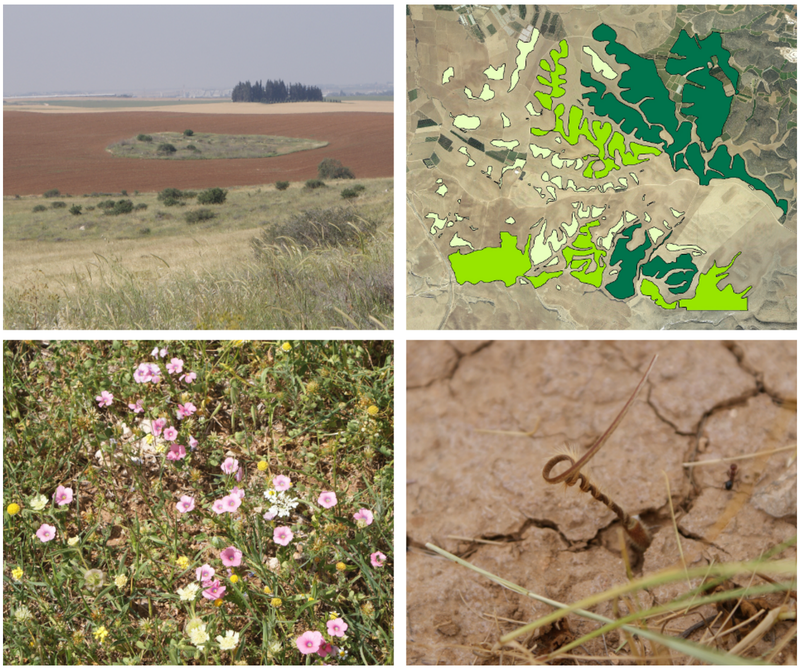
Dissertation

Spatial models of plant diversity and plant functional traits – towards a better understanding of plant community dynamics in fragmented landscapes

Felix May



Plant Ecology & Nature Conservation
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Die Welt, bedacht auf platten Nutzen,
sucht auch die Seelen auszuputzen;
Das Sumpf-Entwässern Wälder-Roden
schafft einwandfreien Ackerboden.
Und schon kann die Statistik prahlen
mit beispiellosen Fortschrittszahlen.
Doch langsam merken's auch die Deppen:
Die Seelen schwinden und versteppen!
Denn nirgends mehr, so weit man sieht,
gibt es ein Seelen-Schutzgebiet:
Kein Wald, drin Traumes Vöglein sitzen,
Kein Bach, drin Frohsinns Fischlein blitzen,
kein Busch, im Schmerz sich zu verkriechen,
kein Blümlein, Andacht draus zu riechen.
Nichts, als ein ödes Feld – mit Leuten
bestellt, es restlos auszubeuten.
Drum, wollt ihr nicht zugrunde gehen,
lasst noch ein bisschen Wildnis stehn!

(Eugen Roth)

Institut für Biochemie und Biologie
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Contents

Summary

The fragmentation of natural habitat caused by anthropogenic land use changes is one of the main drivers of the current rapid loss of biodiversity. In face of this threat, ecological research needs to provide predictions of communities' responses to fragmentation as a prerequisite for the effective mitigation of further biodiversity loss. However, predictions of communities' responses to fragmentation require a thorough understanding of ecological processes, such as species dispersal and persistence. Therefore, this thesis seeks an improved understanding of community dynamics in fragmented landscapes. In order to approach this overall aim, I identified key questions on the response of plant diversity and plant functional traits to variations in species' dispersal capability, habitat fragmentation and local environmental conditions. All questions were addressed using spatially explicit simulations or statistical models.

In chapter 2, I addressed scale-dependent relationships between dispersal capability and species diversity using a grid-based neutral model. In this context, the size of the entire grid is called "landscape size" and the size of the sub-grid, where local species richness was evaluated, is called "survey area". I found that the ratio of survey area to landscape size is an important determinant of scale-dependent dispersal-diversity relationships. With small ratios, the model predicted positive (increasing) dispersal-diversity relationships, while negative (decreasing) dispersal-diversity relationships emerged, when the ratio approached one, i.e. when the survey area approached the landscape size. For intermediate ratios, I found a U-shaped pattern that has not been reported before. With this study, I unified and extended previous work on dispersal-diversity relationships by using a spatially explicit approach and by analysing a wide parameter space with respect to survey areas, landscape sizes and dispersal kernels.

