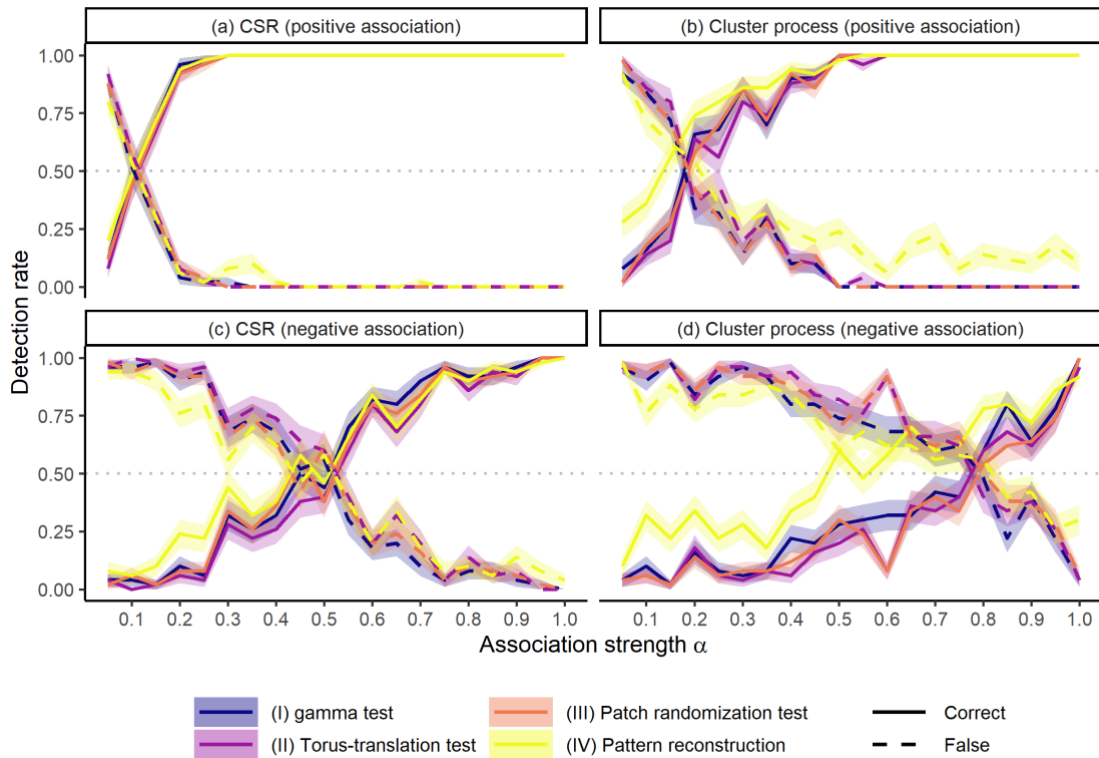
Figure 2-3: *Correct and false detections for all methods and point process models. The association strength α describes the fraction of events in relation to the overall number of events that were added or removed for positive and negative associations, respectively. Starting patterns were simulated using either complete spatial randomness (CSR) or a Thomas (cluster) process. The detection rate summarises 50 repetitions for each association strength α. The solid line represents the mean of correct and false detections, the ribbon the standard error of the mean.*

3.5 Real word data

The forest was mainly dominated by *F. sylvatica* (Appendix Fig. A2-1) and the dbh distribution approximated a reversed J-shaped form (Appendix Fig. A2-2). However, small diameters were underrepresented. The point pattern of all trees showed a clustered pattern up to a distance of approximated $r = 40$ m, but this was mainly dominated by *F. sylvatica* and all other species showed less

28

clustering (Appendix Fig. A2-3). The MRT resulted in four discrete habitat types (Fig. 2-4; Table 2-3) and only the soil water content (summer), the soil acidity and the soil depth had an influence on the habitat classification.
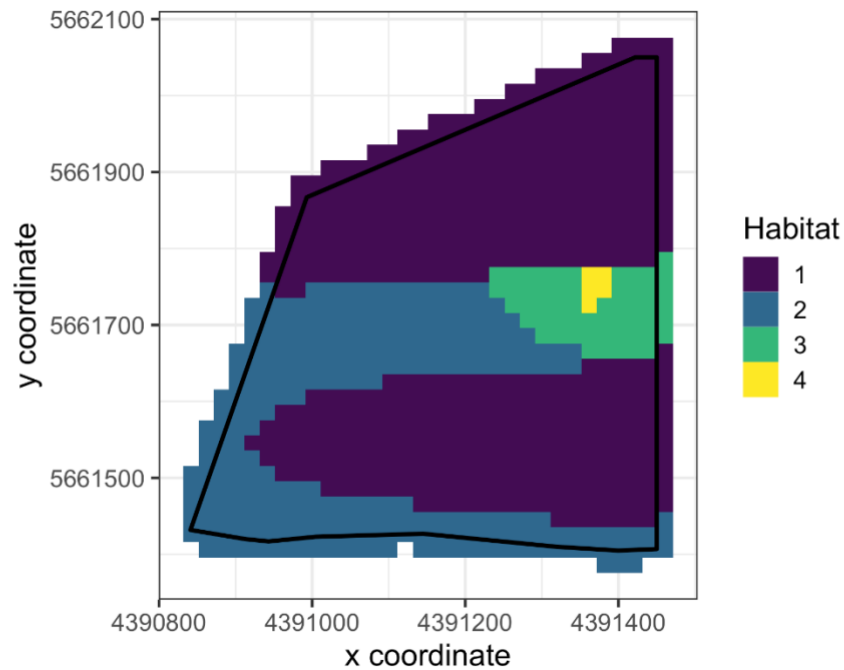
Figure 2-4: *The 28.5 ha forest dynamics plot classified to 846 20×20 m habitat patches. At the edges of the study plot one row and column was added, respectively.*

Table 2-3: *Characteristics of the four classified habitats. The total area is slightly larger than the study plot because of the added rows and columns to ensure each tree can be assigned to a habitat regardless of the non-quadratic study plot area.*

Habitat	Number of cells	Area [ha]	Number of trees	Short description
1	522	20.88	9244	High water content (summer)
2	264	10.56	3523	Low water content (summer), high acidity
3	55	2.20	790	Low water content (summer), low acidity, shallow soil depth
4	5	0.20	43	Low water content (summer), low acidity, deep soil depth
∑	846	33.84	13600	-

3.5.1 Hypotheses 1 & 2

Hypothesis 1 and hypothesis 2 analysed species habitat associations for all species separately and only living trees were included in the analysis (Table 2-4).

Regardless of the used method, *F. sylvatica*, *F. excelsior* and *A. pseudoplatanus* showed significant associations to at least one of the four habitats. Contrastingly, *C. betulus* and all "other" species did not show any significance habitat associations to any habitat. For *F. sylvatica* and *F. excelsior* results differed slightly between methods. However, a clear trend was present. In other words, at least two methods always indicated the same result, while one method differed for some habitats and species (Table 2-4).

For *F. sylvatica*, all methods indicated positive associations to habitat 1 and most likely negative associations to habitat 4 (indicated by two methods). Lastly, two methods showed that there were no associations to habitat 2 and habitat 3. For *F. excelsior* positive associations were present to habitat 4 (shown by two methods). Also, two methods indicated negative associations to habitat 1. Indicated by all three methods, no significant associations were present to habitat 2 and most likely to habitat 3 as shown by two methods (Table 2-4).

Table 2-4: *Results of the habitat association analysis using the gamma-test, randomised-habitats procedure, and pattern reconstruction for all species. Negative associations (blue), positive associations (green) and not significance results (grey) are indicated.*

		Fagus sylvatica	*Fraxinus excelsior*	*Carpinus betulus*	*Acer pseudoplatanus*	others
Habitat 1	*gamma*-test	positive	negative	n.s.	n.s.	n.s.
	Randomised habitats	positve	n.s.	n.s.	n.s.	n.s.
	Pattern reconstruction	positive	negative	n.s.	n.s.	n.s.
Habitat 2	*gamma*-test	n.s.	n.s.	n.s.	n.s.	n.s.
	Randomised habitats	negative	n.s.	n.s.	n.s.	n.s.
	Pattern reconstruction	n.s.	n.s.	n.s.	n.s.	n.s.
Habitat 3	*gamma*-test	n.s.	positive	n.s.	positive	n.s.
	Randomized habitats	n.s.	n.s.	n.s.	n.s.	n.s.
	Pattern reconstruction	negative	n.s.	n.s.	positive	n.s.
Habitat 4	*gamma*-test	negative	positive	n.s.	n.s.	n.s.
	Randomised habitats	n.s.	positive	n.s.	n.s.	n.s.
	Pattern reconstruction	negative	n.s.	n.s.	n.s.	n.s.

3.5.2 Hypothesis 3

For hypothesis 3, all living trees of *F. sylvatica* were classified into small, medium and large sized trees, respectively, as a proxy for the life-history stage (Table 2-5). All other species did not include enough individuals in the corresponding size classes.

All methods showed that small sized trees were positive associated to habitat 1 and negatively associated to habitat 2. No associations to habitat 3 and habitat 4 were present. For medium sized tree, all methods indicated positive associations to habitat 1 and negative associations to habitat 4 and lastly, no significant associations to habitat 3. For habitat 2, two methods showed negative associations. Large sized trees were not significantly associated to habitat 1 and habitat 2 as shown by all methods. Negative associations were indicated by two methods to habitat 3 and habitat 4 (Table 2-5).

Table 2-5: *Results of the habitat association analysis using the randomised-habitats procedure, the gamma test and pattern reconstruction for small, medium and large tree, respectively. Only F. sylvatica was included in the analysis. Negative associations (blue), positive associations (green) and not significance results (grey) are indicated.*

		small	medium	large
Habitat 1	*gamma*-test	positive	positive	n.s.
	Randomised habitats	positive	positive	n.s.
	Pattern reconstruction	positive	positive	n.s.
Habitat 2	*gamma*-test	negative	negative	n.s.
	Randomised habitats	negative	negative	n.s.
	Pattern reconstruction	negative	n.s.	n.s.
Habitat 3	*gamma*-test	n.s.	n.s.	negative
	Randomised habitats	n.s.	n.s.	n.s.
	Pattern reconstruction	n.s.	n.s.	negative
Habitat 4	*gamma*-test	n.s.	negative	negative
	Randomised habitats	n.s.	negative	n.s.
	Pattern reconstruction	n.s.	negative	negative

3.5.3 Hypothesis 4

Again, hypothesis 4 only included *F. sylvatica*, however, also dead trees were considered this time in addition to all living trees (Table 2-6). Following, results for living trees were identical to hypothesis 1 (Table 2-4). For dead trees, all methods indicated a positive association to habitat 1 and no associations to habitat 3 and habitat 4, as well as most likely no associations to habitat 2 as indicated by two methods (Table 2-6).

Table 2-6: *Results of the habitat association analysis using the randomised-habitats procedure, the gamma test and pattern reconstruction for living and dead trees, respectively. Only F. sylvatica was included in the analysis. Negative associations (blue), positive associations (green) and not significance results (grey) are indicated.*

		living	dead
Habitat 1	*gamma*-test	positive	positive
	Randomised habitats	positive	positive
	Pattern reconstruction	positive	positive
Habitat 2	*gamma*-test	n.s.	n.s.
	Randomised habitats	negative	negative
	Pattern reconstruction	n.s.	n.s.
Habitat 3	*gamma*-test	n.s.	n.s.
	Randomised habitats	n.s.	n.s.
	Pattern reconstruction	negative	n.s.
Habitat 4	*gamma*-test	negative	n.s.
	Randomised habitats	n.s.	n.s.
	Pattern reconstruction	negative	n.s.

4. Discussion

4.1 Simulation study

Overall, the methods performed similarly well for different patterns and associations, with exception of pattern reconstruction slightly outperforming the other methods for most starting patterns and association types. However, there are advantages and disadvantages related to all methods. The *gamma*-test is conceptually straightforward, possible for non-quadratic study plots, but with the disadvantage that complex patterns might not be sufficiently describable by a point process model (Wiegand et al., 2009, 2007). The torus-translation test preserves the internal spatial structure of the original data quite well (Wiegand and Moloney, 2014), however, it is only possible for rectangular study plots. Also, if strong gradients are present, this will not be preserved by the torus-translations (Wiegand and Moloney, 2014). Contrastingly, the randomised-habitat procedure is also possible for non-quadratic study plots, but the spatial structure of the data is preserved less well. Especially gradients in the data are not taken

into account and null model data might be rather artificial. Lastly, pattern reconstruction is possible for non-quadratic study plots and able to simulate complex point patterns, however, with the cost of high computational demands (Tscheschel and Stoyan, 2006). Nevertheless, the method is able to preserve the spatial structure of both the environmental data and the point pattern data the best compared to all other methods and thus had the highest correct detection rates.

The performance of all methods was worse for negative habitat associations compared to positive associations. This could have been due to the simulation study design. With increasing habitat association strength, the probability of removing an event from the habitat increased. Following, the overall number of events decreased. Thus, for stronger negative habitat associations the number of remaining individuals might have been too small for a successful analysis (Wiegand and Moloney, 2014).

We could find only one study looking at least partly at the behaviour of one of the methods (Comita et al., 2007). Using random labelling, the authors showed that for an approximated significance level of $\rho \approx 0.05$ only very few false-positive detections were present (between 1 - 4% for most of their five habitats). Since Comita et al. (2007) did only include positive association, this is in accordance with our results showing only a small rate of false detections for positive habitat associations, even though we summarised a total of three different cases as a false detection.

Using data from a tropical forest dynamics plot (Barro Colorado Island, Panama), the randomised-habitats procedure showed 38% less significant habitat associations than the torus translation test (Harms et al., 2001). This is not in agreement with our simulation study. There were no differences between the methods, both in terms of correct and false detections of habitat associations. One reason might be that the randomised-habitat procedure does not necessarily preserve the spatial structure fully, introducing a possible error source. It is possible that the spatial structure of the simulated neutral landscapes could be better imitate by the procedure than the real-world landscape structure and following no differences between the methods could be observed in our simulation study. Additionally,

our modification of the procedure allowing the procedure to jump to a non-neighbouring cell might increase the realism of the simulated null model data, improving the procedure.

With increasing strength of a positive habitat association (i.e. more events within the habitat), the point pattern becomes increasing clustered (Shen et al., 2013; Yamada et al., 2006). Interestingly, using a Poisson process point model for the *gamma*-test did nonetheless result in a high correct detection rate. This indicates that if habitat associations are strong enough, the used point process model and by that the spatial structure of the point pattern is of secondary importance and results should be similar to a generally less conservative χ_2-test (Harms et al., 2001; Plotkin et al., 2000). However, this might be only true for quite strong habitat associations, i.e. many additional events within the habitat, and additionally the χ_2-test does not control for clustering due to biotic processes (Plotkin et al., 2000).

4.2 Real-world data

Only three independent variables were included by the MRT, namely soil water content (summer), soil acidity and soil depth. Similarly, Piedallu et al. (2016) were able to fit species distribution models for temperate forest tree species using only a small subset of the originally provided input variables. Since water availability is assumed to be among the most central factors for tree growth (Bréda et al., 2006), especially the water content is not surprising. This is supported by species distribution models (Piedallu et al., 2016) or boosted regression trees predicting a forest site productivity index (Aertsen et al., 2012), both including variables on soil water availability for temperate forest species. Likewise, soil pH and thereby acidity was important in both studies (Aertsen et al., 2012; Piedallu et al., 2016). One general criticism of this study might be the sampling, interpolation and classification of environmental data introducing possible error sources. Nevertheless, because the topography is rather homogenous in the study area (van Waveren, 2016), however, soil conditions are still heterogeneous (Mund, 2004), we decided not to include topographical data (which was available "continuously" for the forest dynamics plot). This is supported by mainly environmental data improving studies analysing niche processes (Chang et al., 2013).

Even though past human influences can still be seen, the species composition, the spatial pattern of trees and the dbh distribution was typical for an temperate old-growth forest (Butler-Manning, 2007). *F. sylvatica* is expected to be the most dominant species in the region, outcompeting most other species on non-extreme sites (Bolte et al., 2007; Leuschner et al., 2006; Leuschner and Ellenberg, 2017). The reversed J-shaped form of the dbh distribution was, with exception of very small DHB classes, comparable to virgin beech forests in south-eastern Europe (Westphal et al., 2006). Also, the clustered pattern of trees is typical for temperate old-growth forest (e.g. Wang et al., 2010b) and especially smaller beech trees tend to be highly clustered (Janík et al., 2016).

Hypothesis 1 stated that *F. sylvatica* shows the least habitat associations due to its generally assumed broad adaptation to a variety of site conditions (Bolte et al., 2007; Lawesson and Oksanen, 2002; Leuschner et al., 2006) combined with its competitive abilities (Leuschner et al., 2006; Leuschner and Ellenberg, 2017). This was not supported by the data. On the contrary, the species had more significance habitat associations than most other species. *F. sylvatica* was negatively associated to habitat 4. The habitat had a low soil water content during the growing season as well as low soil acidity. Since *F. sylvatica* is most dominant on sites not too dry and with a moderate soil acidity (Bolte et al., 2007; Leuschner and Ellenberg, 2017), the unfavourable conditions for the species might have led to the negative association. The positive association to habitat 1 might be explained by the higher soil water content during the growing season making the habitat generally favourable for tree growth (Aertsen et al., 2012; Bréda et al., 2006). Due to its competitive abilities (Leuschner et al., 2006; Leuschner and Ellenberg, 2017), *F. sylvatica* might be able to outcompete all other species. Once the species is established, this might be supported by the mainly barochorous seed dispersal (Martínez and González-Taboada, 2009), high shade tolerance of saplings (Janík et al., 2016; Petritan et al., 2007), and the lower browsing damage compared to other species (Ratcliffe et al., 2015).

Hypothesis 2 stated that all other species have opposing habitat associations to *F. sylvatica*. This was partly supported by the data. *F. excelsior* showed negative associations to habitat 1 and positive associations to habitat 4. This was just opposing to *F. sylvatica* showing positive associations to

habitat 1 and negative associations to habitat 4. The negative association of *F. excelsior* to habitat 1 might be due to the fact that the species was outcompeted by *F. sylvatica* growing in its optimum habitat. Contrastingly, *F. excelsior* might benefit from the absence of the *F. sylvatica* in habitat 4. Even though a niche overlap between the two species partly exists (Lawesson and Oksanen, 2002), *F. excelsior* still tends to dominant on sites unfavourable for *F. sylvatica* (Dobrowolska et al., 2011). Also, Holzwarth et al. (2011) showed an avoidance of *F. sylvatica* and *F. excelsior* co-occurrence. However, also remnants of human influences are a possible explanation. Most *F. excelsior* trees are rather large (Appendix Fig. A2-1) and probably still standards from a former coppice-with-standards management (Butler-Manning, 2007; Holzwarth et al., 2013). In this case, the trees would have been selectively allowed to growth into the upper forest layer, promoting their survival probabilities. Of course, this could have also led to higher densities of trees within a certain habitat, besides natural processes.

Hypothesis 3 stated that because seedlings and saplings have a higher mortality probability in unfavourable habitats, more species-habitat associations will be present for later life-history stages. This hypothesis is in accordance with niche modelling of temperate forest species showing a niche shift with increasing size and environmental variables being better predictors for large trees than for small ones (Bertrand et al., 2011). Also, studies in the tropical and subtropical forests showed different habitat associations between life-history stages of trees (Comita et al., 2007; Kanagaraj et al., 2011; Lai et al., 2009). On other studies, the number of habitat associations was smaller for later life-history stages and different stages were rarely associated to the same habitat (Comita et al., 2007; Lai et al., 2009). Correspondingly, our results suggested habitat associations differed between life-history stages, however, no clear increase or decrease of habitat associations with increasing tree size was observed. The overall trend was similar to the habitat associations of all *F. sylvatica* trees. Therefore, it seems like the positive habitat association of the overall population to habitat 1 is mainly driven by small and medium trees. This could be due to favourable conditions for establishment and later higher mortality due to increased competition (Comita et al., 2007). Also the higher shade-tolerance of *F. sylvatica* compared to other species (Peltier et al., 1997) might allow a larger number of small trees to firstly

establish in the habitat. However, also *F. sylvatica* needs to escape low-light conditions at some point (Janík et al., 2016) and less trees grow into large size classes. Small and medium trees showed negative associations to habitat 2, which was characterised by a low water content during the growing season and high soil acidity. The unfavourable conditions for the species (Bolte et al., 2007; Leuschner and Ellenberg, 2017), might prevent a successful establishment of regeneration. Another explanation might be that the high soil acidity in habitat 2 is rather a consequence of than a reason for the presence of *F. sylvatica*. Holzwarth et al. (2011) showed that the present of the species lead to lower pH values in the top soil layer due to leaf-litter fall. However, this can be contradicted by the generally high abundance of *F. sylvatica* in the whole study plot. Interestingly, medium and large trees showed negative associations to habitat 3 and habitat 4, respectively. Again, both habitats were characterised by a low water content during the growing season, low soil acidity and a shallow and deep soil depth, respectively. While small trees might still be possible to successfully establish and grow in the habitat, the generally higher nutrient demand of later life-history stages (Bertrand et al., 2011) might lead to a higher mortality and consequently negative association of medium and large trees to the habitats. This is supported by only negative species-habitat associations for medium and large trees in contrast to also positive associations of small trees.

Hypothesis 4 stated that living and dead trees show opposing habitat associations because a higher mortality probability in unfavourable habitats consequently leads to positive associations of dead trees and negative associations of living trees (and vice versa). This was not supported by the data. For dead trees basically the same habitat associations as for living trees or no significant associations were present. The pattern of dead trees seemed to be largely dominated by the pattern of living trees. However, this does not imply that mortality was necessarily completely random. In fact, dead trees were clustered as shown by the mark-connection function and random labelling (Appendix Fig. A2-4), rejecting the random mortality hypothesis (e.g. see Kenkel, 1988). The clustering of dead trees for the overall population of *F. sylvatica* could not be related to our habitat classification and thereby environmental influences. Rather biotic processes, such as growth and competition seemed to be the main drivers of

mortality. Ratcliffe et al. (2015) showed that tree growth is mainly influenced by biotic factors and tree growth indeed was an important driver of tree mortality (Holzwarth et al., 2013). Nevertheless, these possible biotic processes might still have been influenced by abiotic processes in the form of environmental conditions.

5. Conclusions

Our simulation study showed that all methods suggested by the literature to analysis of species-habitat associations were able to detect positive and negative associations in a satisfactory and comparable way. Thereby, negative associations for clustered patterns were detected worse than positive associations for less clustered patterns. Additionally, we proposed to use pattern reconstruction, especially if complex point patterns and/or non-quadratic study plots are analysed. To facilitate the application, we implemented all methods in the open-source and freely available *R* package *shar* (Hesselbarth and Sciaini, 2019).

Our analysis of a temperate old-growth forest showed that species-specific species-habitat associations were present for the two most common species, namely *F. sylvatica* and *F. excelsior*. For *F. sylvatica* habitat associations differed between life-history stages, however, no clear trend was present. Lastly living and dead trees did not show opposing habitat associations, indicating the importance of biotic processes for mortality. Even though our analysis suggested influence of abiotic processes, i.e. environmental heterogeneity, biotic processes seemed to interact. Therefore, further research into the interaction between these two processes is clearly needed.

Chapter 3 - Environmental heterogeneity influences mostly earlier life-history stages in a temperate old-growth forest as shown by individual-based modelling

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Abstract

Environmental heterogeneity and related abiotic processes are assumed to support plant species coexistence on global, landscape and local scales. Many of these abiotic processes lead to spatial clustering of individuals at suitable sites. However, also biotic processes can lead to spatial clustering of individuals. This complicates the analyses of the importance and interactions of these two groups of contrasting processes. One promising approach to study the importance and interactions of abiotic and biotic processes are individual-based simulation models. Individual-based simulation models are able to incorporate interactions between individuals as well as interactions with a heterogeneous environment and allow to gain insights into the underlying processes. To study the importance of environmental heterogeneity in a temperate old-growth forest, we developed an individual-based simulation model with two model versions. While the first model version included the most important biotic processes only (competition, growth, seed dispersal, mortality), the second model version additionally included abiotic interactions with the heterogeneous environment. To validate the model versions, we used non-spatial and spatial patterns from field data in a temperate old-growth forest dominated by *Fagus sylvatica*. Results showed that non-spatial patterns were adequately matched by both model versions. However, spatial patterns were not matched by the purely biotic model version and results differed between different life-history stages, i.e. saplings and adult trees. Inclusion of abiotic processes modifying growth, seed establishment and mortality led to clustered spatial patterns similar to the field data over an extensive period of time. The study highlighted the importance of abiotic processes in temperate forests, especially for earlier life stages. Additionally, we demonstrated that considering several spatially explicit patterns for model validation increased the ability to infer process from pattern.

1. Introduction

Environmental heterogeneity is assumed to be one of the main drivers of plant species coexistence (Chesson, 2000), whereby the relationship between environmental heterogeneity and species richness is scale-dependent (Chase, 2014; Tamme et al., 2010). On landscape and global scales, species richness increases with increasing environmental heterogeneity for many taxa and regions across the world (Báldi, 2008; Stein et al., 2014). Increased environmental heterogeneity normally results in a higher diversity of habitats (Báldi, 2008), as well as in shelters and refuges for species (Stein et al., 2014). While some studies have found similar positive relationships between species richness and environmental heterogeneity on smaller scales (Bergholz et al., 2017; Douda et al., 2012), other studies have found no or even negative relationships (Gazol et al., 2013; Kadmon and Allouche, 2007; Laanisto et al., 2013). Possible explanations for negative relationships include increased asymmetric competition of dominant species (Gazol et al., 2013), increased stochastic extinction due to a decrease of suitable habitat for certain species (Kadmon and Allouche, 2007) or an increase of smaller, isolated microhabitats with increasing environmental heterogeneity (Tamme et al., 2010).

Many proposed processes that lead to positive relationships between environmental heterogeneity and species richness depend on abiotic processes and relate to niche theory and linked coexistence mechanisms (Tilman, 1982; Tilman and Pacala, 1993). On smaller scales, many of these abiotic processes lead to spatially clustered patterns of species in suitable habitats (Comita et al., 2007; Harms et al., 2001; Shen et al., 2013). However, biotic processes, mainly limited seed dispersal, also can result in spatially clustered patterns of plants (Condit et al., 2000; Ramon et al., 2018).

Because both abiotic and biotic processes can lead to similar spatially clustered patterns, there is a long-lasting and ongoing discussion about the relative importance of the two contrasting processes and how to disentangle them in plant populations (e.g. Adler et al., 2007; Chase and Myers, 2011; Chisholm and Pacala, 2010; Diniz-Filho et al., 2012; Furniss et al., 2017; John et al., 2007; Legendre et al., 2009; Mitchell et al., 2017; Schouten and Houseman, 2019). While biotic processes including competition (Coates et al., 2009; Wang et al., 2010a), limited seed dispersal (Martínez and González-Taboada, 2009)

or facilitation (Zhang et al., 2014), have been shown to be important in temperate forests, several studies demonstrate that spatial patterns are also influenced by abiotic processes (Getzin et al., 2008; Shen et al., 2013; van Waveren, 2016), indicated by e.g. species habitat associations (Furniss et al., 2017; Ye et al., 2011).

There are several methods to analyse the influence of abiotic processes and possible interactions with biotic processes, including analytical approaches (Chisholm and Pacala, 2010), spatial autocorrelation analysis (Diniz-Filho et al., 2012), species-habitat associations analysis (Furniss et al., 2017; Harms et al., 2001), principle coordinates of neighbour matrices (Legendre et al., 2009), linear regression models (Mitchell et al., 2017), point pattern analysis (Ramon et al., 2018; Shen et al., 2013) or experimental setups (Schouten and Houseman, 2019). Many methods have in common that conclusions about the acting processes are based on descriptive and inferential analyses of observed field data. However, even though not impossible, linking observed patterns to ecological processes is often neither straightforward nor obvious (Law et al., 2009; McIntire and Fajardo, 2009). Therefore, one promising approach is provided by spatially explicit individual-based simulation models. These models allow variability and interactions between individuals, as well as interactions with a heterogeneous environment and lastly the explicit incorporation of hypothesised processes (DeAngelis and Grimm, 2014; Grimm and Railsback, 2005). This makes them a powerful tool to study the importance and interactions of abiotic and biotic processes. This is especially true for systems that are hard to study experimentally, such as forests, due to the longevity and size of individuals, the temporal scale of processes and the overall complexity of the system (Grimm and Railsback, 2012; Stillman et al., 2015).

Individual-based simulation models are commonly used in forest dynamics research for different forest types and research questions. This includes, besides others, tropical as well as temperate forests and applications dealing with practical management to theoretical issues (e.g. SORTIE; Deutschman et al., 1997; FORMIND; Kohler and Huth, 1998; SILVA; Pretzsch et al., 2002; BEFORE; Rademacher et al., 2004). Even though individual-based models are a powerful tool to study the role of abiotic processes, only a few models exist that explicitly include environmental heterogeneity (but see Cabral

and Kreft, 2012; Jeltsch et al., 1998; Liu and Ashton, 1998; Tietjen et al., 2010) and to our knowledge none in temperate forests.

Pattern-orientated modelling uses patterns in the data to build simple, but realistic models, to parameterise them and to contrast alternative hypotheses (Grimm et al., 2005; Wiegand et al., 2003). This is done by continuously comparing patterns of the model output to patterns of the field data (Wiegand et al., 2003). In this context, patterns are defining characteristics of a study system containing information about acting processes and the system itself (Grimm et al., 2005).

Here, we are going to present an individual-based simulation model to analyse the importance and interactions of abiotic and biotic processes in a temperate old-growth forest dominated by *Fagus sylvatica L.* (European beech). Two model versions, one including only biotic processes and one combining biotic and abiotic processes, will allow insights into the acting processes. Because we have already shown that species-habitat associations are present for *F. sylvatica* (Hesselbarth et al., in prep.) and abiotic processes influence the spatial pattern of trees (van Waveren, 2016) in a temperate forest dynamics plot, we hypothesise that only the model version including biotic and abiotic processes will be able to reproduce non-spatial and spatial patterns of the observed field data.

2. Methods

2.1 Field data from the Hainich National Park

We used field data from a forest dynamics plot situated in the Hainich National Park (Thuringia, Germany) to parametrise and validate the model. The national park was founded in 1997, but already starting from 1965 no major silvicultural activities were carried out in the study plot (Butler-Manning, 2007; Mund, 2004). The old-growth forest is dominated by *F. sylvatica* with a relative abundance of 90.0%, but also *Fraxinus excelsior L.*, *Carpinus betulus L.*, *Acer sp. L.* and other species of low abundance can be found (Butler-Manning, 2007; Huss and Butler-Manning, 2006). The climate is temperate with a mean annual temperature of 6.5 °C and a mean annual precipitation of 720 mm (Butler-Manning, 2007). Soils can be characterised as rendzinas or brown rendzinas covered by a loess layer on shell limestone (Mund, 2004; van Waveren, 2016).

In 1999, 2007 and 2013 the location, species and diameter at breast height (dbh) of all tree individuals with a dbh > 1 cm were mapped (Butler-Manning, 2007; tree individuals are called events in the context of point pattern analysis). The time period allowed the calculation of individual tree growth rates as well as mortality (Holzwarth et al., 2013) leading to the parametrisation of most model processes, with the exception of seed dispersal and establishment. The spatial location of all individuals allowed to use not only non-spatial patterns, but also spatial patterns to construct and optimise the model (Grimm et al., 2005) and finally to discriminate between the two model versions based on the highest agreement of several patterns with the field data (Wiegand et al., 2008, 2003).

2.2 Comparison between model output and field data

Because more insights into the processes can be gained if multiple patterns at different spatial and temporal scales as well as at different hierarchical levels are used (Grimm et al., 2005; Grimm and Railsback, 2012; Wiegand et al., 2003), we included several non-spatial and spatial patterns on the individual- and population-level.

The population size of all living saplings ($1 < \text{dbh} \leq 10$ cm) and adults (dbh > 10 cm) was the simplest pattern we used to compare the model output to the field data. On the individual level, we used the dbh distribution and the mean annual dbh growth.

Spatial patterns included the distribution of a competition value (section 2.3.7) on the individual level and the pair-correlation function $g(r)$ (Stoyan and Stoyan, 1994) on the population level. The pair-correlation function $g(r)$ describes the event density at distance r from the average event of the pattern and thereby allows to determine if a point pattern is random, clustered or regular at different distances r (Velázquez et al., 2016; Wiegand and Moloney, 2014). Because ecological processes also act at several scales (Law et al., 2009), the scale-dependence is an important feature to infer processes from patterns (Brown et al., 2011; Law et al., 2009; McIntire and Fajardo, 2009). A random pattern at distance r is indicated by a value of $g(r) = 1$, while clustering is indicated by a value of $g(r) > 1$ and regularity by a value of $g(r) < 1$. Additionally, we used the mark-correlation function $k_{mm}(r)$ (Stoyan and Stoyan, 1994) to analyse the spatial distribution of the dbh. This summary functions compares the conditional mean

dbh of two events separated by distance *r* to the conditional mean dbh of two randomly selected events and is thereby able to describe spatially positive and negative correlation of the dbh by values of $k_{mm}(r) > 1$ and $k_{mm}(r) < 1$, respectively (Wiegand and Moloney, 2014). We calculated all summary functions using the *spatstat* R package (Baddeley et al., 2015).

2.3 The model

The following model description is in accordance with the ODD protocol (Grimm et al., 2010, 2006). The model code is freely available at <https://zenodo.org/record/3573619>. All R scripts for the analysis can be found at <https://zenodo.org/record/3582922>

2.3.1 Purpose

The purpose of the model was to investigate the importance and interactions of abiotic and biotic processes in a temperate old-growth forest dominated by *F. sylvatica*. Following, two model versions were developed, one including only biotic processes (competition, growth, seed dispersal, mortality) and one combining both biotic as well as abiotic processes (interactions with a heterogeneous environment).

2.3.2 State variables and scales

Individual trees were the only entities of the biotic model version. Trees were described by their stem position (x- and y-coordinate), their dbh and their size group (seedling: dbh <1 cm; sapling: 1 < dbh ≤ 10 cm; adult: dbh > 10 cm; dead). The combined model version additionally included heterogeneous environmental conditions. The cell size of the raster describing the environmental conditions was 1×1 m (spatial grain) and simulations were set in a 28.4 ha study plot (spatial extent) comprising a grid of 651×615 cells (irregularly shaped, Appendix Fig. A3-1). Forest dynamics were simulated every year (temporal grain) for 50 years total (temporal extent). However, in order to match the available time period of the field data (section 2.1), results will be presented after 15 years. Because of the stochasticity of the model, we used 50 repetitions of model runs.

2.3.3 Process overview and scheduling

All processes were modelled in discrete annual time steps. Firstly, competition was simulated for all individual trees based on the local neighbourhood. Secondly, based on the tree size and the previously simulated competition value, annual dbh growth was simulated. Thirdly, seed dispersal and establishment were simulated. The number of seeds was based on the dbh of the source tree. Lastly, mortality was simulated based on a probability depending on the dbh. For the combined model version, all processes but competition were additionally dependent on the environmental conditions at the growing locations of the individual trees.

2.3.4 Design concepts

Emergence: All non-spatial and spatial patterns emerged from the simulated processes of the individual trees. Non-spatial patterns included the number of individuals, the dbh distribution and the mean annual dbh growth. Additionally, we used point pattern analysis summary functions to describe the spatial patterning of individuals.

Sensing: Trees had information about their location in both model versions and thereby also about environmental conditions for the combined model version. Furthermore, trees had information about their dbh as well as their size group. Lastly, the competition value and thus indirectly the local neighbourhood was available for the trees.

Interaction: Trees interacted with each other using an exponential competition kernel describing competition for resources. Thus, the perceived competition for each focal tree depended on the distance to and the size of all other trees in its local neighbourhood.

Stochasticity: Seed dispersal and establishment as well as mortality included a stochastic component. Produced seeds survived with a certain probability and the location of new seedlings was based on a distance-dependent dispersal probability from the source tree (lower probability with increasing distance). The mortality probability was based on the dbh, describing a U-shaped form.

Collectives: Trees were classified as seedlings (dbh ≤ 1 cm), saplings (1 < dbh ≤ 10 cm) and adults (dbh > 10 cm) based on their dbh. However, all processes were simulated individually for each tree and did not necessarily depend on the group. Trees that died during the simulation were not included in any further processes, e.g. did not contribute to the perceived competition of living trees.

Observation: The individual-based characteristic of the model allowed all state variables to be recorded on the level of individual trees and allowed the analysis and comparison against field observations. The same was possible for the spatial patterning on the population level using several point pattern analysis summary functions.

2.3.5 Initialisation

To ensure that model results were not influence by the initialisation, we used two different configurations of trees to initialise the model: the field data recorded in 1999 and a reconstructed point pattern based on the field data. We used pattern reconstruction (Tscheschel and Stoyan, 2006) to create a random, but spatially comparable initialisation. Because not only the spatial patterning of individual trees, but also the spatial distribution of the dbh is an important spatial characteristic (Pommerening and Särkkä, 2013), we used a two-step reconstruction approach. In a first step, using the pair-correlation function *g(r)* and the nearest-neighbour distribution function *G(r)* (Diggle, 2014; Illian et al., 2008) only the spatial structure was reconstructed. In a second step, the spatial dbh distribution was reconstructed using the mark-correlation function $k_{mm}(r)$. To reconstruct the spatial point pattern , we used the *shar* R package (Hesselbarth and Sciaini, 2019). However, because results were similar between the two initialisations, we are going to present only the results of the field data. Also, because the forest was dominated by *F. sylvatica* and not enough data was available to parametrise and validate the model for all other species present, we only used *F. sylvatica* for the analysis.

2.3.6 Input data

For the combined model version, data about environmental conditions describing the suitability for tree growth was required. Because we assumed that a high intensity corresponds to suitable growing conditions (Getzin et al., 2008), we used the intensity *λ(x,y)*, i.e. the event density at a certain location,

of all adult trees of the initial tree configuration (field data census 1999; dbh > 10 cm). Values were linearly scaled to $-1 \leq \lambda_{scaled}(x,y) \leq 1$, where $\lambda_{scaled}(x,y) = -1$ described the least suitable growing condition and $\lambda_{scaled}(x,y) = 1$ described the most suitable growing condition in the study plot. We used the *spatstat* R package to calculate the intensity.

2.3.7 Submodels

Competition: An exponential competition kernel was used to model the competition value for each tree (Pommerening and Maleki, 2014). Advantages of competition kernels include their flexibility to model asymmetric competition continuously in space among plants beyond the nearest-neighbour scale (Pommerening and Maleki, 2014; Purves and Law, 2002; Schneider et al., 2006). Because of their flexibility, the exact shape of the kernel (e.g. exponential or fractional) was shown to be less important (Purves and Law, 2002; Schneider et al., 2006). Because we were only interested in the effect of competition, i.e. a reduction of growth performance (Pommerening and Sánchez Meador, 2018), we assume that the kernel captures both above- and belowground competition. The competition value of a focal tree c_{iraw} aggregated the competition loads of all other trees j in its local neighbourhood (equation 3-1, Fig. 3-1). The size of the competition load depended on the distances to and the dbh of all trees j, whereby small trees that were far away had only a small contribution to the overall competition load. The model parameters in equation 3-1 described the strength of competition (α) and scaled the decrease of competition with increasing distance (β) (Pommerening and Maleki, 2014).

$$c_i^{raw} = \sum_{j \neq i} dbh_j^{\alpha} * \exp\left(-\frac{dist_j}{dbh_j^{\beta}}\right) \tag{3-1}$$

Because how the competition load is perceived also depends on the dbh of the focal tree i, the competition value of tree i was transformed using its own dbh and scaled to $0 < c_{itrans} < 1$ (equation 3-2, Fig. 3-1). The model parameter α in equation 3-2 was identical to the corresponding parameter in equation 1-1 (Pommerening and Maleki, 2014).

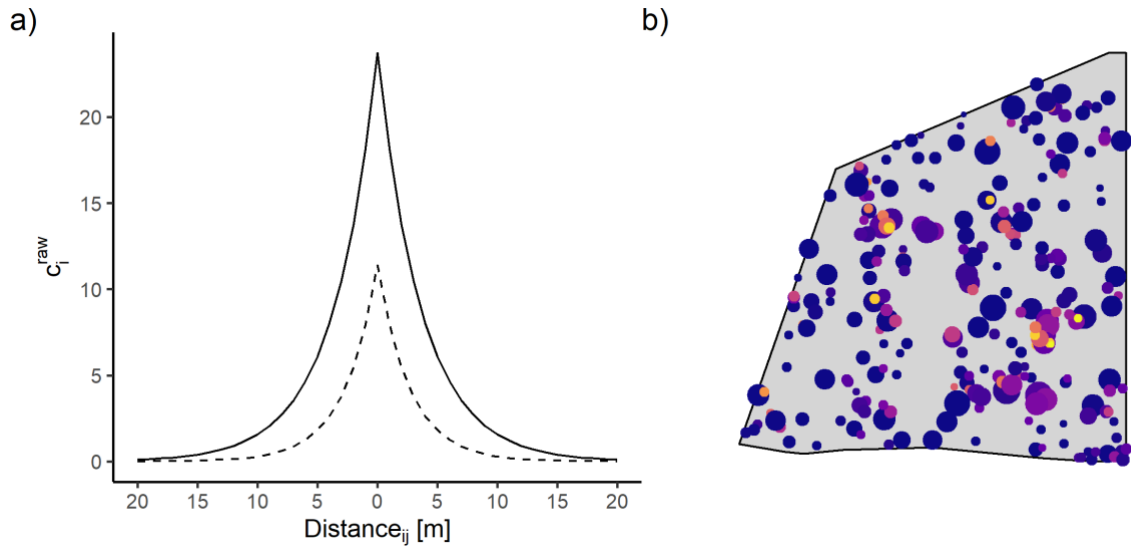$$c_i^{trans} = \frac{c_i^{raw}}{dbh_i^{\alpha} + c_i^{raw}} \tag{3-2}$$

Figure 3-1: *a) Competition kernel for tree individuals with a diameter at breast height (dbh) of dbhⱼ = 10 cm (dashed line) and dbhⱼ = 20 cm (continuous line). b) Exemplary map of perceived competition values of the focal trees i. The colour represents the perceived competition, where blue colours indicate a low and orange colours indicate high competition values cₜᵣₐₙₛ. The size of the circles represents the dbh of the focal tree.*

Growth: We adapted a potential-modifier approach (Botkin et al., 1972; Newnham, 1964) to model annual dbh growth from Pommerening and Maleki (2014). Because of its flexibility, we used the Chapman-Richards growth function (equation 3-3; Pienaar and Turnbull, 1973) to model the potential annual dbh growth of a tree without any competition (Botkin et al., 1972). The model parameters *A*, *k* and *p* of equation 3-3 described the asymptote, scaled the growth rate and described the turning point of the function, respectively (Pommerening and Maleki, 2014).

$$\Delta dbh_{growth}^{potential} = A * k * p * \exp(-k * dbh_i) * (1 - \exp(-k * dbh_i))^{p-1} \qquad (3\text{-}3)$$

The actual dbh growth of tree *i* was then reduced by its perceived competition (equation 3-4.1). For the combined model version, the actual growth was additionally modified by the intensity *λscaled(x,y)* scaled by a parameter *κ* (equation 3-4.2).

$$\Delta dbh_{growth}^{actual} = dbh_{growth}^{potential} * (1 - c_i^{trans}) \qquad (3\text{-}4.1)$$

$$\Delta dbh_{growth}^{actual} = dbh_{growth}^{potential} * \left(1 - c_i^{trans}\right) + dbh_{growth}^{potential} * \kappa * \lambda_{scaled} \qquad (3\text{-}4.2)$$

Seed dispersal and establishment: Seed dispersal was modelled in a two-step approach based on the reduced model of Ribbens et al. (1994). In a first step (equation 3-5), the number of seeds produced was determined by the dbh of the source tree. The parameter *Str* was the standard total recruitment for a tree with a standardised mean dbh = 30 cm (Ribbens et al., 1994).

$$n_{seeds} = Str * \left(\frac{dbh}{30}\right)^{\beta} \qquad (3\text{-}5)$$

The number of seeds was then reduced by a survival probability that accounted for seed survival and browsing (Olesen and Madsen, 2008). For the biotic model version, the seed survival probability was constant throughout the study plot. For the combined model version, we used the standard errors of Olesen and Madsen (2008) to increase and decrease the survival probability if tree seedlings were situated at locations at which the environmental conditions were below or above the 25% and 75% quantiles, respectively.

The locations of the seedlings were simulated using a distance-dependent probability with decreasing probability with increasing distance from the source tree (equation 3-6). The normaliser *n* ensured that the area under the curve equalled one, whereas the model parameters η influenced the probability decrease with increasing distance (Ribbens et al., 1994). Because there were trade-offs between *Str* and β as well as between η and θ and the effects of the parameter pairs were similar, the parameters were fixed to $\beta = 2$ and $\theta = 3$ after an initial data analysis during the parametrisation by Ribbens et al. (1994).

$$dist_{seedlings} = \frac{1}{n}\exp\left(-\eta * dist^{\theta}\right) \qquad (3\text{-}6)$$

Mortality: Because mortality is a binary dependent variable, the mortality probability depending on the dbh was modelled using logistic regression (equations 3-7, 3-8). As explanatory variables, we used the size of the tree and the annual dbh growth. Because mortality depends on the life history stage (Franklin et al., 1987), equation 3-7 was fitted separately for small and large trees and the probabilities added to produce a U-shaped function (equation 3-8; Holzwarth et al., 2013). Even though the mortality depended only on the size, also an indirect effect of competition was included since the growth and thus

the size depended on the competition. Similar to the seed dispersal and establishment process, for the combined model version for trees that were located at the lowest and highest 25% values of the environmental conditions, we used the standard errors of the parameter estimations (Holzwarth et al., 2013) to decrease and increase the mortality parameters, respectively.

$$z = \beta_0 + \beta_1 * dbh + \beta_2 * \Delta dbh \qquad (3\text{-}7)$$

$$p_{annual_i} = \frac{1}{1 + \exp(-z)} \qquad (3\text{-}8)$$

2.4 Parameter estimation

Where possible, we estimated model parameters directly from the field data. This was possible for all submodels with exception of seed dispersal and establishment, because no corresponding data were available (Table 3-1). Model parameters for the mortality submodel were taken from Holzwarth et al. (2013), who used the same field data to fit the logistic regression models for the mortality probability.