In chapter 3, I assessed the type of regional plant community dynamics (meta-community, mainland-island system or island communities) for the study area in the Southern Judean Lowlands (SJL). For this purpose, I parameterised a multi-species incidence-function model (IFM) with vegetation data using approximate Bayesian computation (ABC). I found that the type of regional plant community dynamics in the SJL is best characterized as a set of isolated “island communities” with very low connectivity between local communities. Model predictions indicated a significant extinction debt with 33% - 60% of all species going extinct within 1000 years. In general, this study introduces a novel approach for combining a spatially explicit simulation model with field data from species-rich communities. In contrast to previous correlative approaches, this inverse modelling approach is able to provide quantitative predictions of extinction debts in fragmented landscape.

In chapter 4, I first analysed, if plant functional trait distributions at several spatial scales in the SJL indicate trait convergence by habitat filtering and trait divergence by interspecific competition, as predicted by community assembly theory. For this purpose, I derived several community-level trait indices and applied different null-models of random community assembly. Second, I assessed the interactive effects of fragmentation and the south-north precipitation gradient in the SJL on community-mean plant traits. I found clear evidence for trait convergence, but the evidence for trait divergence fundamentally depended on the chosen null-model. If the null-model accounted for habitat filtering, there was no evidence for trait divergence. All community-mean traits were significantly associated with the precipitation gradient in the SJL. The trait associations with fragmentation indices (patch size and connectivity) were generally weaker, but statistically significant for all traits. Specific leaf area (SLA) and plant height were consistently associated with fragmentation indices along the precipitation gradient. In contrast, seed mass and seed number were interactively influenced by fragmentation and precipitation, i.e. their association with fragmentation indices varied along the precipitation gradient. In general, this study provides the first analysis of the interactive effects of climate and fragmentation on plant functional traits.

Overall, I conclude that the spatially explicit perspective adopted in this thesis is crucial for a thorough understanding of plant community dynamics in fragmented landscapes. The finding of contrasting responses of local diversity to variations in dispersal capability stresses the importance of considering the diversity and composition of the metacommunity, prior to implementing conservation measures that aim at increased habitat connectivity. The model predictions derived with the IFM highlight the importance of additional natural habitat for the mitigation of future species extinctions. In general, the approach of combining a spatially explicit IFM with extensive species occupancy data provides a novel and promising tool to assess the consequences of different management scenarios. The analysis of plant functional traits in the SJL points to important knowledge gaps in community assembly theory with respect to the simultaneous consequences of habitat filtering and competition. In particular, it demonstrates the importance of investigating the synergistic consequences of fragmentation, climate change and land use change on plant communities. I suggest that the integration of plant functional traits and of species interactions into spatially explicit, dynamic simulation models offers a promising approach, which will further improve our understanding of plant communities and our ability to predict their dynamics in fragmented and changing landscapes.

Zusammenfassung

Die Fragmentierung natürlicher Habitate durch anthropogenen Landnutzungswandel ist eine der Hauptursachen für den gegenwärtigen drastischen Verlust an Biodiversität. Angesichts dieser Gefährdung sind Vorhersagen der Reaktion von Artengemeinschaften auf Umweltveränderungen eine wichtige Voraussetzung für eine effektive Verminderung des weiteren Rückgangs der Biodiversität. Vorhersagen der Reaktion von Artengemeinschaften auf Fragmentierung erfordern jedoch ein umfassendes Verständnis ökologischer Prozesse, wie der Ausbreitung und der Persistenz von Arten. Diese Dissertation soll deshalb zu einem besseren Verständnis der Dynamik von Artengemeinschaften in fragmentierten Landschaften beitragen. Dementsprechend werden in dieser Dissertation die Reaktionen von Pflanzen-Diversität und funktionellen Pflanzeneigenschaften auf Veränderungen der Ausbreitungsfähigkeit von Arten, auf Habitatfragmentierung und auf lokale Umweltfaktoren untersucht. Für die Behandlung dieser Fragestellungen werden räumlich explizite Simulationen sowie statistische Modelle entwickelt und ausgewertet.