To estimate parameters of the potential annual dbh growth, we calculated the mean annual dbh growth for each tree of the field data between 1999 - 2013. We classified trees according to their dbh in the year 1999 into 4 cm-diameter classes and used only trees with the top 5% dbh growth of each class. We assumed that the dbh growth of these trees was influenced the least by competition and thus we used quantile regression to estimate the parameters for the potential annual dbh growth. Once parameters for the potential annual dbh growth were estimated, a least square optimisation was used to estimate the remaining parameters of the competition kernel that reduced the potential annual dbh growth to the actual annual dbh growth (Fig. 3-2; Pommerening and Maleki, 2014).
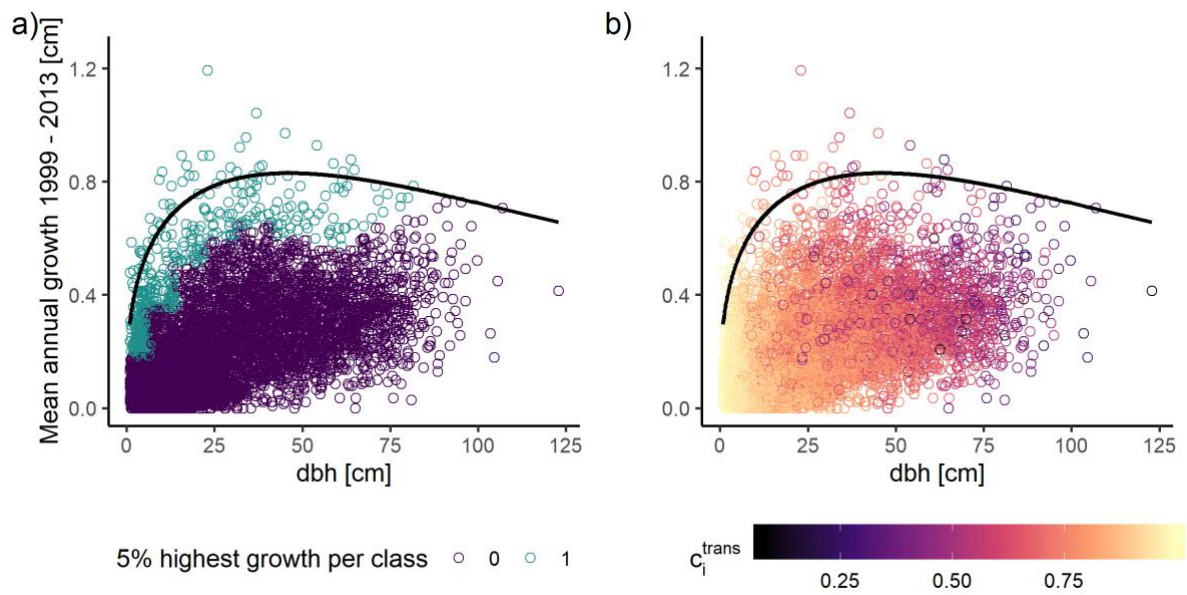
Figure 3-2: *Field data used for the parameter estimation of the competition and growth submodel for the biotic model version. a) The potential annual diameter at breast height (dbh) growth was estimated from trees with the top 5% dbh growth in each 4 cm-dbh class (turquoise points). The black line represents the estimated potential annual dbh growth. b) All trees with less growth than the top 5% dbh growth in each 4 cm dbh-class (violet points in a) were used to estimate the parameters of the competition kernel which reduced the potential to the actual annual dbh growth.*

Table 3-1: *Model parameters of all submodels for Fagus sylvatica. For submodels indicated by *, parameters were estimated directly from the field data. For the combined model version, parameters for trees growing in low and high environmental conditions are given. The last column indicates if the parameter was used for the Sobol' sensitivity analysis.*

Submodel	Equation	Symbol	Description in software	Value biotic version / combined version	Reference	Sobol' sensitivity analysis
Competition*	3-1, 3-2	α	ci_alpha	1.057 / 1.272	(Pommerening and Maleki, 2014)	yes
	3-1	β	ci_beta	0.435 / 0.44	(Pommerening and Maleki, 2014)	yes
Growth*	3-3	A	growth_assymp	204.911	(Pienaar and Turnbull, 1973; Pommerening and Maleki, 2014)	no
	3-3	k	growth_rate	0.006	(Pienaar and Turnbull, 1973; Pommerening and Maleki, 2014)	no
	3-3	p	growth_infl	1.35	(Pienaar and Turnbull, 1973; Pommerening and Maleki, 2014)	yes
	3-4.2	κ	growth_abiotic	- / -0.054	-	no
Seed dispersal and establishment	3-5	Str	seed_str	121.22	(Ribbens et al., 1994)	no
	3-6	η	seed_beta	3.412	(Ribbens et al., 1994)	no
	(3-5)	γ	seed_success	0.005 / low:0.004; high:0.01	(Olesen and Madsen, 2008)	no
Mortality*	3-7	β_0	mort_int_early	1.8 / low: 1.494; high: 2.157	(Holzwarth et al., 2013)	yes
	3-7	β_1	mort_dbh_early	-2.1 / low:-2.253; high:-1.998	(Holzwarth et al., 2013)	yes
	3-7	β_0	mort_int_late	-8.9 / low:-9.461; high:-8.339	(Holzwarth et al., 2013)	yes
	3-7	β_1	mort_dbh_late	0.052 / low:0.042; high:0.061	(Holzwarth et al., 2013)	no
	3-7	β_2	dinc	-1.4 / low:-1.91; high:-0.915	(Holzwarth et al., 2013)	no

2.5 Sensitivity analysis

Sensitivity analysis is a tool to assess how changes of input parameters relate to changes of the model output (Saltelli et al., 2004) and can give insights into the importance of parameters (Railsback and Grimm, 2012). Processes including sensitive parameters, i.e. parameters that have a relative large influence on the general model output, can be assumed to be also important for the pattern formation (Pommerening et al., 2011). To evaluate the influence of the parameters on the model output, we used both non-spatial and spatial patterns. Firstly, we used the number of individuals as non-spatial model output. Secondly, as spatial model output, we used the absolute area between the null model envelope for complete spatial randomness and the observed pair-correlation function $g(r)$ normalised by the total area under the observed pair-correlation function $g(r)$ (i.e. the "area of deviation"; Appendix Fig. A3-2). Using this summarised measure of the pair-correlation function $g(r)_{summarised}$ had the disadvantage of losing the functional characteristic of $g(r)$, however, all sensitivity analysis methods required a single numeric model output (Pianosi et al., 2016; Saltelli et al., 2004).

2.5.1 Local one-at-a-time sensitivity analysis

As a first step to get a general overview of the effect of each parameter (Railsback and Grimm, 2012), we carried out a local one-at-a-time sensitivity analysis. This rather simple approach varies each parameter at a time, while keeping all other parameters constant (Pianosi et al., 2016). The straightforward application, however, comes with the price of not being able to give insights into possible interactions between parameters and not necessarily representing the whole parameters space (Thiele et al., 2014).

We both increased and decreased each parameter by 5% and 10%, respectively. Because of the stochasticity of the model, we run the model 50 times for each parameter combination and calculated the mean difference of the model output between the changed parameters and the baseline parameters. For each repetition, the model was run 50 years.

2.5.2 Global all-at-a-time sensitivity analysis

The local one-at-a-time sensitivity analysis allowed us to reduce the full parameter set to the most sensitive ones, i.e. parameters for which the relative change of the model output exceeded the relative parameter change. This reduced parameter set was used to analyse possible non-linear and non-monotonic relationships between the parameters themselves and the model output (Thiele et al., 2014) using the improved Sobol' method (Sobol' et al., 2007) implemented in the *sensitivity* R package (Iooss et al., 2019).

The improved Sobol' method allowed us to quantify and decompose main effects S_i (the effect of the parameter if all other parameters are constant) and total effects S_{Ti} (main and interaction effects) of all parameters investigated (Thiele et al., 2014). If no interactions between parameters exist, the sum of all main effects equals $S_i = 1$. In this case, total effects S_{Ti} equal main effects S_i. However, if interactions are present, total effects S_{Ti} are larger than main effects S_i and the sum can exceed $S_{Ti} > 1$ (Thiele et al., 2014). If $S_{Ti} < S_i$, parameters are most likely correlated (Wei et al., 2015). To efficiently sample the parameter space, we used Latin hypercube sampling (McKay et al., 1979) and drew 250 samples from the parameter space resulting in 2000 parameters combinations. The parameter space was defined using the confidence intervals of the model fitting. As for the local one-at-a-time sensitivity analysis, the model was run for 50 years.

3. Results

There were no noteworthy differences of the model output for the two different initialisations. Thus, we are going to present the result of the initialisation with field data from the census in 1999 only. For spatial model output, results differed between saplings and adults. Hence, results are presented separately for saplings and adults.

To successfully fit the combined model version, two different values of the standard deviation of the smoothing kernel σ were required when constructing the environmental conditions using the intensity $\lambda(x,y)$. For fitting the competition and growth parameters, a smaller value $\sigma = 5$ was used, while for seed establishment and mortality a larger value $\sigma = 15$ was used (Appendix Fig. A3-1).

3.1. Sensitivity analysis

The local one-at-a time analysis showed that both the non-spatial and the spatial model output was more sensitive to parameters changes for saplings than for adults (Appendix Fig. A3-3, Fig. A3-4). For the number of individuals, two mortality parameters (*mort_int_early*, *mort_dbh_early*), two parameters related to the competition value (*ci_alpha*, *ci_beta*) and one growth parameter (*growth_infl*) were the most sensitive parameters. The relative differences of the model output between the changed parameters and the baseline parameters exceeded the magnitude of the relative parameter changes for these parameters (Appendix Fig. A3-3). The summarised pair-correlation function $g(r)_{summarised}$ was mainly sensitive to mortality (*mort_int_early*, *mort_int_late*, *mort_dbh_early*), competition (*ci_alpha*, *ci_beta*) and growth (*growth_infl*). Also here, the relative differences of the model output between the changed parameters and the baseline parameters exceeded the magnitude of the relative parameter changes (Appendix Fig. A3-4).

The Sobol' indices using the most sensitive parameters identified by the local one-at-a time analysis showed that the model was mostly additive for the number of individuals (saplings: $\sum S_i = 0.94$; adults: $\sum S_i = 0.84$). Two mortality parameters (*mort_dbh_early*, *mort_int_early*) had the largest contribution to the overall main effects with $S_i = 0.30$ and $S_i = 0.48$ for saplings and $S_i = 0.40$ and $S_i = 0.36$ for adults. The large total effects showed that only small interaction effects between the parameters existed. This was supported by the total effects S_{Ti}, which where only marginally larger than the main effects S_i for all parameters. For saplings, interaction between parameters were slightly more prominent than for adults (saplings: $\sum S_{Ti} = 1.09$; adults: $\sum S_{Ti} = 1.03$) (Fig. 3-3, upper panels).

For the summarised pair-correlation function $g(r)_{summarised}$, the main effects of all parameters were fairly small for saplings and adults with sums of $\sum S_i < 0.1$ for both life-history stages. Total effects S_{Ti} (saplings: $\sum S_{Ti} = 1.1$; adults: $\sum S_{Ti} = 1.68$) exceeded the main effects S_i for all parameters. Thus, for the summarised pair-correlation function $g(r)_{summarised}$ as model output interaction between parameters were more important compared to the number of individuals (Fig. 3-3, lower panels).
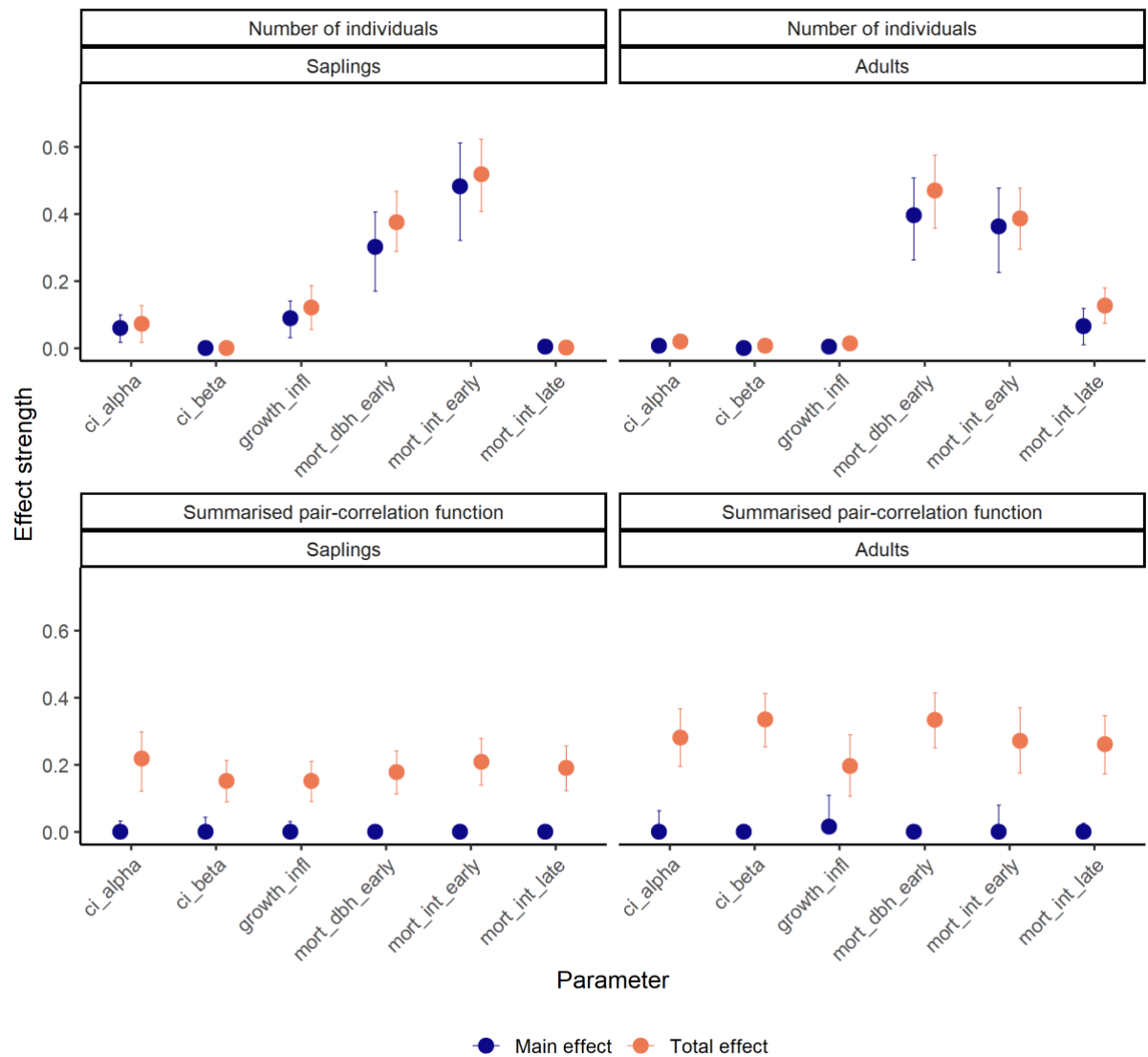
Figure 3-3: *Sobol' indices sensitivity analysis for the number of individuals and the summarised the pair-correlation function g(r)*_{summarised} *as model output for saplings and adults separately. A subset of important parameters indicated by a local one-at-a-time sensitivity analysis were used. To sample the parameters space, Latin hypercube sampling was used. The circles show the sensitivity index value, error bars 95% confidence intervals of 10000 bootstrap repetitions. Colours indicate main effect S_i (blue) and total effects S_{Ti} (orange).*

3.2 Model output

3.2.1 Non-spatial patterns

For the field data from 1999 - 2013, the number of individuals was relatively stable for adults and decreased for saplings by about 1000 individuals (Table 3-2). A similar trend was observed for the biotic model version. While the number of adult trees was more or less stable during the first 15 simulation years, the number of saplings decreased by about 1000 individuals. Interestingly, after 50 simulation

years this trend changed and the number of saplings increased, whereas the number of individuals decreased compared to the initialisation. Contrastingly, for the combined model version, both the number of saplings and well as the number of adults decreased in all simulation years. This decrease was even more prominent for saplings compared to adults (Table 3-2).

Table 3-2: *Number of Fagus sylvatica individuals for the field data and the biotic and combined model version separated by size group. Trees with a 1 < dbh ≤ 10 are classified as saplings, trees with a dbh > 10 cm as adults. The number of individuals for the model runs described the mean of 50 simulation runs as well as the standard deviation (parenthesis). Because field data was not available in 5-year steps, results were compared to the next nearest year steps of the simulation model.*

Year		Field data		Biotic model version		Combined model version	
Field data	Model data	Sapling	Adult	Sapling	Adult	Sapling	Adult
0	0	7049	6204	7049	6204	7049	6204
8	10	5790	6094	6036.36 (45.2)	6077.06 (18.2)	5565.54 (45.0)	6004.64 (16.4)
14	15	6080	6207	6091.96 (58.7)	6005.96 (22.1)	5230.56 (48.6)	5897.20 (21.2)
-	50	-	-	7953.42 (72.3)	5318.42 (25.8)	4137.40 (61.3)	5113.46 (27.3)

For the biotic model, there was a good fit of the relative dbh distribution between the model results and the field data. Only the relative frequency of trees with a dbh 10 ≤ dbh < 20 cm was slightly less for the biotic model version compared to the field data (Fig. 3-4). However, similar to the number of individuals, after 50 simulation years the relative frequency of trees with a dbh < 10 cm was higher for the biotic model version compared to the field data. While about 50% of all trees had a dbh < 10 cm in both censuses of the field data, about 60% were in the corresponding dbh class for the biotic model version. At the same time, for all other dbh classes the relative frequency for the biotic model version was smaller than for the field data (Appendix Fig. A3-5).

For the combined model version, the relative frequency of trees with a dbh < 10 cm was slightly less compared to the field. For all larger dbh classes the relative frequency for the combined model version showed a satisfactory fit between the model data and the field data (Fig. 3-4). Again, after 50 simulation

years discrepancies between the model data and the field data increased and the relative frequencies of trees with a dbh < 10 cm and a 10 ≤ dbh < 20 cm were smaller, while for all other dbh classes the relative frequency was slightly larger for the combined model version compared to the field data (Appendix Fig. A3-5).
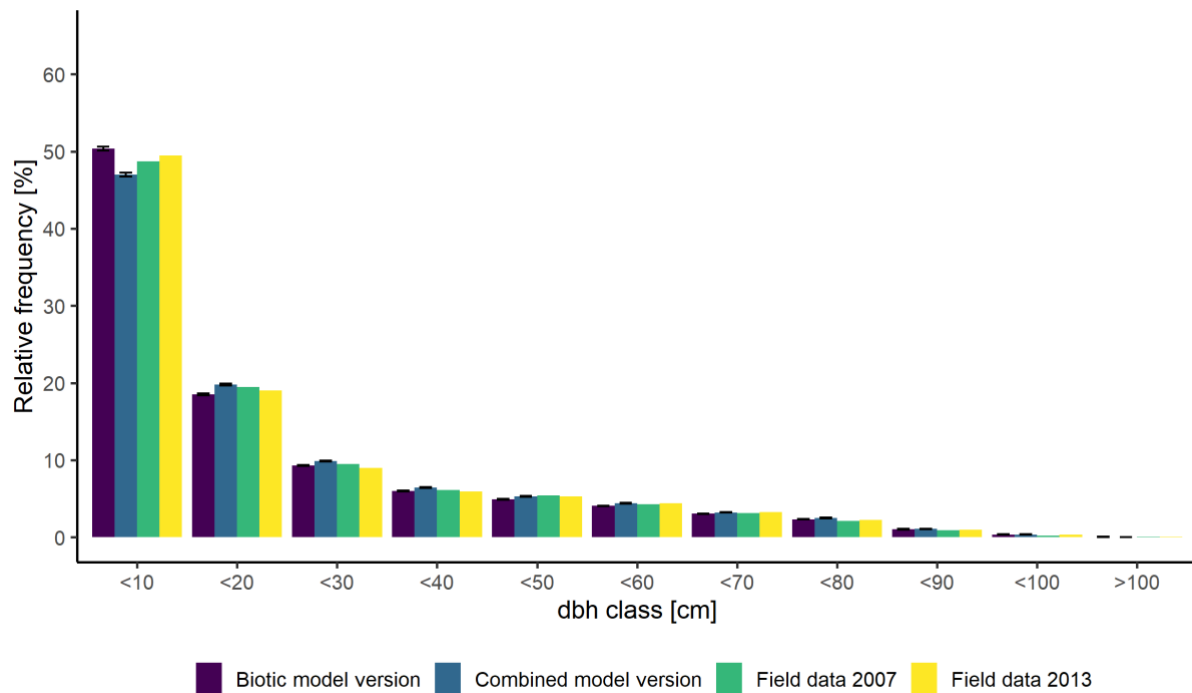

Figure 3-4: *Distribution of diameter at breast height (dbh) classes for the biotic and the combined model version after 15 simulated years and for field data of the censuses in 2007 and 2013. The dbh was classified using 10 cm classes. The last class included all trees with a dbh > 100 cm.*

The mean annual dbh growth did not differ between the biotic and the combined model version (Fig. 3-5). For both model versions the dbh growth of trees with a dbh < 10 cm at the start of the simulation was smaller compared to the field data. For the remaining dbh classes, there was a satisfactory agreement between the model data and the field data, even though the simulated dbh growth was always slightly less compared to the field data. While the field data showed a decrease of mean annual dbh growth for larger trees (dbh > 100 cm), no such decrease was observed for the model data. Consequently, the growth of large trees was larger for by both model versions compared to the field data (Fig. 3-5). However, this was based on only few individuals.
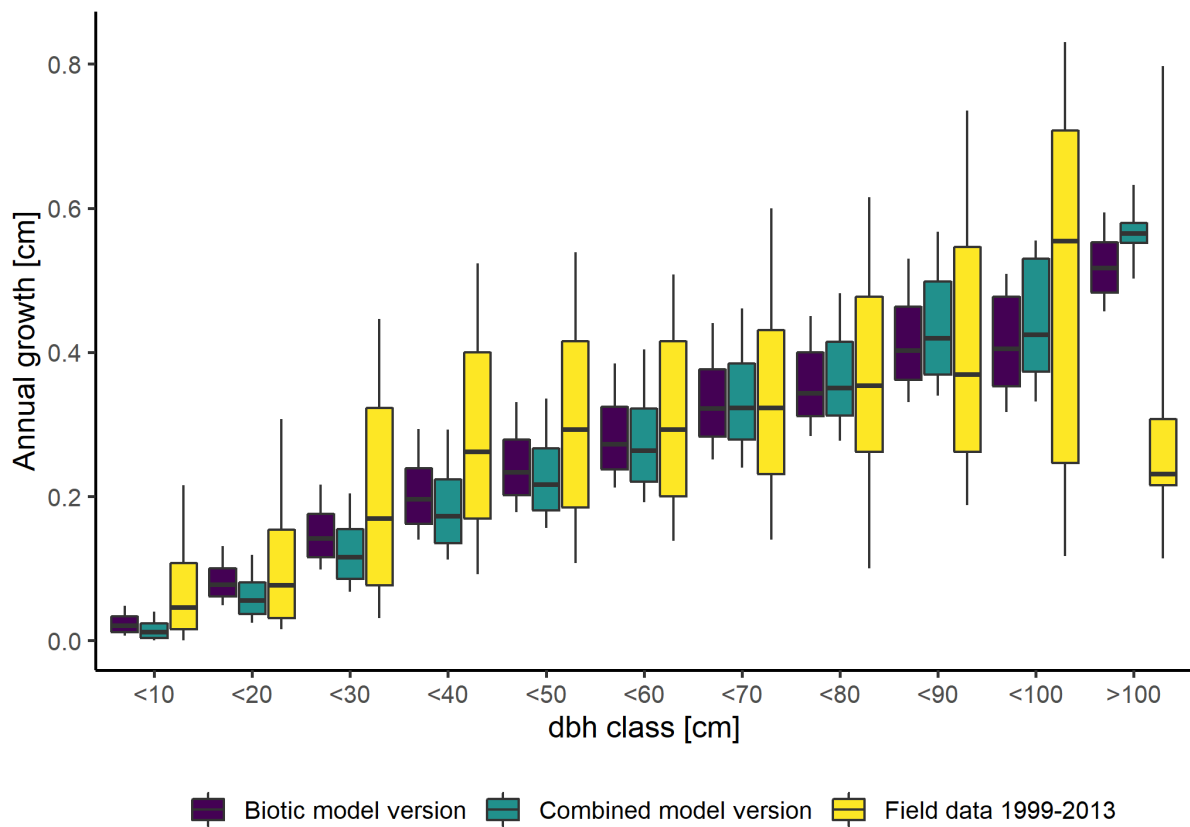
Figure 3-5: *Annual diameter at breast height (dbh) growth for 15 simulated years of the biotic and the combined model version as well as for the field data based on the censuses in 1999 and 2013. The boxes include the middle 50% of the data and the whiskers include 10 - 90% of the data. The median is represented by the solid line. Trees were classified to dbh classes (class width 10 cm) based on their dbh in 1999. The last class included all trees with a dbh > 100 cm.*