In Kapitel 2 werden skalenabhängige Beziehungen zwischen Ausbreitungsfähigkeit und Diversität mit Hilfe eines gitter-basierten, neutralen Modells untersucht. In diesem Zusammenhang werden die Größe des gesamten Gitters als „Landschaftsgröße“ und die Größe des Teilgitters, in dem die Artenzahl ausgewertet wurde, als „Erhebungsfläche“ bezeichnet. Es zeigte sich, dass der Quotient von Erhebungsfläche zu Landschaftsgröße eine entscheidende Einflussgröße für skalenabhängige Ausbreitungs-Diversitäts Beziehungen ist. Für niedrige Quotienten sagte das Modell positive (ansteigende) Ausbreitungs-Diversitäts Beziehungen vorher, während negative (absteigende) Ausbreitungs-Diversitäts Beziehungen entstanden, wenn der Quotient nahe eins war, d.h. wenn die Erhebungsfläche sich der Landschaftsgröße annäherte. Für mittlere Quotienten ergab sich ein U-förmiges Muster der Ausbreitungs-Diversitäts Beziehung, das in vorherigen Studien noch nicht beschrieben wurde. Mit dieser Studie werden somit frühere Arbeiten zu Ausbreitungs-Diversitäts-Beziehungen durch die Verwendung eines räumlich-expliziten Modells zusammengeführt und um die Untersuchung eines

umfassenden Parameterraumes im Hinblick auf Erhebungsflächen, Landschaftsgrößen und Ausbreitungsdistanzen erweitert.

In Kapitel 3 wird der Typ der regionalen Dynamik der Pflanzengemeinschaften (Meta-Gemeinschaft, Festland-Insel System oder Insel-Gemeinschaften) im Untersuchungsgebiet Süd-Judäisches-Hügelland (engl. Southern Judean Lowlands – SJL) analysiert. Zu diesem Zweck wurde ein Modell für die Auftretenswahrscheinlichkeit von Arten (engl. Incidence-Function Model – IFM) mit Hilfe eines approximativen Bayes'schen Verfahrens (ABC) parametrisiert. Der Typ der regionalen Dynamik der Pflanzengemeinschaften im SJL konnte am plausibelsten als Ensemble von isolierten Insel-Gemeinschaften mit sehr geringer Konnektivität zwischen den lokalen Gemeinschaften charakterisiert werden kann. Das Modell sagte eine signifikante „extinction debt“, d.h. eine beträchtliche Zahl an zukünftigen Extinktionsereignissen voraus. Innerhalb von 1000 Jahren würden demnach zwischen 33% und 60% aller Arten aussterben. Damit liefert diese Studie einen neuen Ansatz für die Verknüpfung räumlich expliziter Modelle mit Felddaten artenreicher Gemeinschaften. Im Gegensatz zu bisherigen korrelativen Ansätzen ist der hier vorgestellte inverse Modellierungsansatz in der Lage quantitative Vorhersagen über die Anzahl zukünftig aussterbender Arten in fragmentierten Landschaften zu treffen.

In Kapitel 4 wird zum einen untersucht, ob Verteilungen von funktionellen Pflanzeneigenschaften auf verschiedenen räumlichen Skalen im SJL die Vorhersagen aktueller Theorien zur Zusammenstellung von Pflanzengemeinschaften bestätigen. Demzufolge führt die Anpassung an lokale Umweltbedingungen („habitat filtering“) zu Konvergenz und zwischenartliche Konkurrenz zu Divergenz von funktionellen Eigenschaften bei gemeinsam auftretenden Arten. Zum anderen werden die interagierenden Auswirkungen der Fragmentierung und des Süd-Nord Niederschlagsgradienten im SJL auf die mittleren Eigenschaften der Pflanzengemeinschaften („community-mean traits“) analysiert. Zu diesem Zweck wurden aus den funktionellen Eigenschaften mehrere Indizes zur Charakterisierung der Pflanzengemeinschaften berechnet und verschiedene Null-Modelle für die zufällige Zusammenstellung von Pflanzengemeinschaften verwendet. Die Konvergenz von funktionellen Eigenschaften durch „habitat filtering“ konnte klar nachgewiesen werden. Im Gegensatz dazu war der Nachweis der Divergenz von funktionellen Eigenschaften durch zwischenartliche Konkurrenz grundlegend abhängig von dem verwendeten Null-Modell. Sobald das Null-Modell „habitat-filtering“ berücksichtigte, zeigten die Daten keine Divergenz der funktionellen Eigenschaften.