3.2.1 Spatial patterns

For the field data, competition values did not show clear differences between the censuses in 2007 and 2013, however, clear differences were apparent between different size groups with high competition values dominating the density of adult trees (Fig. 3-6). Both model versions resulted in distributions of competition values for adult trees comparable to each other. While the biotic model version fitted the field data well, the density peak of the combined model version was shifted towards higher competition values compared to the field data (Fig. 3-6). For saplings, both model versions resulted in less higher competition values ($c_{itrans} \approx 0.65$) compared to the field data (Fig. 3-6). After 50 simulation years, higher competition values for adults, but especially saplings were less present for both model versions compared to the field data (Appendix Fig. A3-6).
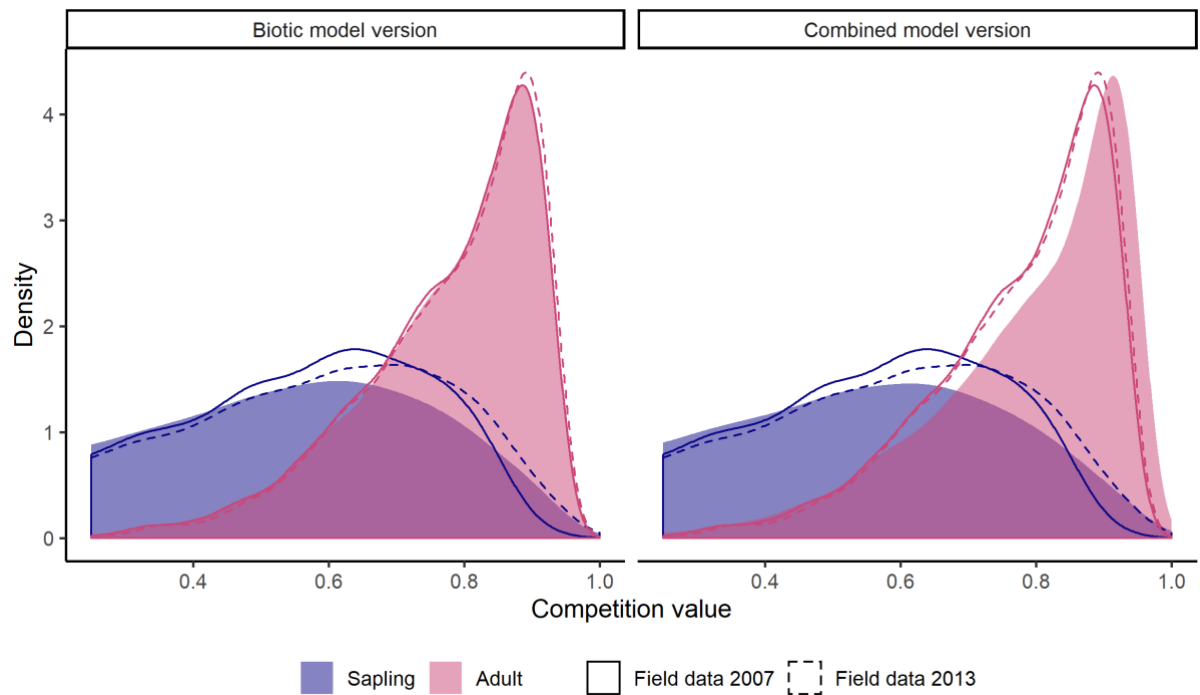
61

Figure 3-6: *Distribution of competition values for the biotic and combined model version after 15 simulated years (surfaces) and field data census in 2007 (solid line) and 2013 (dashed line). Colours indicate size groups; saplings (blue) are classified by a 1 < dbh ≤ 10 cm and adults (red) by a dbh > 10 cm.*

The pair-correlation function *g(r)* showed a clustered pattern at small distances *r* for saplings in both censuses, respectively. This clustering was stronger in 2013 compared to 2007 due to a few high-density clusters. Contrastingly, adults showed a segregated pattern at small distances *r* in the 2007 and 2013 censuses (Fig. 3-7). After 15 simulation years, the biotic model version indicated a segregated pattern of adults and a clustered pattern of saplings at small distances *r*. For larger distances, the patterns of both size groups tended towards complete spatial randomness (Fig. 3-7, left panel). Thereby, the clustering of saplings for the biotic model version was weaker than for the field data. This trend carried on with increasing simulation years and after 50 years the spatial characteristics of saplings resembled the spatial characteristics of adults, i.e. all clustering at small distances *r* disappeared (Appendix Fig. A3-7). Similar to the biotic model version, the combined model version indicated a segregated pattern for adult trees at short distances *r* as well. However, at medium and larger distances *r* the pattern showed weak aggregation regardless of the distance *r*. On the other hand, saplings were clustered at small distances *r* and tended towards complete spatial randomness with increasing distance *r*, similar to

the field data. Nevertheless, the strength of the clustering was slightly weaker for the combined model version compared to the field data (Fig. 3-7, right panel). Contrastingly to the biotic model, the clustering of saplings was still present for the abiotic model version after 50 simulations years. At the same time, the weak clustering of adults at medium and larger distances r increased (Appendix Fig. A3-7).
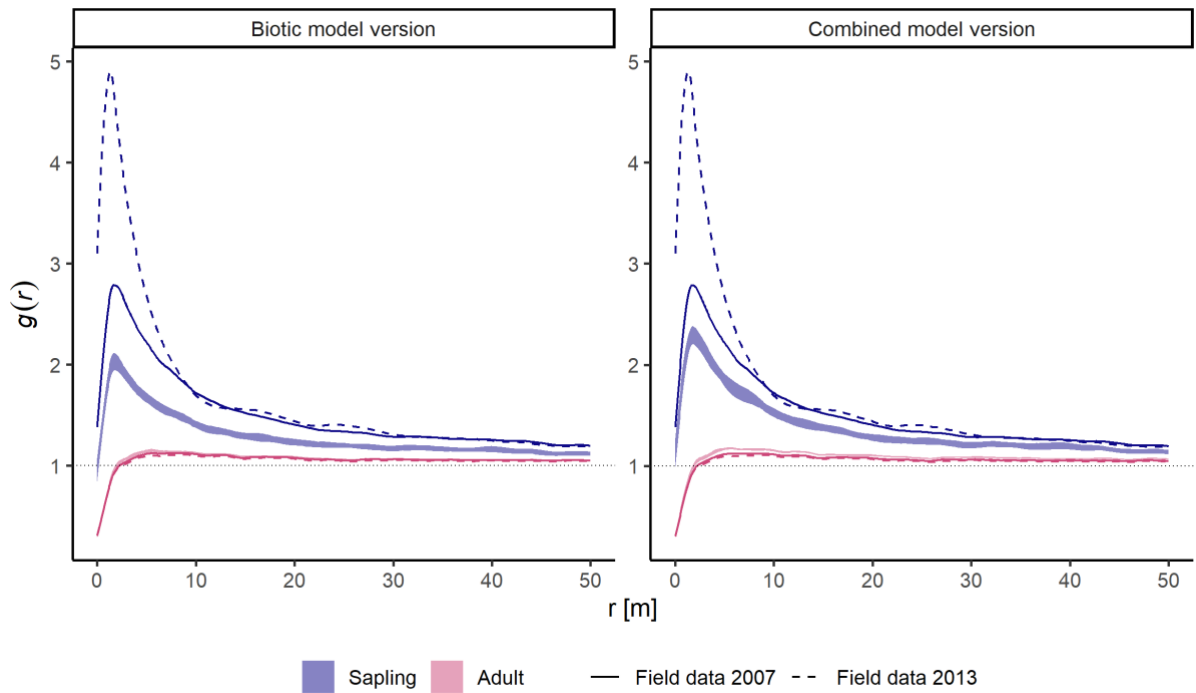

Figure 3-7: *Pair correlation function g(r) for the biotic model version and the combined model version (envelopes) after 15 simulation years and the field data censuses in 2007 (solid line) and 2013 (dashed line). Individuals are classified to size groups (sapling: 1 < dbh ≤ 10 cm, adult: dbh > 10cm) indicated by colour (saplings: blue; adults: red).*

For the field data, the negative correlation of the mark-correlation function $k_{mm}(r)$ at small distances r indicated that adult trees growing close to each other tended to be smaller. With increasing distance, this trend developed towards no correlation (randomness) at larger distances r. Interestingly, for saplings, there was a distinctive difference between the censuses in 2007 and 2013. Whereas the faintly negative correlation was independent of distance r in 2007, a negative correlation at short distances r as for adults was present in 2013 (Fig. 3-8). Both model versions were able to reproduce the mark-correlation function $k_{mm}(r)$ for adult trees after 15 simulation years compared to the field data. However, while the biotic model versions simulated a positive correlation for saplings, the combined model version

simulated only weak positive to no correlations for saplings at all. For the biotic model version, the positive correlation was the strongest at short distances r and decreased with increasing distance. For the combined model version, the dependency on distance r was comparable to the field data in 2007, however, with a random overall $k_{mm}(r)$ value (Fig. 3-8). After 50 simulation years the positive associations for saplings at small distance r increased for the biotic model version. Interestingly, a similar pattern developed for the combined model version at short distances r. At larger distances, the mark-correlation function $k_{mm}(r)$ tended towards no correlation (Appendix Fig. A3-8).
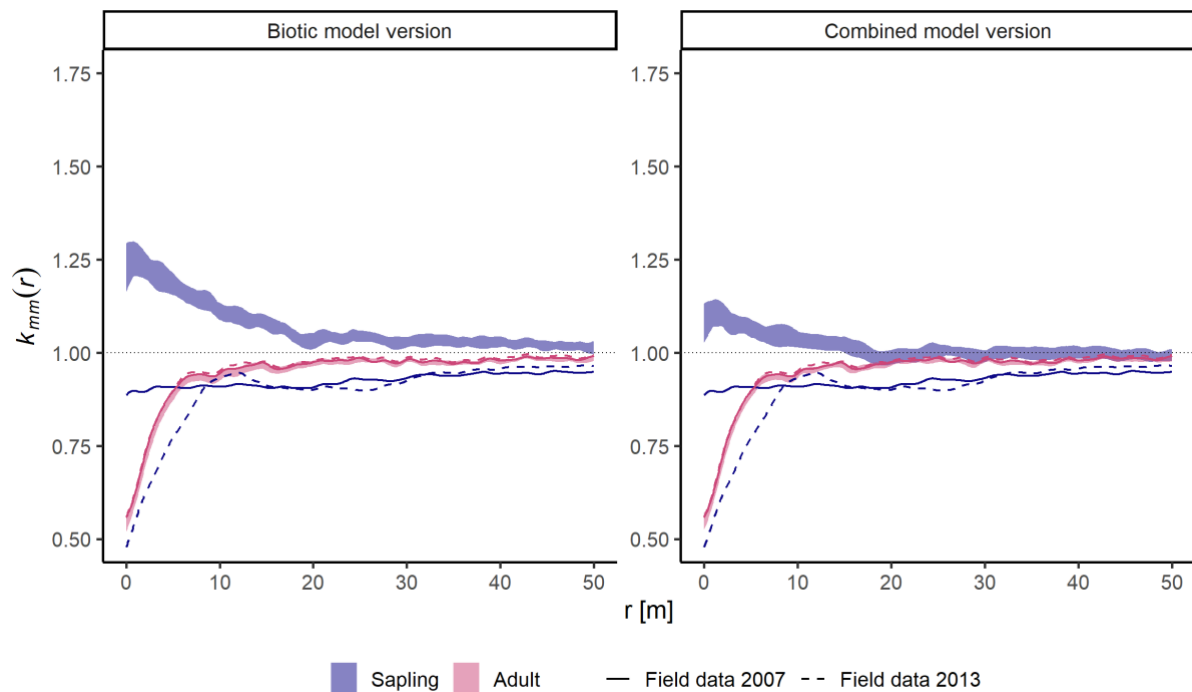

Figure 3-8: *Mark-correlation function $k_{mm}(r)$ for the biotic model version and the combined model version (envelopes) after 15 simulation years and the field data censuses in 2007 (solid line) and 2013 (dashed line). Individuals are classified to size groups (sapling: $1 < dbh \leq 10$ cm, adult: $dbh > 10cm$) indicated by colour (saplings: blue; adults: red).*

4. Discussion

We developed an individual-based simulation model to study the importance of abiotic processes, i.e. environmental heterogeneity, in a temperate old-growth forest dominated by *F. sylvatica*. While biotic process are important in temperate forests (Coates et al., 2009; Martínez and González-Taboada, 2009; Wang et al., 2010a; Zhang et al., 2014), abiotic processes have also been shown to influence

64

dynamics (Getzin et al., 2008; Shen et al., 2013; van Waveren, 2016). To study the importance of the contrasting processes, we developed two model versions, one including only biotic processes and one combining biotic and abiotic processes. To validate the model versions, we compared non-spatial and spatial model output to a forest dynamics plot. Even though former silviculture imprints are still present in the forest dynamics plot, the species composition and structure already developed towards and resembles an old-growth beech forest (Butler-Manning, 2007; Huss and Butler-Manning, 2006). Results showed that only the combined model version was able to simulate spatial patterns comparable to field data. Similar to our model, Jeltsch *et al.* (1998) showed that introducing environmental heterogeneity linked to tree establishment and survival improved their ability to model realistic and stable tree-grass coexistence in a savanna system compared to a first model version without abiotic processes (Jeltsch et al., 1998).

One basic requirement of pattern-oriented modelling was demonstrated by our study, namely that several non-spatial and spatial patterns on different hierarchical levels should be considered (Grimm et al., 2005; Janssen et al., 2009; Wiegand et al., 2003). While both model versions were able to fit one or two patterns satisfactorily, no model version was able to fit multiple patterns simultaneously; a circumstance also experienced by other studies (May et al., 2016, 2015). However, also the failure of the model versions can help to identify important (missing) ecological processes and questions that need further research (May et al., 2015). In our study, especially including spatial patterns was a powerful "filter" of non-realistic processes and helped to develop a more structurally realistic model (Wiegand et al., 2003). This also highlighted the importance of explicitly including scale and space into ecological analysis and modelling (Brown et al., 2011; Chase, 2014; Wallentin, 2017).

Basically, all processes in the model depended on the dbh. Thus, when introducing environmental heterogeneity, firstly only the growth process was modified. However, this did not lead to noteworthy changes of the model output. Environmental heterogeneity influences seedling survival and establishment (Beckage and Clark, 2003; Gómez-Aparicio, 2008; Lin et al., 2017; Terborgh et al., 2014) and preferred habitats exist for seedlings (Masaki et al., 2015). Similarly, also general mortality was

shown to be influenced by environmental heterogeneity (Getzin et al., 2008). Therefore, to simulate spatial model output comparable to the field data to a higher degree, we additionally modified seed establishment and the mortality process.

The combined model version required the calculation of environmental heterogeneity based on the intensity $\lambda(x,y)$ with two different standard deviations of the smoothing kernel σ (Baddeley et al., 2015). Thus, the parameter can be understood as a spatial scaling parameter of environmental heterogeneity. A smaller σ parameter was used for growth processes compared to seed establishment as well as the mortality process. Because mortality was most dominant for seedlings, this might reflect that habitat associations differ between different life-history stages (Comita et al., 2007; Lai et al., 2009) and site requirements change over ontogeny (Bertrand et al., 2011; Masaki et al., 2015). However, it is also possible that the intensity of adult trees as a proxy for suitable growing conditions throughout the study area (Getzin et al., 2008) did not reflect suitable growing conditions for seedlings and saplings.

On a population level, the biotic model was able to realistically simulate the number of individuals. Contrastingly, the combined model version resulted in a too small population size already during the first simulation years. Interestingly, differences between the model output and the field data became evident also for the biotic model version after the time period used for data fitting was exceeded (Holzwarth et al., 2013). The sensitivity analysis revealed that mortality is the most important process for the number of individuals. The accuracy of mortality models relies on the similarity between data used for model fitting and data used for model validation (Hülsmann et al., 2017). With increasing simulation years, this similarity might have decreased, leading to larger differences between model data and field data.

At the same time, both model versions were able to reproduce a relative dbh distribution similar to the field data. The dbh distributions were characterised by a high number of trees in smaller dbh classes and a decrease of trees with a larger dbh. Similar shaped diameter distributions can be found in European virgin beech forests (Westphal et al., 2006). This shows that even though the absolute number of individuals and mortality contradicted between both model versions and the field data, the relative dbh

structure could be simulated by both model versions with the exception of small dbh classes. Because mortality was most prominent in smaller dbh classes, again a too high mortality seemed to be the reason for the larger differences of the combined model version. Similar to the number of individuals, discrepancies increased with increasing simulation years. Because mortality was also the most influential process for the dbh distribution, the similarity between data used for model fitting and data used for model validation probably decreased and thereby the accuracy of the mortality model decreased (Hülsmann et al., 2017). Possibly because structural and spatial differences were larger between the biotic model version output and the field data compared to the combined model version, the discrepancies were larger for the biotic model version than for the combined model version.

Comparing spatial patterns showed increased inconsistencies between both model versions. Interestingly, even though the initialisation pattern was clustered at small distances *r* and seed dispersal was spatially limited, the biotic model version output showed a decrease of clustering already after 15 simulation years and even a mostly random pattern after 50 simulation years. Possible processes that could counteract a clustering of seedlings include increased competition or decreased survival probability of seedlings close to conspecific adult trees due to host-specific seed predators, herbivores and pathogens (Janzen-Connell hypothesis; Comita et al., 2014). However, the spatial pattern of *F. sylvatica* seedlings, saplings and understory trees was shown to be clustered at small distances (Janík et al., 2016; Kunstler et al., 2004; Nagel et al., 2006). This is often explained by spatially limited barochorous seed dispersal of the relatively heavy seeds of *F. sylvatica* (Wagner et al., 2010), leading to an increased number of seeds close to the source tree (Butler-Manning, 2007; Martínez and González-Taboada, 2009) and positive associations between seedlings and adult trees (Martínez et al., 2013). Yet, our model showed that limited seed dispersal could not maintain a clustered pattern of seedlings over a longer time period.

Positive and negative habitat associations reflect the idea that individuals are more or less frequent in certain habitats caused by habitat-related performance (Harms et al., 2001), which leads to clustering in favourable growing conditions (Shen et al., 2013). In temperate forests, positive and negative habitat

associations are present at the sapling stage (Hesselbarth et al., in prep.; Ye et al., 2011). Strong clustering at small distances r was only achieved over a longer simulation period when increased and decreased seed survival and mortality at favourable and unfavourable growing conditions was introduced for the combined model version. The strong clustering of the field data in 2013 was not reached, but this was caused by few high-density clusters for the field data. However, with increasing temporal extent, the clustering decreased for the combined model version. This might have indicated that with the used parameterisation, the influence of environmental heterogeneity was not strong enough on the spatial patterns of trees.

Adult trees showed a regular pattern at short distances r and a random pattern at medium and longer distances r as well as negative associations of the dbh at short distances r for the field data. Generally, this is related to competition, because density-dependent mortality leads to a maximisation of tree-to-tree distances and prevents large trees from neighbouring each other (Stoll and Bergius, 2005; Suzuki et al., 2008; Wälder and Wälder, 2008). Even though competition was high for adult trees for the abiotic model as well, the pair-correlation function $g(r)$ resembled "virtual aggregation" (Wiegand and Moloney, 2004). "Virtual aggregation" describes clustered spatial patterns with few or no individuals present in larger areas of the study area (Velázquez et al., 2016; Wiegand and Moloney, 2004). While including abiotic processes improved the model fit for saplings, the virtual aggregation of adults might indicated again that abiotic conditions and processes differ between saplings and adult trees (Comita et al., 2007; Ye et al., 2011). This was also supported by the sensitivity analysis showing that the sensitivity of both the non-spatial and spatial model outputs differed between saplings and adults.

The mark-correlation function $k_{mm}(r)$ for the biotic model version suggested facilitation effects for saplings at smaller distances r. The stress gradient hypothesis predicts that facilitation is more common in harsh environments (Callaway, 2007), but facilitation is also important under moderate conditions (Holmgren and Scheffer, 2010). However, competition, especially for light, was shown to be important for *F. sylvatica.* (Collet and Chenost, 2006; Wagner et al., 2009). The negative associations of the mark-correlation function of the field data rather suggested competition among saplings. Even though also the

combined model version indicated a positive correlation for saplings at small distances r, contrastingly to the biotic model version the correlation tended towards no correlation with increasing distance r. For the combined model version, competition values were marginally higher due to higher densities at suitable growing conditions. This might have led to decreased growth within these high-density clusters and following a lower mark-correlation function $k_{mm}(r)$ at short distances r. However, similar to the pair-correlation function $g(r)$, the influence of environmental heterogeneity on the spatial pattern might not have been strong enough with the used parametrisation.

We demonstrated in this study that the explicit consideration of environmental heterogeneity resulted in a better agreement between model data output and field data of a temperate old-growth forest. The first implementation and parametrisation of the individual-based simulation model presented here allows further improvements of the model as well as further research questions. Pattern-orientated modelling can be a powerful tool to parametrise the model (Grimm et al., 2005; Wiegand et al., 2003). Especially the seed dispersal and establishment process would benefit from further optimisations of the parameters using field data. This could also include e.g. long-distance dispersal events by animals (Martínez and González-Taboada, 2009). Related to this, another improvement could be to physically restrict successful seedling establishment at locations a tree is already growing.

Another possible improvement of the model could be a different competition kernel. Especially for larger trees, the annual dbh growth was larger for both model versions compared to the field data. Because larger trees were mostly neighboured by smaller trees and distances between larger trees were generally greater (Appendix Fig. A3-9), one possible explanation was a too short-sighted competition kernel. This could have resulted in a too small growth reduction for larger trees. However, another commonly used competition kernel (Uriarte et al., 2004) resulted in a similar shape, but was even more short-sighted. Thus, a completely different kernel shape (e.g. sigmoidal) might be worth considering. Alternatively, a higher influence of smaller trees on larger trees could be an improvement of the used competition kernel.

As already discussed, using the intensity of adult trees might not have been a good proxy for the growing conditions of seedlings and saplings. Therefore, using different ways to characterise environmental heterogeneity would be another possible improvement. For this, it would be possible to use non-linear scaling approaches for the intensity layer or different layers for different size groups. Of course, not using the intensity as a proxy, but meaningful field data describing soil conditions to characterise the growing conditions would be the most desirable possibility to characterise environmental heterogeneity (Chang et al., 2013).

As a next step, extending the model to a multi-species setting would allow the study of questions related to species coexistence (Hart et al., 2017; Masaki et al., 2015). In this context, because tree growth was shown to be influenced differently by intra- and interspecific competition of neighbouring trees (Canham et al., 2006; Coates et al., 2009; Ratcliffe et al., 2015), the importance and influence of intra- and interspecific competition between individuals on the spatial model output would be of interest.

In conclusion, the comparison between the biotic and combined model versions showed that especially spatial patterns could not be matched by the biotic model version. Only including environmental heterogeneity and a modification of almost all processes considering this heterogeneity produced a satisfactory fit to spatial patterns of field data from a temperate old-growth forest. This was mainly related to processes of earlier life-history stages, namely to seed establishment and survival of seedlings and saplings under favourable growing conditions.

Acknowledgments

Chapter 4 - *landscapemetrics*: An open-source *R* tool to calculate landscape metrics

Abstract

Quantifying landscape characteristics and linking them to ecological processes is one of the central goals of landscape ecology. Landscape metrics are a widely used tool for the analysis of patch-based, discrete land-cover classes. Existing software to calculate landscape metrics has several constraints, such as being limited to a single platform, not being open-source, or involving a complicated integration into large workflows. We present *landscapemetrics*, an open-source *R* package that overcomes many constraints of existing landscape metric software. The package includes an extensive collection of commonly used landscape metrics in a tidy workflow. To facilitate the integration into large workflows, *landscapemetrics* is based on a well-established spatial framework in *R*. This allows pre-processing of land-cover maps or further statistical analysis without importing and exporting the data from and to different software environments. Additionally, the package provides many utility functions to visualise, extract, and sample landscape metrics. Lastly, we provide building-blocks to motivate the development and integration of new metrics in the future. We demonstrate the usage and advantages of *landscapemetrics* by analysing the influence of different sampling schemes on the estimation of landscape metrics. In so doing, we demonstrate the many advantages of the package, especially its easy integration into large workflows. These new developments should help with the integration of landscape analysis in ecological research, given that ecologists are increasingly using *R* for the statistical analysis, modelling, and visualisation of spatial data

1. Introduction

Understanding how landscape characteristics affect ecological processes and the spatial distribution of species and communities is central to ecology (Kupfer, 2012; Turner, 2005, 1989). Thereby, one major challenge is how to describe and quantify landscape characteristics (Lausch et al., 2015; Turner,

2005). Typically, landscapes are characterised as discrete patches of different land-cover classes (Forman, 1995; Forman and Godron, 1986; Wiens, 1995) which has several benefits. These include a straightforward application and communication (Lausch et al., 2015; McGarigal et al., 2009), especially in human-dominated landscapes where the distinction between different land-cover classes is rather clear-cut (Lausch et al., 2015). While other landscapes may be better described by a gradient-based description of landscape structure (Cushman et al., 2010; McGarigal et al., 2009), the landscape-mosaic model remains the dominant paradigm (Kupfer, 2012; With, 2019).

To quantify the composition (number and abundance) and configuration (spatial arrangement) of different land-cover classes, numerous landscape metrics have been developed and extensively applied to the analysis of landscape structure (Gustafson, 2019, 1998; Uuemaa et al., 2013). Such landscape metrics are commonly used to facilitate comparisons among different landscapes; to quantify how landscapes change over time, especially in response to different types of disturbances or land-use pressures; and to investigate the relationship between landscape characteristics and other ecological patterns (Uuemaa et al., 2009). Some recent examples of these sorts of applications include studies of how landscape characteristics of temperate forests differ between years of low and high natural disturbance activities (Senf and Seidl, 2018), how land-use intensity affects agricultural landscapes and associated biodiversity (Decaëns et al., 2018), and how distributional patterns of birds with different habitat affinities are related to landscape heterogeneity (Herrera et al., 2018).

One commonly used software to calculate landscape metrics is the stand-alone software *FRAGSTATS* (McGarigal et al., 2012). First published in 1995, *FRAGSTATS* was the first software to provide an extensive collection of landscape metrics, and subsequently, revolutionised landscape pattern analysis (Gustafson, 2019; Kupfer, 2012). However, ecologists are increasingly turning to *R* (Sciaini et al., 2018), a language originally developed for statistical computing (R Core Team, 2019). Nowadays, *R* is more and more used for the analysis, modelling, and visualisation of spatial data (e.g. Fletcher and Fortin, 2018). One benefit of *R* is its active community that constantly develops software packages for specific tasks. The *R* package *SDMTools* (VanDerWal et al., 2019) includes a small subset of landscape

metrics, but until now there is no comprehensive, dedicated *R* package to calculate landscape metrics. Therefore, the development of new software that facilitates the application of landscape metrics is still necessary to keep pace with the changing needs and expectations of ecologists wanting to perform landscape analysis.

Here, we present *landscapemetrics*, an extensive collection of widely used landscape metrics for the analysis of discrete land-cover maps, including the most commonly used metrics (Cushman et al., 2008; Lustig et al., 2015; Schindler et al., 2008), as well as some recent ones (e.g. joint entropy; Nowosad and Stepinski, 2019). To demonstrate its application, we present an analysis of how different sampling schemes influence the estimation of landscape metrics using neutral landscape models that vary in spatial autocorrelation by adopting a virtual ecologist approach (Zurell et al., 2010; Appendix Fig. A4-1).

2. The *R* package *landscapemetrics*

The core of *landscapemetrics* comprises functions to calculate landscape metrics and uses raster data as input. Therefore, the package is mainly based on the well-established *raster* package (Hijmans, 2019), but the use of next-generation frameworks is also possible (*stars* package, Pebesma, 2019).

At present, *landscapemetrics* primarily includes the so-called *FRAGSTATS*-style metrics (Kupfer, 2012; McGarigal et al., 2012), but other types of metrics are planned for future updates. The current software version includes metrics on all available levels, namely patch-, class-, and landscape-level. Patch-level metrics describe every patch in a landscape (a patch being defined as contiguous cells belonging to the same land-cover class). Class-level metrics describe all patches belonging to a certain land-cover class. Lastly, landscape-level metrics describe the characteristics of the entire landscape (McGarigal et al., 2012). Additionally, landscape metrics can be classified according to the characteristics of the landscape they (conceptually) describe (McGarigal et al., 2012; Šímová and Gdulová, 2012). *landscapemetrics* includes area and edge metrics, shape metrics, core area metrics, aggregation metrics, diversity metrics, as well as complexity metrics. For a full list of all metrics, see the package documentation (<https://r-spatialecology.github.io/landscapemetrics>).

2.1 Improvements over existing software tools

Though popular, *FRAGSTATS* has certain drawbacks (Table 4-1). As a stand-alone software, it requires data import to the software for integration into large workflows. If the resulting metrics are the basis for further analysis, they must then be exported to yet another program. Additionally, the analysis of several input layers or the use on high-performance clusters is rather laborious. Also, *FRAGSTATS* is not open-source software and only available for *Windows* operating systems. This can complicate transparency and reproducibility of the analysis workflow, and collaboration among researchers using different computing platforms.

Contrastingly, *R* is open-source and available for most common operating systems (including *Windows*, *macOS,* and *Linux*). The existing *R* package *SDMTools* calculates a limited number of landscape metrics, and thereby overcomes some of the above-mentioned limitations of *FRAGSTATS*. But, as this package was primarily developed for species distribution modelling rather than landscape analysis, it cannot fully replace *FRAGSTATS* (Table 4-1). The use of the package for landscape analysis is rather cumbersome. To calculate patch-level metrics, the data must first be converted to a matrix and a loop through all land-cover classes implemented (Example 4-1). Furthermore, *SDMTools* does not permit a sub-selection of metrics and no further parameterisation of metrics is possible. Additionally, the user must specify the cell resolution manually for all area- and distance-related calculations, introducing a possible error source. Also, the output format makes integration of the results into large workflows difficult. Lastly, to our knowledge, *SDMTools* is not actively developed anymore.

Table 4-1: *Main characteristics and features of FRAGSTATS, SDMTools and landscapemetrics. The available metric levels are abbreviated: p = patch level, c = class level, l = landscape level.*

Characteristics	FRAGSTATS	SDMTools	landscapemetrics
open-source software	no	yes	yes
cross-platform compatibility	no	yes	yes
available metric levels	p, c, l	p, c	p, c, l
parametrisation of metrics	yes	no	yes
tidy data format	no	no	yes
easy integration into workflows	no	no	yes
utility functions	sampling	no	various
restrictions due to numeric precision	yes[1]	no	no

[1]FRAGSTATS does not allow a cell resolution <0.005 map units of the input raster.

landscapemetrics provides an extensive collection of widely used landscape metrics for discrete land-cover maps, including most of the commonly used metrics used in landscape analysis (Cushman et al., 2008; Lustig et al., 2015; Schindler et al., 2008), as well as some recent ones (e.g. joint entropy; Nowosad and Stepinski, 2019). Because *landscapemetrics* is written in the *R* programming language, it operates across operating platforms. Given the variety of *R* packages, this also enables the user to run the software easily in parallel or on high-performance clusters. To ensure integration into large workflows, *landscapemetrics* is based on a well-established spatial framework in *R* (mainly the *raster* package). This allows pre-processing of data, calculation of metrics, and further analysis of the results, all within the same software environment. This also facilitates its usage with other spatial objects in *R* (e.g. *sp* spatial points, Pebesma and Bivand, 2005). Additionally, the use of raster data has advantages in having all required spatial information included and eliminating possible error sources, such as a misspecified cell size. To simplify integration further, the output of all metric functions is tidy (sensu Wickham, 2014) and type stable, meaning the returning data frame is identically structured regardless of the level or metric (Table 4-2). This facilitates reproducible workflows (Sandve et al., 2013). The package is open-source, which allows users to comprehend and improve upon existing metrics, as well as to contribute new functions. All functions were designed to calculate landscape metrics in a

straightforward way (Example 4-1). Lastly, the package provides several utility functions (Table 4-3) to facilitate visualisation, extraction, sampling, and development of metrics.

2.2 Calculation of landscape metrics

The first step of every analysis should be a check if the input raster is suitable for *landscapemetrics* using `check_landscape()`. The function checks if the coordinate reference system is projected, if the cell units are in meters, if the classes are decoded as integer values, and if the number of different values is reasonable (in other words if discrete land-cover classes are present). In case the input is not or only partially suitable, a corresponding warning is produced. This means that a calculation of metrics is still possible, but some results must be interpreted with caution (e.g. area- and distance-related metrics).

To get an overview of all available metrics, *landscapemetrics* provides the function `list_lsm()`. It is possible to specify metrics by name, level, and/or type. Of course, all specifications can be combined. Also, rather than a data frame, it is possible to return a vector with function names. For example, the vector format makes it straightforward to get only the function names of all patch- and class-level aggregation metrics for later use by `list_lsm(level = c("patch", "class"), type = "aggregation metric", simplify = TRUE)`.

All functions to calculate landscape metrics are consistently named in *landscapemetrics*. Functions to calculate a given metric have the prefix "`lsm_`" followed by an abbreviation for the level ("`p`", "`c`" or "`l`" for patch-, class- and landscape-level, respectively) and lastly for the metric itself. For example, the class area for each land-cover class is calculated simply by `lsm_c_ca()`. All functions can handle several landscapes as input (either a list of RasterLayers or a RasterStack/RasterBrick).

Several metrics, regardless of the level, can easily be combined into one data frame because the resulting output is always an identically structured data frame (Table 4-2). Therefore, the results of the desired metrics can be combined using, for example, `rbind(lsm_p_area(x), lsm_l_ai(x))`. Because all output is tidy following widely accepted data science standards, further analysis of the resulting data frame is possible without laborious data import/export or formatting (see Section 3).

77

Table 4-2: Structure of the output table used for all metrics in landscapemetrics. The output is type stable, which simplifies integration into larger workflows.

layer	level	class	id	metric	value
<integer>	<character>	<integer>	<integer>	<character>	<double>
ID of landscape	Level of metric	ID of class; NA for landscape level	ID of patch; NA for class and landscape level	Abbreviation of metric	Value of metric

Many functions provide additional parametrisation, such as the edge depth or the cell neighbourhood rule for patch delineation. For example, to change the patch delineation rule for the patch area, only the argument `directions` must be changed from its default using the "queen's case" (eight neighbouring cells) to the "rook's case" (four neighbouring cells), i.e. `lsm_p_area(x, directions = 4)`. Of course, all arguments are consistently named across metrics.

```
library(dplyr)

library(landscapemetrics)

library(SDMTools)

library(raster)


#### SDMTools ####

result_patch <- list() # preallocate list

classes <- unique(landscape) # all present classes


# loop through all classes

for(i in seq_along(classes)) {

    landscape_matrix <- as.matrix(landscape) # convert to matrix

    landscape_matrix[landscape_matrix != i] <- 0 # binarize landscape

    landscape_matrix[landscape_matrix == i] <- 1 # binarize landscape

    ccl <- ConnCompLabel(landscape_matrix) # get patches

    result_patch[[i]] <- PatchStat(ccl, cellsize = 1) # patch metrics

}


result_patch <- bind_rows(result_patch,

                          .id = "classID") # combine to one df


result_patch <- filter(result_patch,

                       patchID != 0) # only present classes


area_SDM <- result_patch[, c(1, 2, 7)] # select only area

perim_SDM <- result_patch[, c(1, 2, 9)] # select only perimeter


#### landscapemetrics ####

area_lsm <- lsm_p_area(landscape) # calculate patch area

perim_lsm <- lsm_p_perim(landscape) # calculate patch perimeter
```

Example 4-1: *Comparison of SDMTools and landscapemetrics workflows to calculate patch area and patch perimeter. SDMTools requires a loop through all present land-cover classes and a binarisation of the input to 1 for the current class and 0 for all other classes. Also, the desired metrics must be filtered from the resulting data frame.*

The `calculate_lsm()` wrapper can be used to calculate several metrics simultaneously. Similar to `list_lsm()`, this wrapper allows specifying a subset of metrics using the name, level, and/or type, such as `calculate_lsm(x, level = "landscape", type = "diversity metric")`. Alternatively, a vector (e.g. previously created using `list_lsm()`) with function names can be provided as `what`-argument. The returning data frame is identical to the output of all single metric functions.

2.3 Utility functions

An additional advantage of *landscapemetrics* over existing software tools for landscape analysis lies in its utility functions (Table 4-3). These functions are designed to facilitate the application, visualisation, extraction, sampling, and development of landscape metrics.

Visualisation functions, which help to understand and communicate metrics, start with the prefix "`show_`" followed by the subject to visualise. It is possible to include either all classes in one plot (`class = "global"`), all classes but each plotted separately (`class = "all"`), or just selected classes (`class = c(1, 3)`). Patches in a landscape can be visualised by `show_patches()` (Fig. 4-1B), or to visualise only the core area, there is `show_cores()` (Fig. 4-1C). Additionally, patches can be filled with the value of any patch level metric, such as the patch area using `show_lsm(x, what = "lsm_p_area")`. It is also possible the get the result as a RasterLayer, using `spatialize_lsm()`. In the returning RasterLayer, each cell has the value of the corresponding patch for any chosen metric. Correlations between metrics can be problematic (Cushman et al., 2008; Nowosad and Stepinski, 2018; Schindler et al., 2008) and the selection of mainly uncorrelated metrics can be a challenge. Providing a data frame with metric results, `show_correlations()` returns a correlation matrix plot.

Table 4-3: *Overview of utility functions in the landscapemetrics package.*

Area of application	Function name	Description
Visualisation	show_patches()	Plot patches in the landscape
Visualisation	show_cores()	Plot core areas in the landscape
Visualisation	show_lsm()	Plot landscape filling cells with patch level metric value
Visualisation	show_correlation()	Show correlation between metrics
Sampling	sample_lsm()	Sample metrics in a buffer around sample points
Sampling	extract_lsm()	Extract landscape metric of patches enclosing sample points
Sampling	window_lsm()	Moving window analysis
Building block	get_adjacencies()	Get class cell adjacencies
Building block	get_boundaries()	Get boundary cells of patches
Building block	get_circumscribingcircle()	Get diameter of the smallest circumscribing circle around patches
Building block	get_nearestneighbour()	Get minimum Euclidean distance between classes
Building block	get_patches()	Patch delineation
Various	check_landscape()	Check if input fulfils package requirements
Various	list_lsm()	List all available metrics
Various	spatialize_lsm()	Assign patch metric to each cell

There are several functions to sample landscape metrics. Sample locations can be provided either as a matrix including x- and y-coordinates or as *sp*-objects and for all sampling functions, the metrics can

be specified similar to `list_lsm()`. The function `extract_lsm()` returns the patch-level metric values of each patch in which sample points are located. To calculate metrics in a buffer around sample points, `sample_lsm()` can be used, allowing to specify the shape (circle, square, or rectangle) and the area of buffers around sample points, and then calculates the specified metrics. Landscape metrics are known to be scale dependent (Lausch and Herzog, 2002; Lustig et al., 2015; Wu, 2004) and using a moving window can be an approach to deal with this (e.g. Su et al., 2011). The moving window assigns to each focal cell in the landscape the metric value of its local neighbourhood specified by a neighbourhood matrix (McGarigal et al., 2012). The resulting raster describes the landscape in regard to the local variability of the chosen metric (Hagen-Zanker, 2016). Within *landscapemetrics*, a moving window approach can be applied by using `window_lsm()`. The local neighborhood can be specified using, for example, `window <- matrix(1, nrow = 5, ncol = 5)`, followed by `window_lsm(x, window = window, what = c("lsm_l_pr", "lsm_l_joinent"))`.
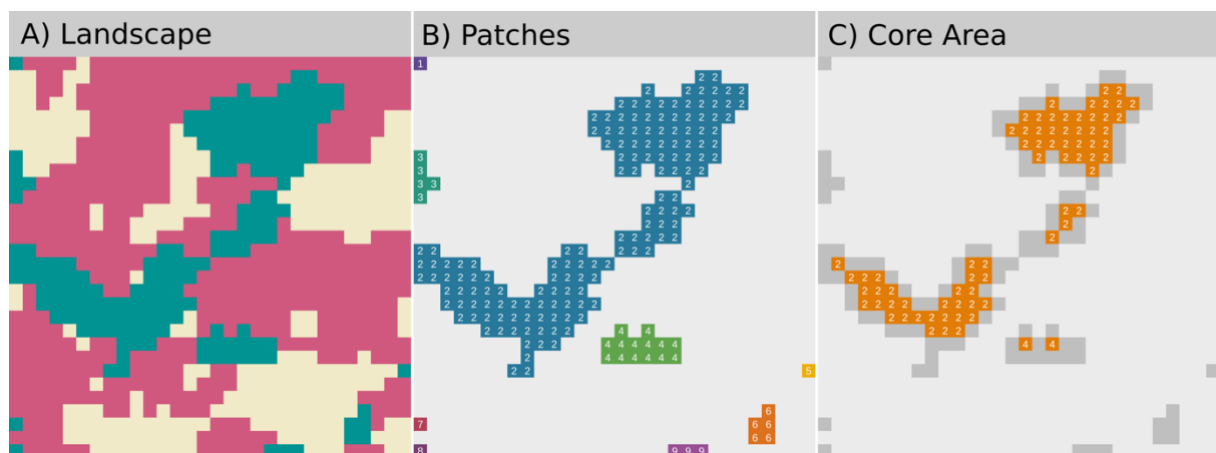
Figure 4-1: *Visualisation of an example landscape (a) using the utility functions* `show_patches()` *(b) and* `show_cores()` *(c) for a selected class.*

Lastly, *landscapemetrics* provides several building-blocks to develop and contribute new metrics. These functions all start with the prefix "`get_`" and are mainly computationally fast *C/C++* implementations of common raster procedures. Of these, `get_patches()` is the most fundamental, as it returns all connected cells as patches and is used in most metrics. Another useful function is `get_adjacencies()`, which returns the adjacency matrix of all cells, and is easier to use, faster, and more memory efficient than its equivalent in the *raster* package (Example 4-2). Finally,

`get_nearestneigbhour()` returns the minimum Euclidean distance between patches of the same class, and `get_circumscribingcircle()` returns the diameter of the smallest circumscribing circle around each patch.

```
library(landscapemetrics)

library(dplyr)

library(bench)


#### raster ####

adj_raster <- function(x) {

    # get cell ids of neighboring cells

    adjacencies <- raster::adjacent(x, cells = 1:raster::ncell(x))

    # table of values of neighboring cells

    table(x[adjacencies[, 1]], x[adjacencies[, 2]])

}


adj_raster(landscape)


#### landscapemetrics ####

get_adjacencies(landscape)


#### benchmark of both options ####

mark(adj_raster(landscape),

     get_adjacencies(landscape),

     iterations = 10000, check = FALSE)


# A tibble: 2 x 3

  expression                     mean      mem_alloc

  <chr>                          <bch:tm>  <bch:byt>

1 adj_raster(landscape)          8900 µs    1470 KB

2 get_adjacencies(landscape)      562 µs       6 KB
```

Example 4-2: *Comparison between raster and landscapemetrics to get the cell adjacency matrix of a raster. Not only is the landscapemetrics solution much easier, but it is also computationally faster and more memory efficient. The benchmark was done on Windows 10 (32 GB RAM, Intel i7 core, 3.4 GHz), using R 3.5.1 and 10000 iterations of each function.*

3. Use Case

Here, we aim to demonstrate some of the advantages of the package, especially its easy integration into large workflows. To this end, we apply *landscapemetrics* to analyse the effect of different sampling schemes on the estimation of landscape metrics. All code to reproduce the use case can be found at <https://zenodo.org/record/2597976>.

Although the collection, processing, and analysis of spatial data across landscape and regional scales has become commonplace, ecologists still need to subsample data from a larger landscape. Possible reasons are atmospheric conditions, logistical or budget constraints, or the use of unmanned aerial vehicles, resulting in high-resolution imagery but with limited extent (Getzin et al., 2012). Even though landscape metrics are known to be sensitive to various scaling issues (Lausch and Herzog, 2002; Lustig et al., 2015; Wu, 2004), the quality of the sample mean as an estimator has only been investigated for a subset of metrics and specific sampling schemes (Hassett et al., 2012; but see Ramezani et al., 2010; Ramezani and Holm, 2011).

We used the virtual ecologist approach (Zurell et al., 2010; Appendix Fig A4-1) which can be summarised in four major steps: *i)* a virtual ecological simulation model of an ecosystem (or landscape, in this case), *ii)* a virtual sampling process, sampling data from the virtual ecosystem or landscape, *iii)* analyses of the sampled data, and *iv)* an evaluation of the results against the true value for the full virtual ecosystem or landscape (Zurell et al., 2010). Following this approach, we first simulated neutral landscapes (500×500 cells) containing five classes (relative proportion of 20% each) with either low, medium, or high spatial autocorrelation, respectively (*NLMR* package, Sciaini et al., 2018). For each landscape, we calculated all available landscape-level metrics that were invariant to the absolute plot area (Appendix Table A4-1). Within each landscape, we sampled data using all 54 possible combinations of plot size, landscape area sampled, plot shape, and spatial arrangement (Table 4-4). We used the sample mean to estimate the landscape properties for the whole landscapes and evaluated the estimated metrics against the true metrics using the root-mean-square error (RMSE, Hyndman and Koehler, 2006) normalised by the mean as $nRMSE = \frac{\sqrt{\frac{Var(\bar{x})}{n-1}+(\bar{x}-\mu)^2}}{\bar{x}}$.

Table 4-4: Components of the sampling scheme. All 54 possible unique combinations were used for the analyses.

Size [cells]			Sampled landscape [%]			Shape			Arrangement	
2500	7500	20000	~10	~35	~75	Rectangle	Square	Circle	Random	Regular

The metrics "area_cv", "area_sd", "core_cv", "core_sd", "lsi", and "mesh" were estimated with a *nRMSE* > 125% for all sampling schemes and spatial autocorrelations, and were thus removed from further analyses. In general, we found that the accuracy and precision of the estimator decreased with increasing spatial autocorrelation (Fig. 4-2). Across all metrics and spatial autocorrelations, the median *nRMSE* decreased slightly as the area sampled increased (Fig. 4-2A). The median *nRMSE* across all metrics and spatial autocorrelations was similar among plot shapes, but the extreme deviations slightly increased for square and circular plots with increasing spatial autocorrelation (Fig. 4-2B). Finally, the spatial arrangement of plots had no clear influence on accuracy and precision of the estimator (Fig. 4-2C).