Alle gemittelten Eigenschaften der Pflanzengemeinschaften zeigten einen signifikanten Zusammenhang mit dem Niederschlagsgradienten im SJL. Der Zusammenhang der Eigenschaften mit Fragmentierungs-Indizes (Patch-Größe und Patch-Konnektivität) war generell schwächer, aber statistisch signifikant für alle gemittelten Eigenschaften. Die spezifische Blattfläche (SLA) und die Pflanzenhöhe zeigten einen konsistenten Zusammenhang mit den Fragmentierungs-Indizes über den gesamten Niederschlagsgradienten. Im Gegensatz dazu wurden die mittlere Samenmasse und Samenanzahl durch die Interaktion von Fragmentierung und Niederschlag bestimmt, d.h. der Zusammenhang zwischen diesen Eigenschaften und den Fragmentierungs-Indizes veränderte sich signifikant über den Niederschlagsgradienten. Diese Studie analysiert erstmals die interagierenden Auswirkungen des Klimas und der Fragmentierung auf funktionelle Pflanzeneigenschaften.

Zusammenfassend lässt sich schlussfolgern, dass die in dieser Arbeit verwendete räumlich explizite Betrachtungsweise von grundlegender Bedeutung für ein umfassendes Verständnis der Dynamik von Pflanzengemeinschaften in fragmentierten Landschaften ist. Das Ergebnis von gegensätzlichen Reaktionen der lokalen Diversität auf Veränderungen der Ausbreitungsfähigkeit macht deutlich, dass Diversität und Zusammensetzung der potentiellen Meta-Gemeinschaft berücksichtigt werden müssen, wenn beispielsweise durch Naturschutzmaßnahmen die Habitat-Konnektivität erhöht werden soll. Die Modellvorhersagen des IFM verdeutlichen die Bedeutung von zusätzlichen Flächen für natürliche Sukzession, um zukünftige Extinktionen zu vermeiden. Generell bietet die Verknüpfung eines räumlich expliziten IFM mit Daten zur Verbreitung von Arten einen neuen und vielversprechenden Ansatz für die Untersuchung der Auswirkungen verschiedener Management-Szenarien. Die Analyse der funktionellen Pflanzeneigenschaften im SJL zeigt wesentliche Wissenslücken auf, vor allem in Bezug auf die simultanen Auswirkungen abiotischer Umweltbedingungen und biotischer Interaktionen. Insbesondere verdeutlicht die Studie die hohe Relevanz der Untersuchung von Synergie-Effekten der Konsequenzen von Fragmentierung, Klimawandel und Landnutzungswandel auf Pflanzengemeinschaften. Die Integration von funktionellen Eigenschaften und biotischen Interaktionen in räumlich explizite, dynamische Simulationsmodelle bietet einen vielversprechenden Ansatz zum einen zur Vertiefung des Verständnisses von Artengemeinschaften und zum anderen zur Verbesserung von Vorhersagen der Dynamik von Artengemeinschaften in fragmentierten Landschaften.

Chapter 1

General introduction

1.1 Motivation – habitat fragmentation and biodiversity loss

Currently, we witness a rapid and unprecedented decline of biodiversity, which is expected to continue or even accelerate during the next decades (Sala *et al.* 2000; Millennium Ecosystem Assessment 2005). This alarming decline has been primarily caused by human activities, with the most important drivers of biodiversity loss being land use change, climate change, invasive species, overexploitation of ecosystems, and increased nutrient loadings (Millennium Ecosystem Assessment 2005). Among these drivers, the fragmentation of natural habitats caused by anthropogenic land use changes poses one of the greatest threats to biodiversity (Fahrig 2003; Millennium Ecosystem Assessment 2005). In an extensive global assessment, Sala *et al.* (2000) predicted that land use change will be the most important driver of biodiversity loss up to 2100. Furthermore, drivers such as habitat fragmentation and climate change do not influence biodiversity independently, but will likely affect populations, communities and ecosystems synergistically (Sala *et al.* 2000; Travis 2003; Opdam & Wascher 2004; Ewers & Didham 2006; Brook *et al.* 2008; Jeltsch *et al.* 2011).