We found that most landscape metrics were able to provide a fairly accurate and precise assessment of landscape structure for landscapes with a low spatial autocorrelation, likely because individual plots captured more of the inherent spatial heterogeneity present within the overall landscape (Hassett et al., 2012; Wiens, 1989). Accuracy and precision decreased with increasing spatial autocorrelation, likely due to increasing between-plot variability (Hassett et al., 2012). Accuracy and precision of the estimator increased as the area sampled within the landscape increased because estimators increasingly converged on the true landscape value. Although this has been found by others (Ramezani and Holm, 2011), the influence was smaller than expected, perhaps because the same region of the landscape might have been resampled due to overlapping sample plots. There were no clear differences between the three plot shapes investigated (rectangular, circular, square). When spatial autocorrelation was low, the "salt and pepper" properties of the landscapes were adequately captured by all plot shapes. Contrastingly, with increasing spatial autocorrelation, rectangular plots provided a slightly more accurate and precise estimation of landscape properties than did circular and square plots. Most likely, rectangular plots

captured more spatial heterogeneity. A similar effect can be observed for species richness counts, where more species can be found in elongated plots (Güler et al., 2016). Both regular and random arrangements of sampling plots were able to capture landscape properties similarly well. This is not surprising for landscapes with a low spatial autocorrelation, because the finer scale of heterogeneity means all sampling distributions should perform similarly. However, in landscapes with high spatial autocorrelation, a regular sampling array should better capture landscape structure than a random sampling scheme, given the coarser scale of heterogeneity (Ramezani et al., 2010).
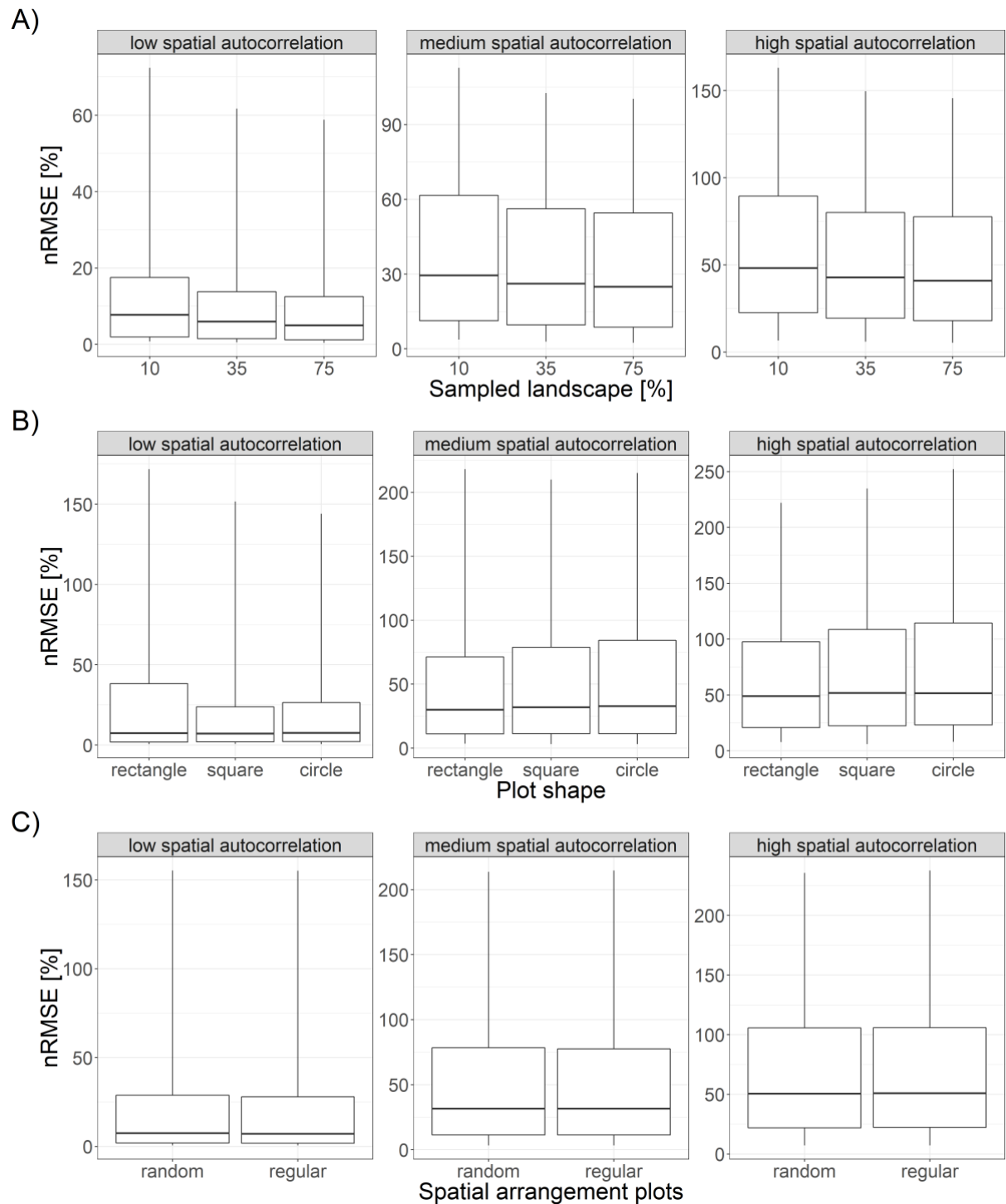
Figure 4-2: *Normalised root-mean-square error (nRMSE) for different sampling schemes. The nRMSE is summarised for all metrics and sampling schemes components not present on the corresponding x-axis. For a) the sampled landscape is increased, for b) different sampling plot shapes, and for c) different spatial arrangements of sampling plots are used. The solid lines represent the median, the boxes the middle 50% of the data and the whiskers include 1% to 99% of the data. The y-scales differ among panels to highlight differences between the sampling schemes.*

4. Discussion

The use case demonstrated many advantages of the *landscapemetrics* package, especially the easy integration into large analysis workflows without the need of importing/exporting to or from different software environments. This also facilitates usage in combination with other spatial *R* packages, such as *raster, sp*, or *NLMR*.

Although the aimless calculation of landscape metrics is not recommended (Gustafson, 2019), in cases where many metrics need to be calculated, *landscapemetrics* can calculate these with ease either in parallel or on high-performance clusters. This lessens one disadvantage of *landscapemetrics* being computationally slower for the calculation of some landscape metrics compared to *FRAGSTATS* and *SDMTools*. The use of *landscapemetrics* in parallel computing or on high-performance clusters can also be a huge advantage for studies where only a small number of metrics need to be calculated, but for many landscapes, as in the use case demonstrated here with its large factorial design (see section 3).

The type-stable and tidy output also allows users to process results without much data formatting, using data manipulation packages such as *dplyr* (Wickham et al., 2019), and furthermore, to produce figures using plotting packages such as *ggplot2* (Wickham, 2016).

Finally, being open-source and hosted on *GitHub* improves the transparency of the package and users can easily file bug reports to ensure a rapid fix. This can also lead to the development of new functions when requested by users on *GitHub,* as evidenced by several new functions that have been implemented since the first release of the *landscapemetrics* package.

5. Summary

landscapemetrics is the first *R* package that allows calculation of most of the commonly employed landscape metrics found in the ecological literature (Cushman et al., 2008; Lustig et al., 2015; Schindler et al., 2008). Along with the package, a dedicated website introduces the basic concepts and usage of *landscapemetrics* <https://r-spatialecology.github.io/landscapemetrics>.

Many characteristics, such as including a large set of landscape metrics, working across platforms, being open-source, and the ability to analyse a comprehensive variety of spatial data within larger

88

workflows, are all advantages of the package. The included utility functions that permit the visualisation, extraction, sampling, and development of metrics, provide additional benefits over existing software. We hope this helps integrate *landscapemetrics* more easily into larger workflows, enhances transparency and reproducibility, and simplifies landscape analyses in ecological investigations.

Software availability

landscapemetrics is available on the Comprehensive *R* Archive Network (*CRAN*): <https://cran.r-project.org/package=landscapemetrics> and is also hosted on *GitHub*: <https://www.github.com/r-spatialecology/landscapemetrics>. *landscapemetrics* is distributed under GNU Public License Version 3 (GPLv3). To cite *landscapemetrics* or acknowledge its use, cite this Software note as follows, substituting the version of the application that you used for 'version 0': Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J. 2019. *landscapemetrics*: an open-source R tool to calculate landscape metrics. - Ecography 42(10): 1648-1657 (ver. 0).

Chapter 5 - General discussion

The aim of this thesis was to use spatial patterns to infer ecological processes and more precisely the role of environmental heterogeneity. Because non-random patterns contain information about the underlying processes, analysing spatial patterns can be a powerful tool to infer the processes (Brown et al., 2016, 2011; Law et al., 2009). However, because the pattern-process link can be ambiguous (McIntire and Fajardo, 2009), different approaches including spatial point pattern analysis, individual-based simulation modelling as well as landscape metrics were presented here to infer process from pattern. Field data from a temperate old-growth forest was used and the role of abiotic processes and possible interactions with biotic processes analysed. Naturally, biotic processes where shown to influence the spatial patterns of trees (Coates et al., 2009; Martínez and González-Taboada, 2009; Wang et al., 2010b; Zhang et al., 2014), but also abiotic processes can have similar effects on spatial patterns (Furniss et al., 2017; Getzin et al., 2008; Shen et al., 2013; van Waveren, 2016; Ye et al., 2011). While many former studies are regionally biased towards species-rich tropical forests (e.g. Brown et al., 2013; Chisholm and Pacala, 2010; Jara-Guerrero et al., 2015; Lin et al., 2017; Ramon et al., 2018), only a few studies are present in temperate forests (but see Furniss et al., 2017; Ye et al., 2011).

Studying species-habitat associations is a widely used approach to show the influence of environmental heterogeneity on the spatial pattern of trees. In the context of spatial point pattern analysis (SPPA), two contrasting approaches to randomize the null model data exist (Harms et al., 2001; Plotkin et al., 2000). In chapter 2, using a simulation study, it was firstly shown that the power of all methods to detect species-habitat associations was comparable to each other. Nevertheless, all methods had both advantages and disadvantages related to them. Even though pattern reconstruction had the highest computational demand, the method was favoured because of its high accuracy and applicability regardless of the study plot shape and the spatial pattern of the individuals. In accordance with similar studies (Furniss et al., 2017; Ye et al., 2011), results of chapter 2 showed that abiotic processes in form of species-habitat associations influenced the spatial pattern of tree species in the temperate old-growth forest. In contrast to the hypotheses of chapter 2, this was also true for *Fagus sylvatica L.,* the most dominant species in the study area and central Europe in general (Leuschner and Ellenberg, 2017). As

90

also shown for other forests (Comita et al., 2007; Kanagaraj et al., 2011; Lai et al., 2009; Ye et al., 2011), species-habitat associations differed between life-history stages. Lastly, living and dead trees did not show contrasting species-habitat associations as hypothesised. Concluding, chapter 2 demonstrated the power of SPPA and species-habitat associations to show an influence of abiotic processes on the pattern of forest trees. However, also the complexity of linking observed patterns to underlying processes was exposed. Albeit patterns were significantly non-random and the simulation study confirmed that species-habitat associations lead to identifiable patterns in the data, conclusions about the processes were mostly hypothetical based on general ecological knowledge.

To overcome the limitations of chapter 2 and to model the pattern-process link in more detail (An et al., 2009), an individual-based simulation model (IBM) was developed in chapter 3. Because variability between individuals and interactions with a heterogeneous environment are easy to incorporate into spatially explicit IBMs (An et al., 2009; DeAngelis and Grimm, 2014; Wallentin, 2017), IBMs are highly appropriate to study the role of abiotic processes on tree populations. This is further supported by their emergent higher level patterns based on discrete individuals (An et al., 2009; Grimm and Railsback, 2005). The model had two model versions, one including biotic processes only and one model version combining both biotic and abiotic processes. Spatial patterns for the biotic model version developed towards complete spatial randomness for longer simulation periods. However, especially seedlings, saplings and understory trees were shown to be clustered in the field (Janík et al., 2016; Kunstler et al., 2004; Nagel et al., 2006). In order to model the clustered pattern of saplings in the field data, several abiotic processes needed to be included into the model. In addition to growth, also seedling establishment and mortality had to be influenced by environmental heterogeneity. Remarkably, two different scales of environmental heterogeneity were required, which pointed towards differences of abiotic processes depending on the life-history stage (Bertrand et al., 2011; Comita et al., 2007; Lai et al., 2009; Masaki et al., 2015). This supported the results of chapter 2 showing that species-habitat associations also differed between life-history stages. Lastly, because single patterns could be modelled by both model versions, chapter 3 demonstrated the power of patterns in combination with IBMs to infer

underlying processes, however, only if several patterns are used simultaneously (Grimm et al., 2005; Janssen et al., 2009; Wiegand et al., 2003).

Because science is not only driven by ideas, but also by tools (Dyson, 2012), in chapter 4 the open-source software tool *landscapemetrics* was introduced. In order to study the role of environmental heterogeneity, one basic step is to quantify the heterogeneity. Landscape metrics are widely used to quantify the spatial composition and configuration of land-cover classes. Despite that landscape metrics are widely used (Kupfer, 2012; Uuemaa et al., 2013, 2009; With, 2019), existing software has several drawbacks. This includes a complicated integration into larger workflows, not being open-source, being limited to certain operating systems or not including a comprehensive collection of metrics. Contrastingly, the *R* package *landscapemetrics* overcomes these drawbacks. Thus, it improves the transparency and reproducibility of research (Powers and Hampton, 2018) and facilitates the consideration of environmental heterogeneity in ecological studies, as already confirmed by its usage in various studies (Bajaru et al., 2019; Gasparini et al., 2019; Heisler et al., 2019; Kendall et al., 2019; Lucash et al., 2019; Maxence et al., 2019). The importance of considering environmental heterogeneity even in apparently fairly homogenous conditions was clearly demonstrated by chapter 2 and chapter 3 of this thesis.

Future directions

Using spatial point pattern analysis, individual-based simulation models and landscape metrics allowed to quantify environmental heterogeneity and link processes to patterns. However, there are several options to describe and model the pattern-process link in more detail.

Even though this might be difficult for the whole study system, a supporting approach would include specifically designed laboratory experiments on individuals (Grimm and Railsback, 2012; Stillman et al., 2015). For this, especially the specific influence of environmental heterogeneity on seedlings would be of interest. This is because firstly, the physical and temporal dimension related to seedlings would allow such experiments and secondly, regeneration processes are often assumed to be crucial for the overall population (Martin and Canham, 2010; Shibata et al., 2010). Because the quality of the

environmental data has a large influence on the results (Chang et al., 2013), experiments might also allow to improve how and which data about environmental heterogeneity should be sampled for future research.

A better understanding of temperate old-growth forest dynamics will logically improve the ability to conserve and protect them (Brang, 2005). Because forests provide many ecosystem services and refuges for species (Wirth et al., 2009), this is especially important in times of climate change and biodiversity loss. However, most forests in Europe are under management (Kuemmerle et al., 2016; Tieskens et al., 2017). Nevertheless, a better understanding of old-growth forest dynamics can result in better near-to-nature management, a policy commonly applied in central Europe (Puettmann et al., 2015). In the context of this thesis, this could be realised in two different ways. Firstly, the IBM could be extended by management submodels and the outcome of different management strategies analysed. Secondly, similar studies could be implemented in comparable, but managed forests. This would allow to show similarities and differences between unmanaged and managed forests and thus allow to deduce strategies to mimic natural dynamics during management.

The role of environmental heterogeneity is scale dependent (Chase, 2014; Tamme et al., 2010). Therefore, trying to scale results of the IBM to larger landscape scales could be an interesting direction to take. However, not a trivial one. Scaling from smaller scales on which studies are reasonably feasible to larger landscape or even global scales is an issue ecologists struggle with for many years now (Denny and Benedetti-Cecchi, 2012; Henle et al., 2014). Nevertheless, local dynamics were shown to be able to model landscapes patterns under various circumstances (Lischke et al., 2006). This could allow to use SPPA on local scales to analyse the spatial structure very precisely. This information could be used to construct and parametrise IBMs also on larger scales, e.g. by "assembling" a large landscape with several local IBMs (i.e. a mosaic of local IBMs). Lastly, emerging patterns on landscape scale could be evaluated using landscape metrics. Thus, such an approach would allow to link local descriptors of spatial patterns across spatial scales to descriptors of spatial patterns on larger scales.

As demonstrated by this thesis, environmental heterogeneity should be considered spatially explicit in probably most ecological studies and spatial patterns can be a powerful tool to do so. Especially the here presented combination of different methods is a promising approach to deal with the complexity of possible interactions of abiotic and biotic processes. Nevertheless, of course countless other combinations with different approaches exit and will hopefully be explored in future research.

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Appendix

Chapter 2
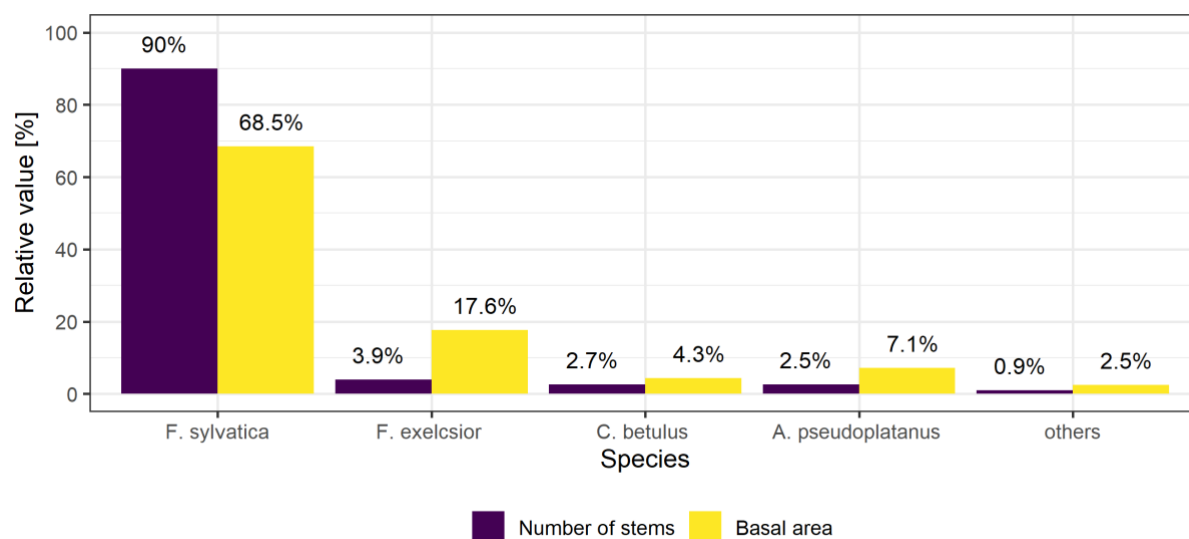
Figure A2-1: *Relative abundance and basal area of all present species in the study plot. The study plot is dominated by F. sylvatica in terms of both number of stems and basal area. The relatively high basal area of F. excelsior in combination with the comparable low number of stems indicates few but large individuals.*
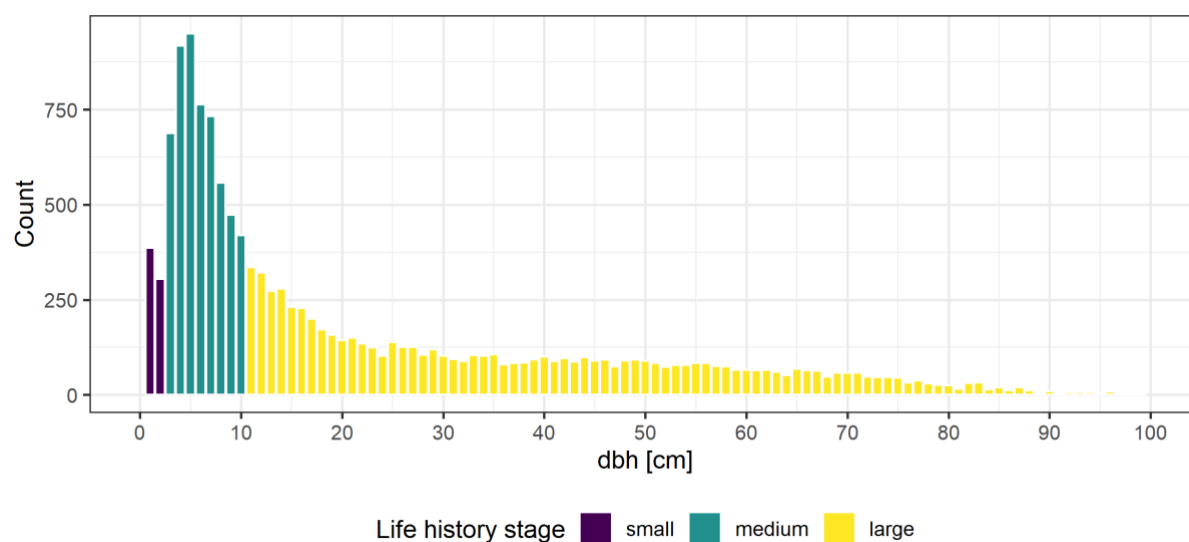
Figure A2-2: *Distribution of the diameter at breast height (dbh) for all living trees. The dbh is classified into 1 cm classes. The minimum and maximum diameters were 0.2 cm and 135.5 cm, respectively.*
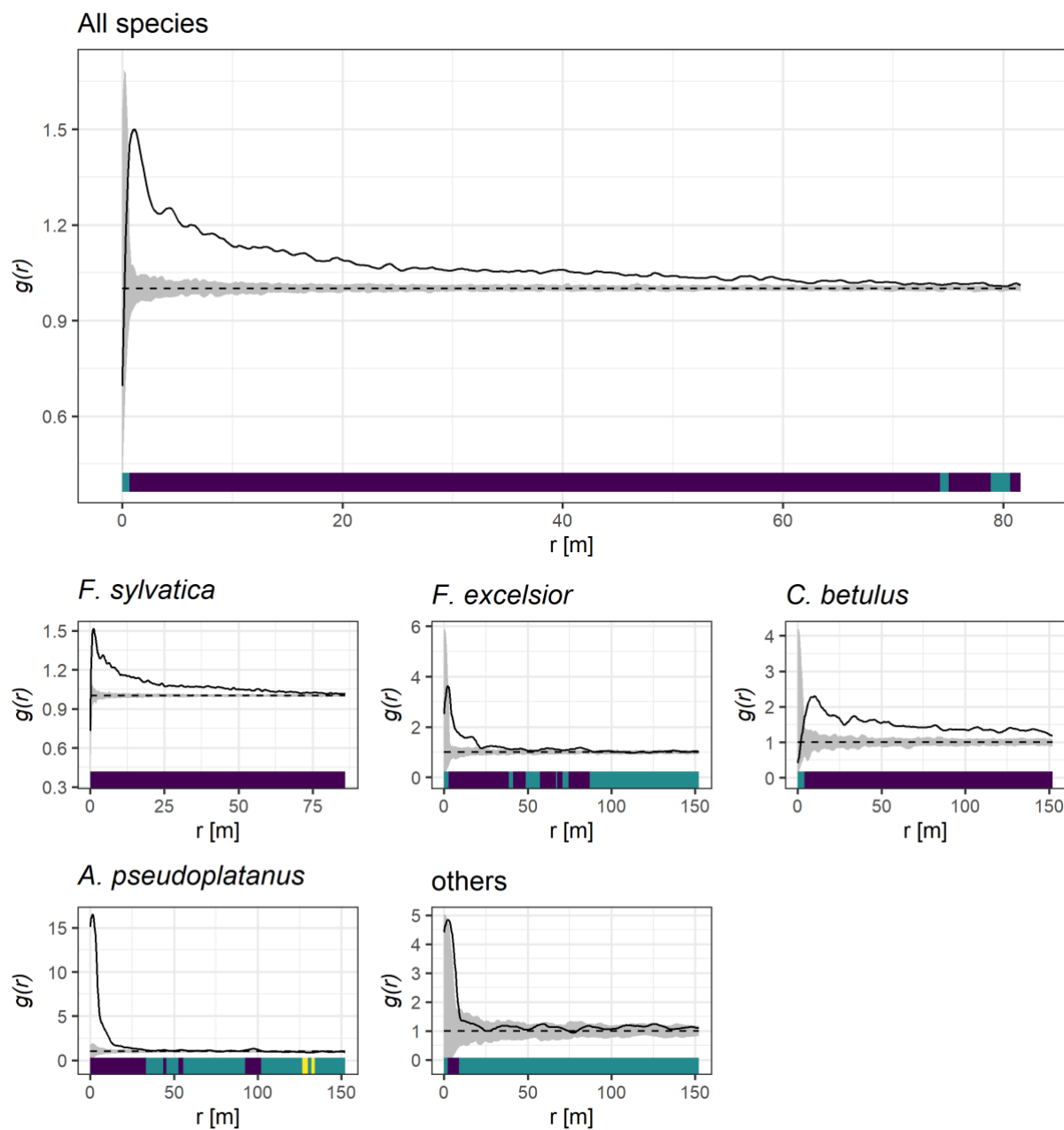
Figure A2-3: *Pair correlation functions g(r) for all trees and separated by species. The solid, black line reflects the observed pattern, the grey envelopes 199 simulations of the null model of complete spatial randomness (CSR) and the dashed line the theoretical value for CSR. A location of the observed values above the simulation envelopes indicates clustering, a location below regularity (as indicated by the colour bars below).*

109
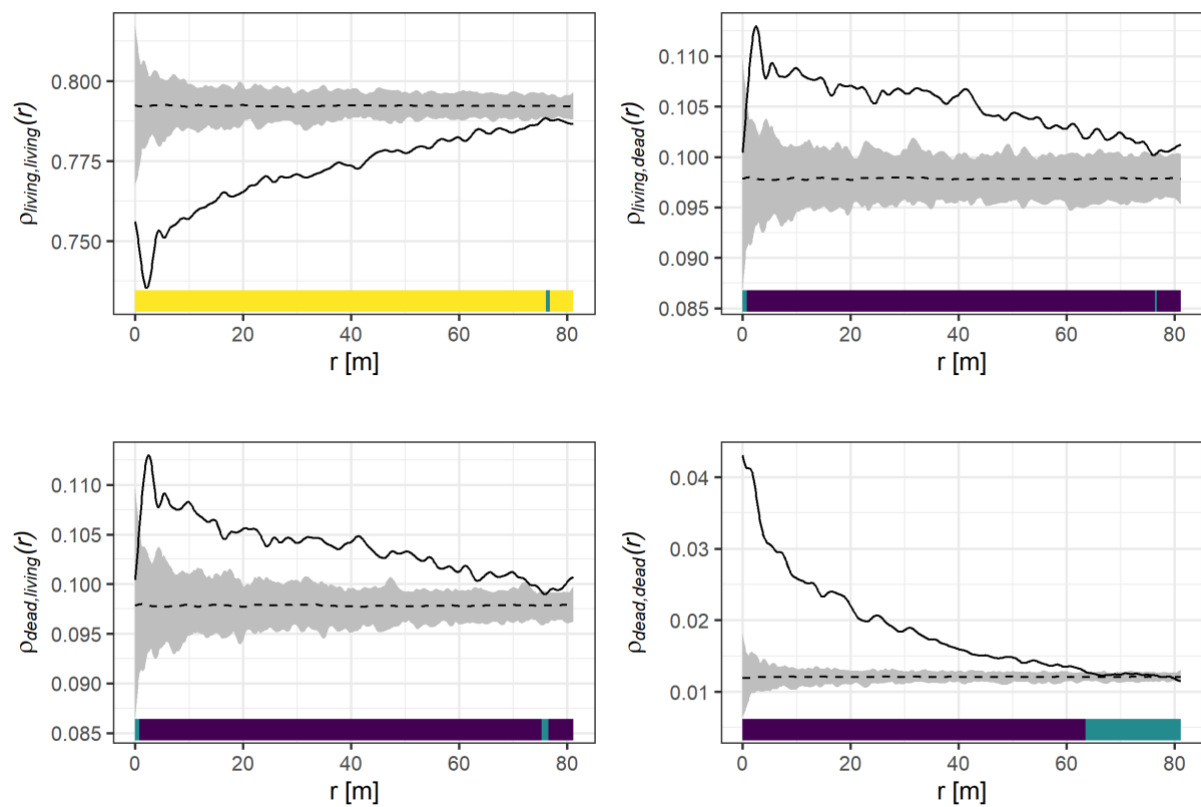
Figure A2-4: *Mark-connection functions $\rho_{i,j}(r)$ for dead and living F. sylvatica trees. The solid, black line reflects the observed pattern, the grey envelopes 199 simulations of the null model of random labelling. The dashed lines represent the theoretical values of the null model. A location of the observed values above the simulation envelopes indicates a positive correlation of marks, i.e. a higher probability of finding an event with mark j at distance r from the focal event with mark i. Analogously, a negative correlation is indicated by a location of the observe values below the simulation envelopes.*

Chapter 3
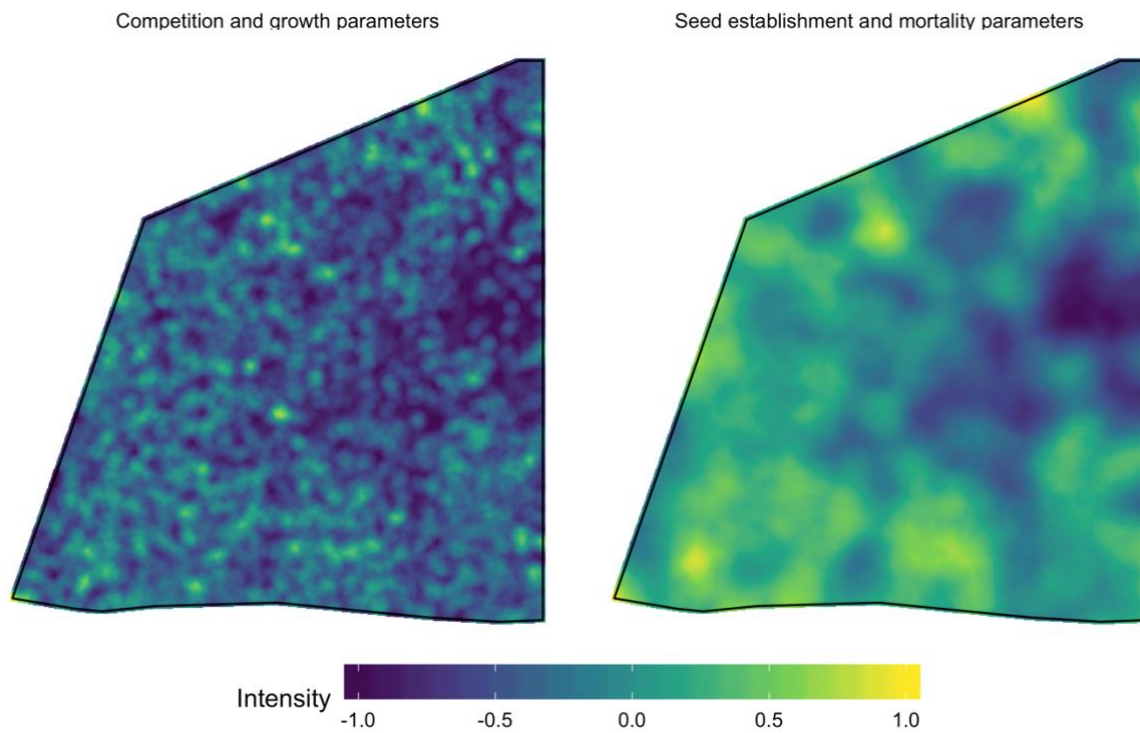
Figure A3-1: *Abiotic conditions used for the parameterisation and simulation of the combined model version. For parametrising the competition and growth parameters, a smaller standard deviation of the smoothing kernel was used (left panel) than for successful seed establishment and mortality processes (right panel). Low intensity values describe unsuitable growing conditions, while high intensity values describe suitable growing conditions based on the intensity λ(x,y) of trees with a dbh > 10 cm.*
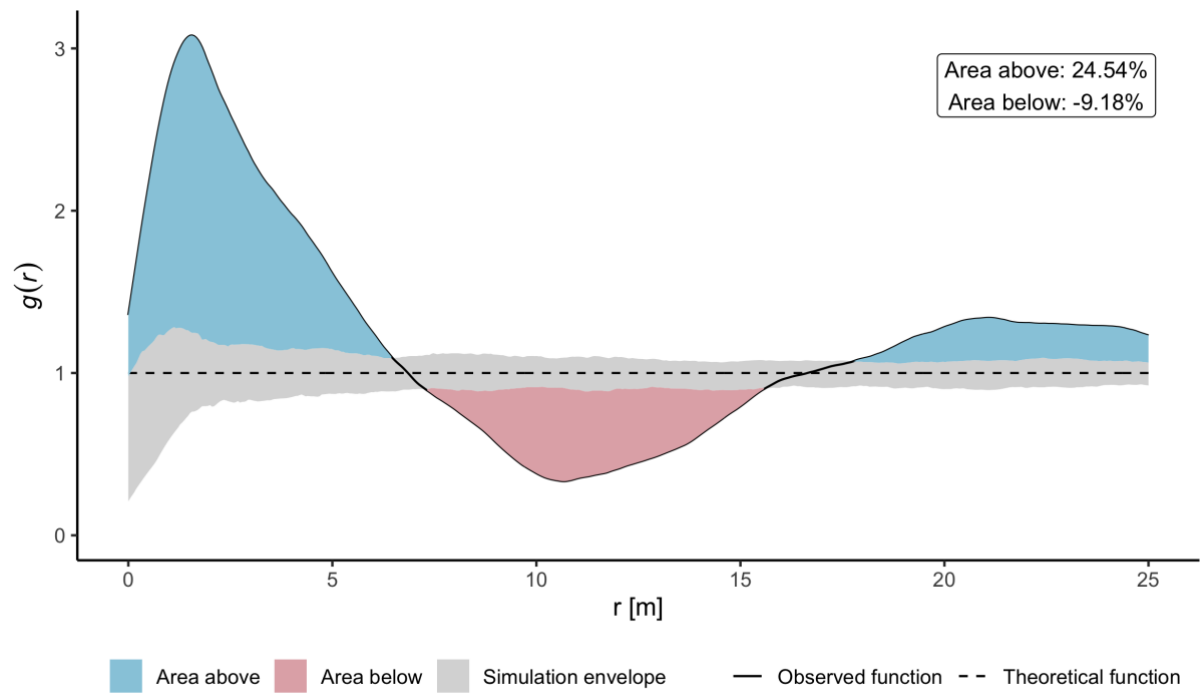
Figure A3-2: Example pair-correlation function g(r) to illustrate how it was summarised for the sensitivity analysis. The absolute area above (blue) and below (red) the null model envelope (grey) for complete spatial randomness (CSR) was summed and normalised by the total area under the observed curve. If the area above the envelope was larger than the area below the envelope, the absolute area was positive and vice versa.
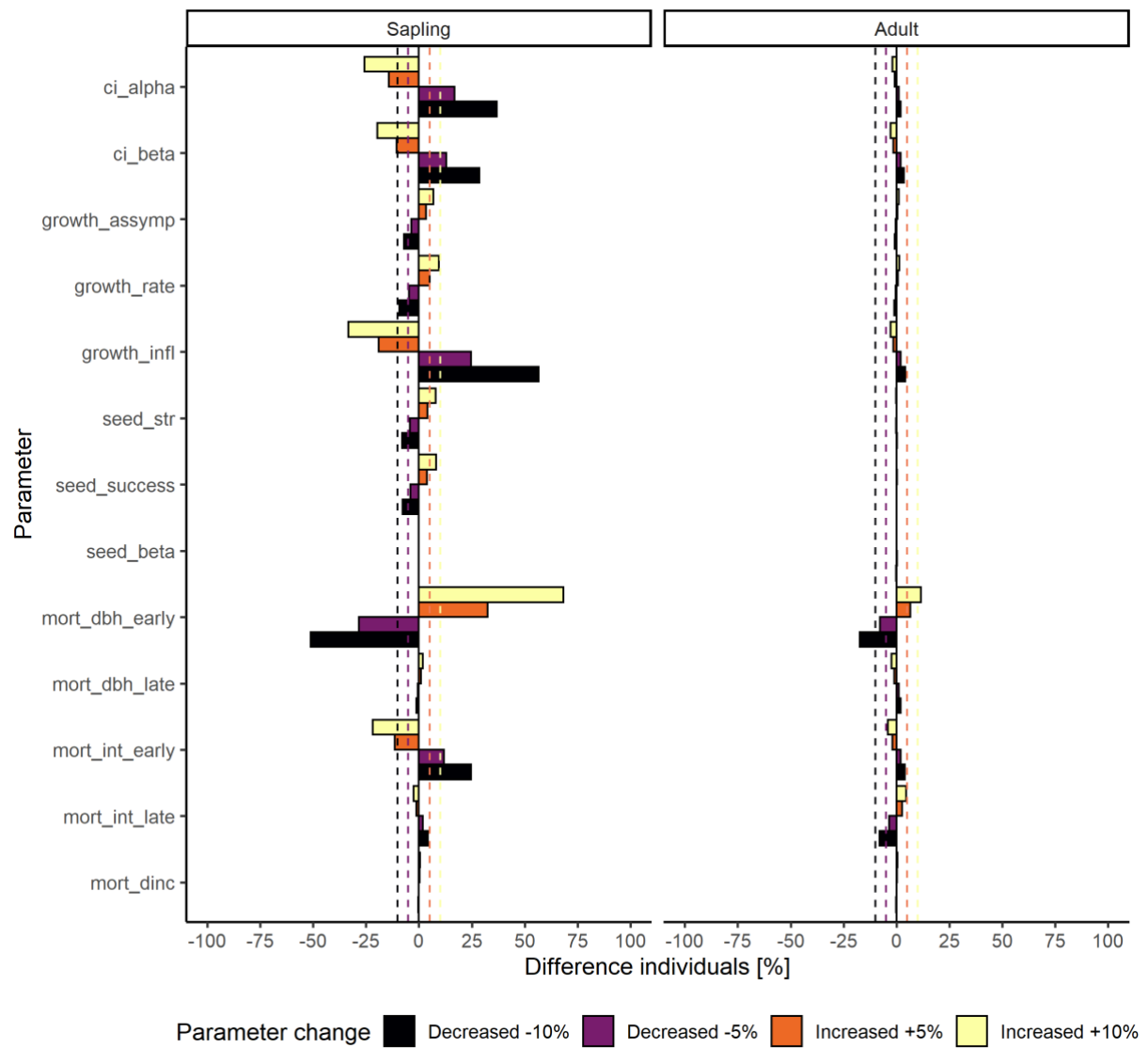
Figure A3-3: *Local one-at-a-time sensitivity analysis with the number of individuals as model output. The relative difference of individuals after 50 simulation years between the baseline parameters and the one-at-a-time decreased and increased parameters are depicted.*
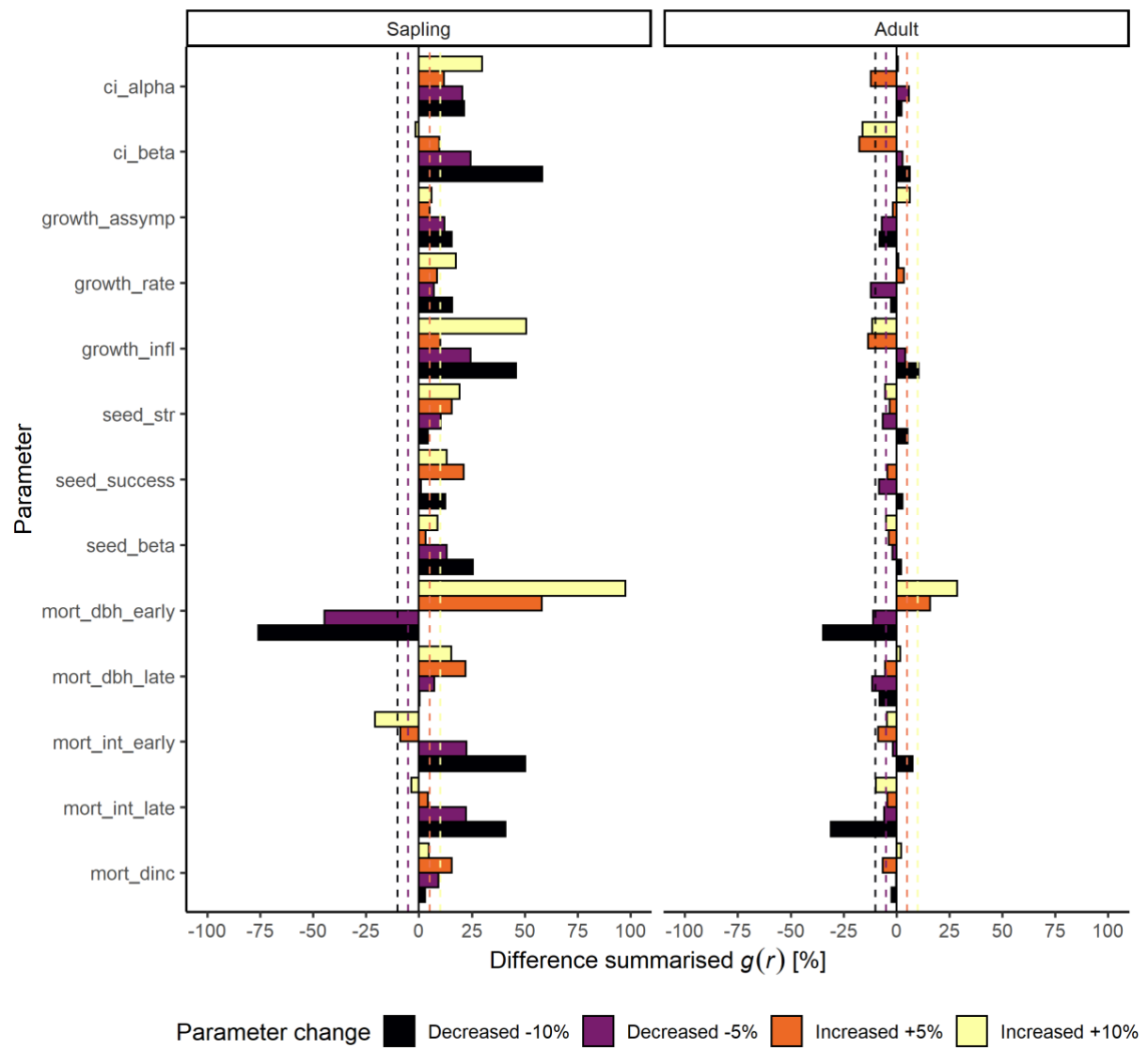
Figure A3-4: *Local one-at-a-time sensitivity analysis with the integral of the pair-correlation function as model output. The relative difference of the integral after 50 simulation years between the baseline parameters and the one-at-a-time decreased and increased parameters are depicted.*
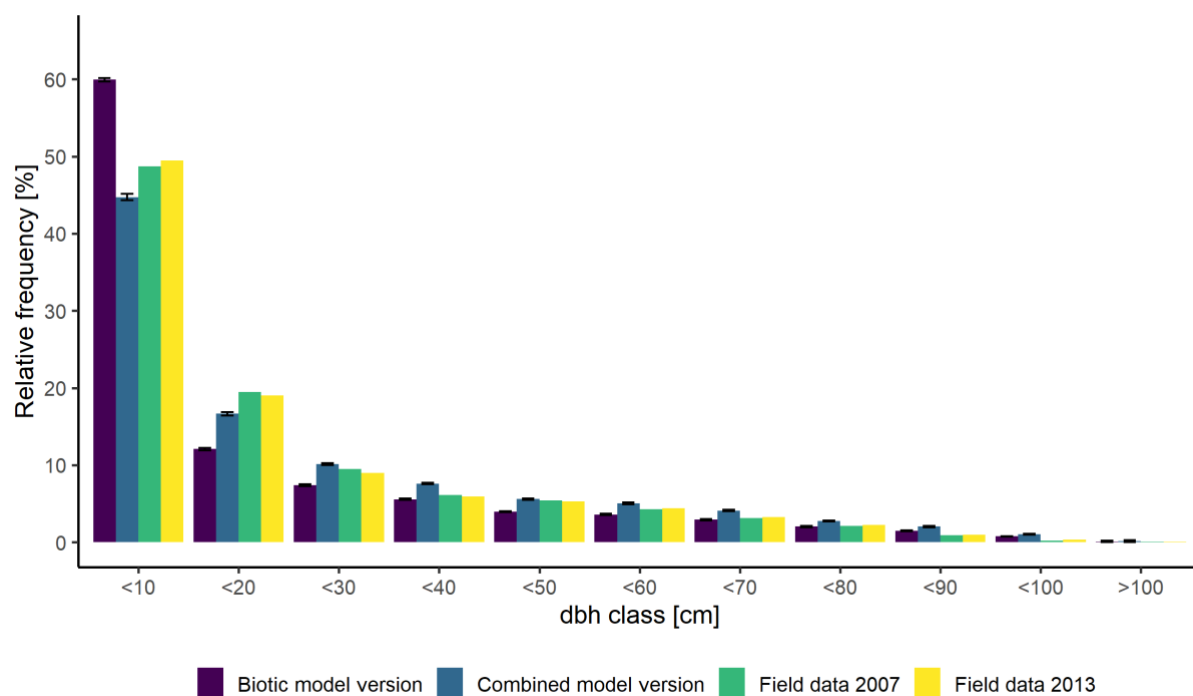
Figure A3-5: *Distribution of diameter at breast height (dbh) classes for the biotic and the combined model version after 50 simulated years and field data of the censuses in 2007 and 2013. The dbh was classified using 10 cm classes.*
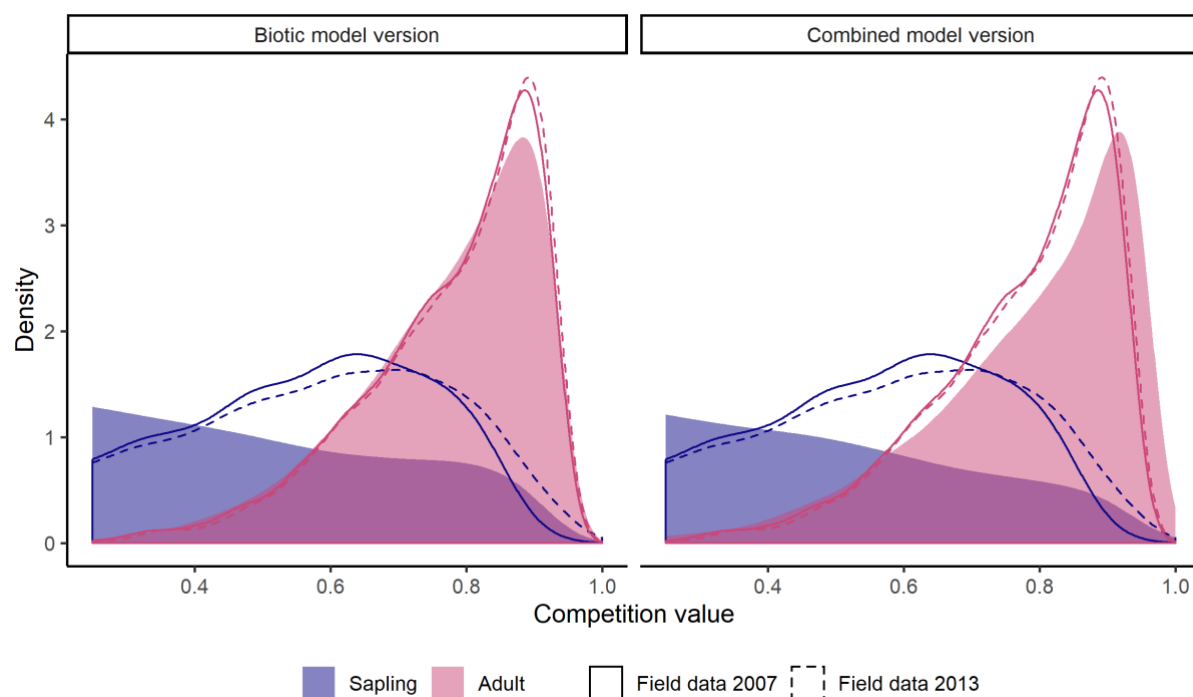
Figure A3-6: *Density of competition values for the biotic and combined model version after 50 simulated years (surface) and field data census in 2007 (solid line) and 2013 (dashed line). Colours indicate size groups; saplings (blue) are classified by a 1 <dbh ≤ 10 cm and adults (red) by a dbh > 10 cm.*

115
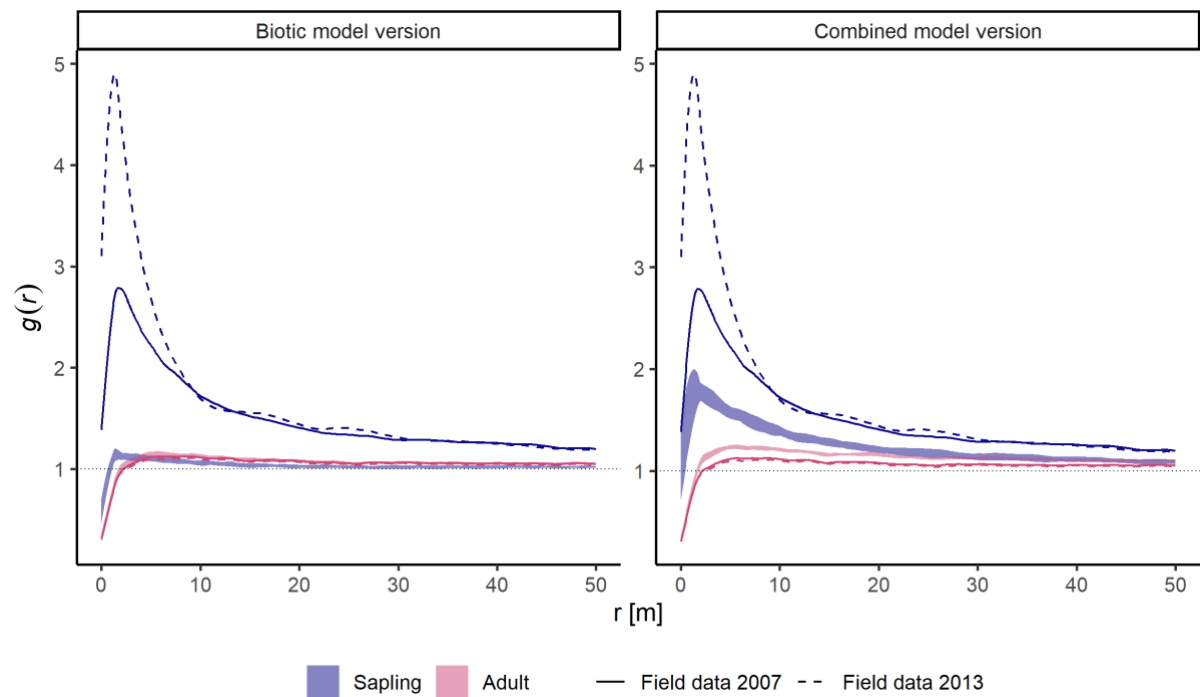
Figure A3-7: *Pair correlation function g(r) for the biotic model version and the combined model version (envelopes) after 50 simulation years and the field data censuses in 2007 (solid line) and 2013 (dashed line). Individuals are classified to size groups (sapling: 1 < dbh ≤ 10 cm, adult: dbh > 10cm) indicated by colour (saplings: blue; adults: red).*
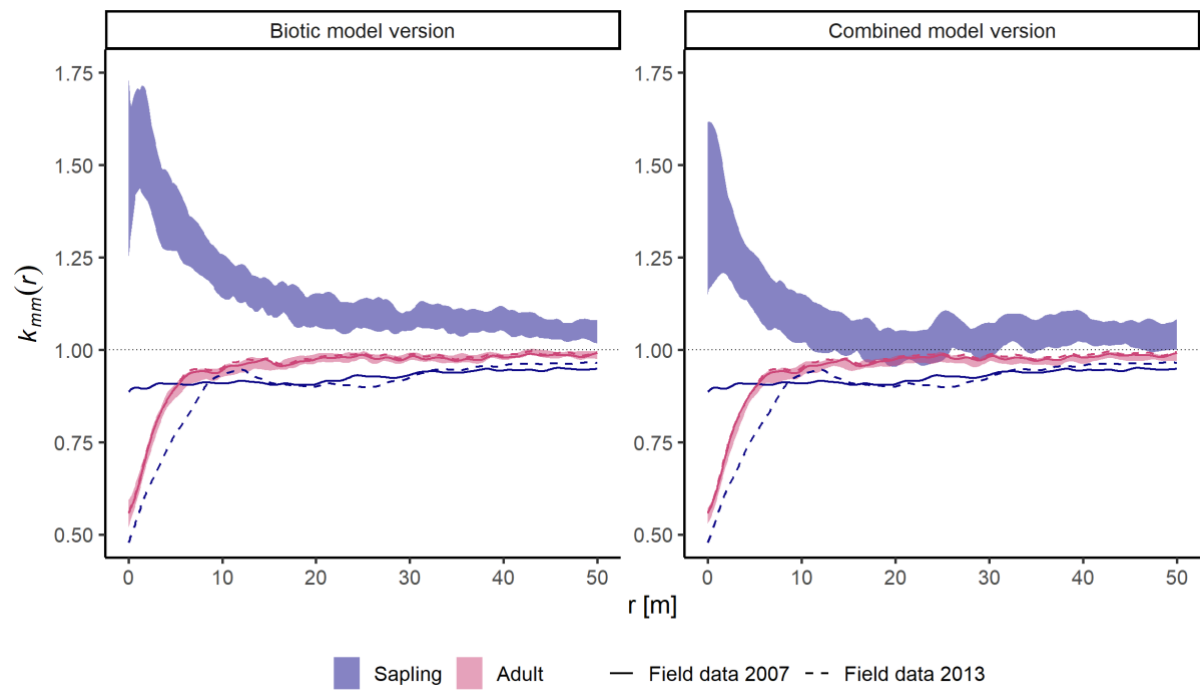
Figure A3-8: Mark-correlation function k_{mm}(r) for the biotic model version and the combined model version (envelopes) after 50 simulation years and the field data censuses in 2007 (solid line) and 2013 (dashed line). Individuals are classified to size groups (sapling: 1 < dbh ≤ 10 cm, adult: dbh > 10cm) indicated by colour (saplings: blue; adults: red).
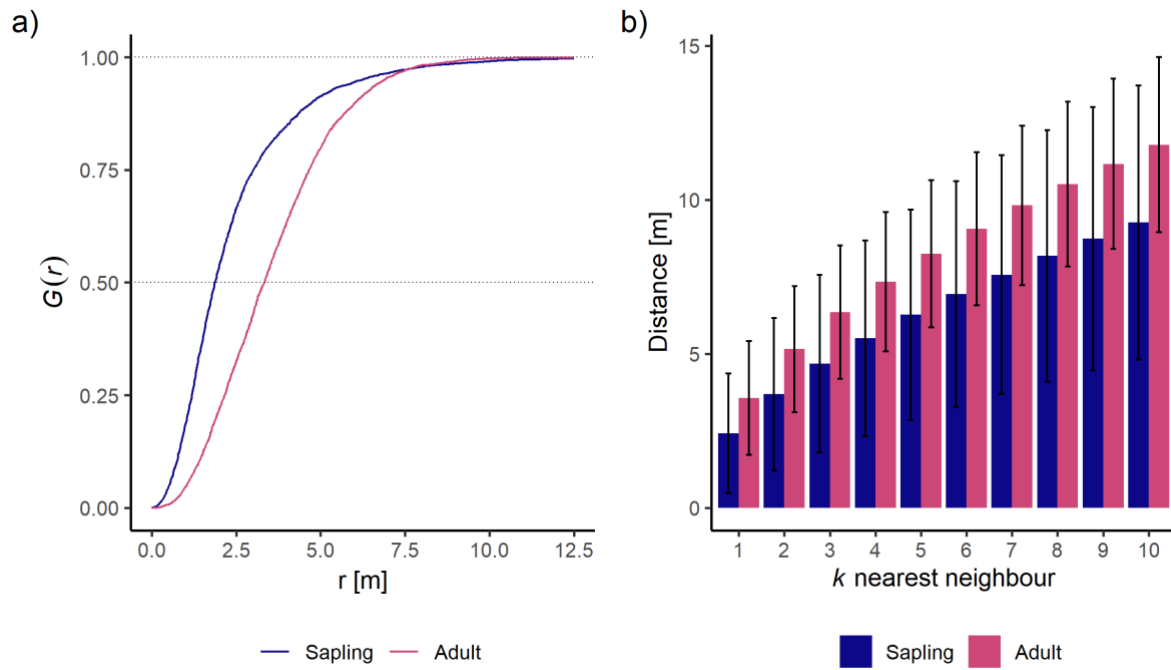
Figure A3-9:a) The nearest-neighbour distribution function G(r) for saplings (solid blue line) and adults (solid red line). The dashed grey lines indicate 50% and 100% of all individuals with the nearest neighbour at distance r. b) Mean distance and standard deviation to the k nearest neighbour for saplings (blue) and adults (red). Both figures indicate the distance to the nearest neighbour is smaller for saplings compared to adults.

Chapter 4

Table A4-1: All landscape metrics used for the simulation study analysing the influence of different sampling schemes on the ability of sampled data to estimate the statistical properties of a larger landscape. The groups are based on the FRAGSTATS classification (McGarigal et al. 2012) with the exception of the "Complexity metrics", which are based on Nowosad and Stepinski (2019). For detailed information on all metrics see <https://r-spatialecology.github.io/landscapemetrics/>.

Group	Metric	n
Aggregation metrics	ai	13
	cohesion	
	contag	
	division	
	enn_cv	
	enn_mn	
	enn_sd	
	iji	
	lsi	
	mesh	
	pd	
	pladj	
	split	
Area and edge metrics	area_cv	8
	area_mn	
	area_sd	
	ed	

	gyrate_cv	
	gyrate_mn	
	gyrate_sd	
	lpi	
	cai_cv	
	cai_mn	
	cai_sd	
	core_cv	
Core area metrics	*core_mn*	*10*
	core_sd	
	dcad	
	dcore_cv	
	dcore_mn	
	dcore_sd	
	msidi	
	msiei	
	prd	
Diversity metrics	*rpr*	*8*
	shdi	
	shei	
	sidi	
	siei	

Complexity metrics	condent	4
	ent	
	joinent	
	mutinf	
Shape metrics	circle_cv	15
	circle_mn	
	circle_sd	
	contig_cv	
	contig_mn	
	contig_sd	
	frac_cv	
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	frac_sd	
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	para_mn	
	para_sd	
	shape_cv	
	shape_mn	
	shape_sd	
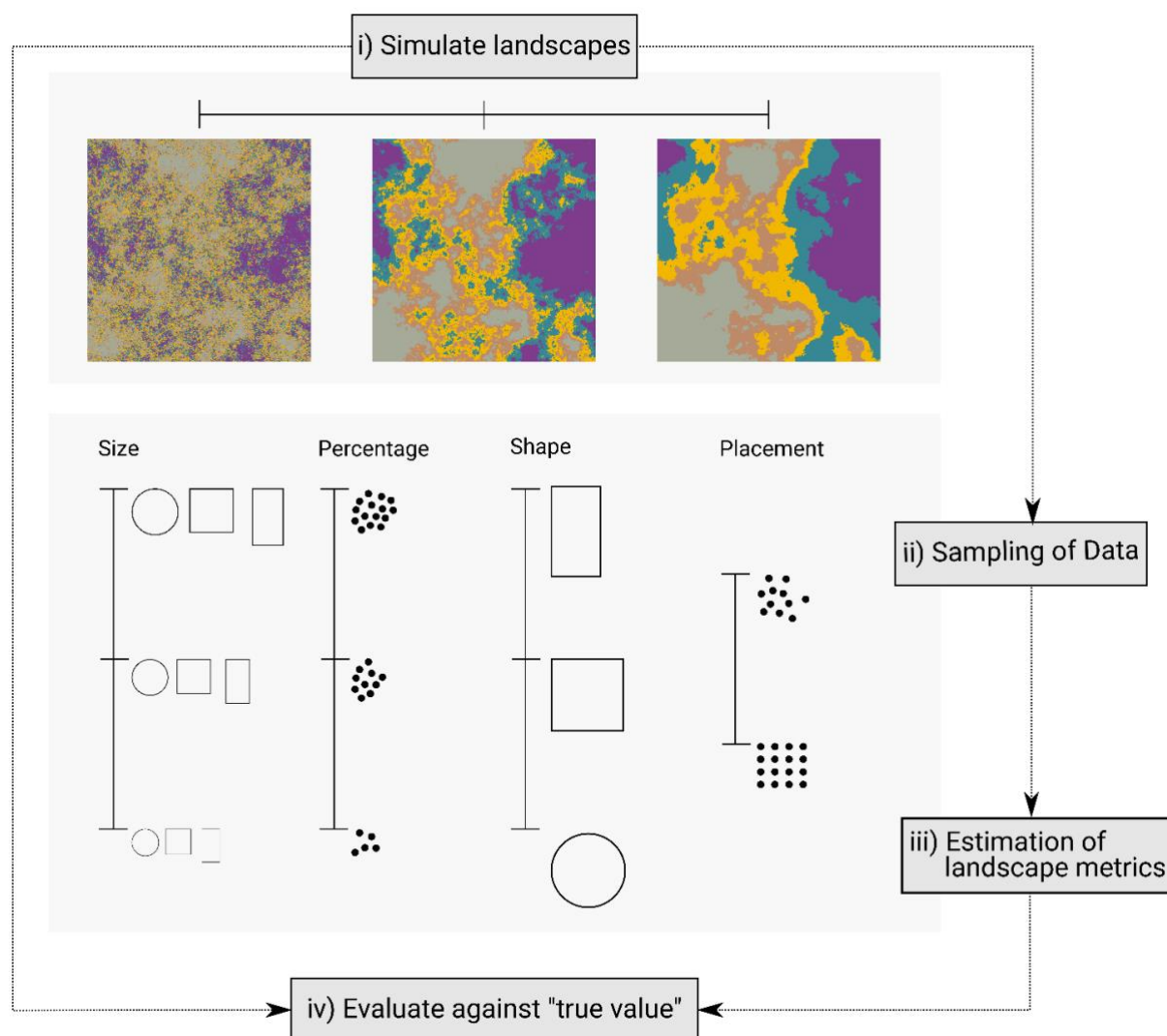
Figure A4-1: *Schematic visualisation of the "virtual ecologist" approach (Zurell et al. 2010) to analyse the influence of different sampling schemes on the estimation ability.*

Abstract

One of the main goals of ecology is to understand processes underlying patterns. Because presumably all ecological processes are spatially explicit, especially spatial patterns can contain a lot of information about the processes shaping them. Nevertheless, the pattern-process link can be ambiguous. Reasons for this include different processes that lead to similar patterns, interacting processes that lead to random patterns or patterns that lead to processes and not the other way around. However, many of these issues can be dealt with using appropriate analysis methods. This includes meaningful ecological hypotheses, precise descriptions of patterns in the data as well as null models and model simulations to strengthen the pattern-process link.

Biotic and abiotic processes were shown to interact in plant populations and to result in similar clustered spatial patterns. The clustering can be introduced by limited seed dispersal as an example of biotic processes, but also by higher densities of individuals at suitable growing conditions as an example of abiotic processes. Even though challenging, analysing spatial patterns in the data can be a powerful tool to disentangle the importance and interactions of these two processes.

The aim of this thesis was to present approaches that use the power of spatial patterns to study the role of environmental heterogeneity. The methods included spatial point pattern analysis, individual-based simulation models as well as tools to quantify environmental heterogeneity to link spatial patterns to underlying processes. To this end, field data from a temperate old-growth forest was used.

In chapter 2, a simulation study of commonly used spatial point pattern analysis methods to study species-habitat associations as indicator of abiotic processes showed that all methods were able to indicate species-habitat associations from patterns. Furthermore, species-habitat associations were shown to be present in the temperate old-growth forest for the most common species. Thereby, possibly to avoid competition, some species showed opposing associations to the most dominant species *Fagus sylvatica*. Furthermore, species-habitat associations differed between life-history stages. However, using species-habitat associations as indicator of abiotic processes demonstrated one issue of the pattern-process link. Many conclusions were, even though based on ecological knowledge, rather hypothetical.

As a next step in chapter 3, an individual-based simulation model was developed to model the pattern-process link in more detail. Individual-based simulation models allow to explicitly incorporate assumed underlying processes and discriminate between alternative hypotheses. Hence, two model version were implemented. In the first model version only biotic processes were included and in the second model version biotic and abiotic processes combined. Only the combined model version was able to simulate clustered patterns of individuals for earlier life-history stages comparable to the field data over a longer time period. Interestingly, in order to do so, an influence of environmental heterogeneity on three processes, namely growth, seedling establishment and mortality, needed to be implemented. Additionally, two different scales of environmental heterogeneity were needed. This indicated that environmental heterogeneity influenced several biotic processes, however, the influence differed between life-history stages.

Lastly in chapter 4, a new open-source software tool to quantify environmental heterogeneity for discrete land-cover classes was introduced in this thesis. Quantifying composition and configuration of environmental heterogeneity is one of the fundamental steps in any study trying to establish a pattern-process link. Nevertheless, existing software tools have several drawbacks and constraints that the here introduced *R* package tries to overcome. The software allows an integration into reproducible and transparent workflows and thereby hopefully facilitates future research using patterns of environmental heterogeneity.

Overall, the thesis demonstrated how spatial patterns can be used to explore underlying ecological processes, even if contrasting processes lead to similar patterns as for biotic and abiotic processes. To successfully link pattern to process, *i)* meaningful ecological hypotheses are needed, *ii)* patterns in the data need to be described precisely using suitable methods and *iii)* appropriate null models as well as model simulations need to be applied to link pattern to process as unambiguously as possible.

Deutsche Zusammenfassung

Eines der Hauptziele in der Ökologie ist es, die zugrunde liegenden Prozesse von Mustern zu verstehen. Da vermutlich alle ökologischen Prozesse räumlich explizit sind, können insbesondere räumliche Muster eine Vielzahl von Informationen über die sie gestaltenden Prozesse enthalten. Der Zusammenhang zwischen Muster und Prozess ist jedoch nicht immer eindeutig. Gründe hierfür sind verschieden Prozesse die zu ähnlichen Mustern führen, interagierende Prozesse die zu zufälligen Mustern führen oder Muster die Prozesse beeinflussen und nicht entgegengesetzt. Vielen dieser Schwierigkeiten kann allerdings mit geeigneten Methoden begegnet werden. Dazu gehören sinnvolle ökologische Hypothesen, genaue Beschreibungen der Muster, sowie Nullmodelle und Simulationsmodelle um die Muster-Prozess Verbindung zu stärken.

Biotische und abiotische Prozesse interagieren in Pflanzenpopulationen und können in vergleichbaren, geklumpten Mustern resultieren. Die Klumpung kann durch räumlich limitierte Samenverbreitung verursacht werden als Beispiel für biotische Prozesse, aber auch durch eine höhere Dichte von Individuen an geeigneten Wuchsbedingungen als Beispiel für abiotische Prozesse. Die Analyse räumlicher Muster kann ein leistungsstarkes Werkzeug sein, um die Rolle und Interaktionen dieser zwei Prozesse zu entwirren.

Das Ziel dieser Dissertation war es, Ansätze zu präsentieren, die räumlichen Mustern benutzt um die Rolle von Umweltheterogenität zu studieren. Die Methoden umfassten sowohl räumliche Punktmusteranalyse, Individuen-basierte Simulationsmodelle, als auch Werkzeuge um die Umweltheterogenität zu quantifizieren, um räumliche Muster mit den zugrundeliegenden Prozessen zu verbinden. Dazu wurden Felddaten aus einem gemäßigten Naturwald verwendet.

Eine Simulationsstudie gängiger räumlichen Punktmusteranalyse Methoden zur Untersuchung von Art-Habitat-Assoziationen als Indikator für abiotische Prozesse in Kapitel 2 zeigte, dass alle Methoden in der Lage waren, vorhandene Assoziationen aufzuzeigen. Auch die häufigsten Arten im untersuchten gemäßigten Naturwald zeigten Art-Habitat-Assoziationen. Vermutlich um Konkurrenz zu vermeiden, zeigten einige Arten gegensätzliche Assoziationen zur dominantesten Art *Fagus sylvatica*. Des Weiteren unterschieden sich Art-Habitat-Assoziationen in den verschiedenen Entwicklungsstadien. Die Verwendung von Art-Habitat-

Assoziationen als Indikator für abiotischer Prozesse zeigte jedoch, dass viele Schlussfolgerungen eher hypothetisch waren, wenn auch auf Grundlage ökologischer Erkenntnisse.

Als nächsten Schritt wurde in Kapitel 3 ein Individuen-basiertes Simulationsmodell entwickelt, um den Zusammenhang zwischen Muster und Prozess detaillierter zu modellieren. Individuen-basiertes Simulationsmodelle erlauben es, explizit angenommene zugrundeliegende Prozesse zu integrieren und zwischen alternativen Hypothesen zu unterscheiden. Daher wurden zwei Modellversionen implementiert. Während in der ersten Modellversion nur biotische Prozesse einbezogen wurden, wurden in der zweiten Modellversion biotische und abiotische Prozesse kombiniert. Dabei konnte nur die kombinierte Modellversion ein geklumptes Muster von Individuen frühere Entwicklungsstadien über einen längeren Zeitraum simulieren, die mit den Felddaten vergleichbar war. Interessanterweise musste dazu der Einfluss von Umweltheterogenität auf drei Prozesse, nämlich Wachstum, Samenverbreitung und Mortalität, implementiert werden. Zusätzlich mussten für die Umweltheterogenität zwei unterschiedliche Skalen berücksichtigt werden. Dies deutete darauf hin, dass Umweltheterogenität mehrere biotische Prozesse beeinflusst, die sich zusätzlich in den verschiedenen Entwicklungsstadien unterschieden.

Außerdem wurde in Kapitel 4 eine neue Software eingeführt, um Umweltheterogenität für diskrete Landschaftsklassen zu quantifizieren. Die Beschreibung von Komposition und Konfiguration der Heterogenität, ist einer der grundlegenden Schritte um die Muster-Prozess Verbindung herzustellen. Existierende Software hat dennoch einige Nachteile und Beschränkungen, die das hier vorgestellte *R* Paket zu überwinden versucht. Die Software erlaubt eine Einbindung in reproduzierbare und transparente Arbeitsabläufe und verbessert dadurch hoffentlich zukünftige Forschung welche Muster von Umweltheterogenität verwendet.

Die vorliegende Dissertation zeigte, wie Muster verwendet werden können, um zugrunde liegende ökologische Prozesse zu erforschen, auch wenn unterschiedliche Prozesse zu ähnlichen Mustern führen (wie bei biotischen und abiotischen Prozessen). Um Muster erfolgreich mit Prozessen zu verknüpfen, bedarf es *i)* aussagekräftigen ökologischen Hypothesen, *ii)* geeigneten Methoden um Muster in Daten präzise beschreiben zu können und *iii)* zusätzlich geeignete Nullmodelle und Simulationsexperimente, um Muster so eindeutig wie möglich mit Prozessen zu verknüpfen.

Acknowledgements

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18/10/2017 - 21/12/2017 | Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames (USA)

Workshops

07/09/2013 - 22/09/2013 | Fire protection and management, Cyprus Forestry College, Podromos (Cyprus)

02/04/2017 - 07/04/2017 | Advances in spatial analysis of multivariate ecological data: Theory and practice, Port Talbot (UK)

18/01/2018 – 19/01/2018 | Deep learning with *Keras* and *TensorFlow*, Solingen (Germany)

26/03/2018 - 30/03/2018 | Spatial modelling *inlabru*, St. Andrews (GB)

Conferences

29/04/2017 – 05/05/2017 | Young Modellers in Ecology, Freiburg (Germany)

10/09/2018 – 14/09/2018 | 48th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, Vienna (Austria)

01/07/2019 - 05/07/2019 | 10th World Congress International Association of Landscape Ecology, Milano (Italy)

Publications

Articles

- Hesselbarth, M.H.K.; Wiegand, K.; Dreber, N.; Kellner, K.; Esser, D.; Tsvuura, Z. (2018). Density-dependent spatial patterning of woody plants differs between a semi-arid and a mesic savanna in South Africa. Journal of Arid Environments. 157, 103-112. <https://doi.org/10.1016/j.jaridenv.2018.06.002>

- Hesselbarth M.H.K.; Sciaini M.; With, K.A.; Wiegand, K.; Nowosad, J (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography. 42 (10), 1648-1657. <https://doi.org/10.1111/ecog.04617>

- Borthwick, R., de Flamingh, A., Hesselbarth, M.H.K., Parandhaman, A., Wagner, H.H., Abdel Moniem, H.E. (2020). Alternative quantifications of landscape complementarity to model gene flow in banded longhorn beetles [Typocerus v. velutinus (Olivier)]. Frontiers in Genetics 11, 307. <https://doi.org/10.3389/fgene.2020.00307>

Poster / Talks

- Hesselbarth, M.H.K.; Wiegand K. (2018). A simulation study comparing methods to analyze species-habitat associations of forest trees. 48th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland. Vienna (Austria). Conference poster.

- Hesselbarth, M.H.K.; Sciaini, M.; Nowosad, J.; Hanss; S. (2019). landscapemetrics: introducing a new R tool to characterise landscapes. 10th World Congress International Association of Landscape Ecology. Milano (Italy). Conference poster.

Software

- Hesselbarth, M.H.K.; Sciaini, M., Nowosad, J., Hanss, S. (2019). landscapemetrics: Landscape Metrics for Categorical Map Patterns. R package version 1.4.3. <https://cran.r-project.org/package=landscapemetrics>

- Hesselbarth, M.H.K.; Sciaini, M. (2019). shar: Species-Habitat Associations in R. R package version 1.1. <https://cran.r-project.org/package=shar>

Doktoranden-Erklärung der Georg-August-Universität Göttingen

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Ich beabsichtige, eine Dissertation zum Thema „Analysing and modelling spatial patterns to infer the influence of environmental heterogeneity using point pattern analysis, individual-based simulation modelling and landscape metrics" an der Georg-August-Universität Göttingen anzufertigen.
Dabei werde ich von Frau Prof. Dr. 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.

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Des Weiteren ist mir bekannt, dass Unwahrhaftigkeiten hinsichtlich der vorstehenden Erklärung die Zulassung zur Promotion ausschließen bzw. später zum Verfahrensabbruch oder zur Rücknahme des erlangten Grades berechtigen.

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