In face of these threats to biodiversity, the tasks of projecting communities' responses to environmental changes and of developing effective conservation measures have gained high priority in ecological research during the last decades (Clark *et al.* 2001a; Dawson *et al.* 2011; McGill *et al.* 2006). However, the response of ecological communities to habitat fragmentation is inherently linked to species' habitat requirements and ecological processes, such as dispersal, regeneration, persistence and biotic interactions (Geertsema *et al.* 2002; Ewers & Didham 2006). Therefore, a thorough understanding of ecological processes and their relationship to environmental drivers is a fundamental requirement in order to project communities' responses to fragmentation and to implement effective conservation measures (Clark *et al.* 2001a; Dawson *et al.* 2011; McGill *et al.* 2006).

The ability of organisms to move, migrate or disperse within fragmented landscapes is a pivotal process for their response to habitat fragmentation and their survival in changing environments (Trakhtenbrot *et al.* 2005; Nathan *et al.* 2008). Plants, as sessile organisms, can only move once in their life cycle – as a seed – and are therefore expected to "perceive" habitat fragmentation differently than mobile animals (Damschen *et al.* 2008). The specific characteristics of seed dispersal and plant species persistence have fuelled a controversial and on-going debate on plant population and community dynamics in fragmented landscapes (Eriksson 1996; Freckleton & Watkinson 2002, 2003; Ehrlén & Eriksson 2003; Alexander *et al.* 2012). This debate indicates that our knowledge concerning the dynamics of plant communities at the landscape scale is still limited. However, understanding plant species dispersal and persistence is crucial in order to project the response of plant diversity to fragmentation. Consequently, this thesis was motivated by the need to improve our mechanistic understanding of plant community dynamics in fragmented landscapes. With the research presented in this thesis I aimed at developing and testing tools for the assessment of plant community dynamics and for projections of plant community responses to present and future habitat fragmentation.

1.2 Theories and concepts of plant population and community dynamics in fragmented landscapes

During the last decades, different concepts and theories emerged that highlight habitat availability and configuration as important determinants of population and community dynamics in heterogeneous or fragmented landscapes. One theory that profoundly influenced ecologists' perspective on community dynamics in fragmented landscapes is MacArthur's and Wilson's equilibrium theory of island biogeography (MacArthur & Wilson 1963, 1967). According to their ideas, the species richness of communities on islands emerges as a dynamic equilibrium balancing species immigrations and extinctions. MacArthur & Wilson (1963) suggested that this dynamic equilibrium is primarily determined by the area of an island and its distance to the "mainland". The mainland is assumed to contain a constant species pool and to provide a propagule rain of potential immigrants to the islands. The immigration rate into an island – measured as number of species per unit time – is assumed to decrease with increasing distance between island and mainland, as most propagules are expected to be dispersed over short distances and only few over long distances from the mainland. With respect to species persistence, smaller islands are expected to hold smaller populations, which face a higher risk of extinction due to higher demographic stochasticity. Therefore, the extinction rate of an island is assumed to increase with decreasing island size.

The equilibrium theory of island biogeography drastically changed the prevailing view on biogeography and community dynamics in two important aspects: First, the theory does not focus on static species-environment relationships, but stresses a dynamic perspective on biodiversity, considering the processes dispersal, colonization, survival and extinction. Second, by assuming a decrease of immigration rates with increasing mainland-island distance, the theory highlights dispersal limitation as an essential determinant of community dynamics at the landscape scale (Hubbell 2001).

Later studies modified several simplifying assumptions of MacArthur's and Wilson's original theory, for instance by considering species survival in the matrix, edge effects, differences between islands other than size and distance to the mainland, and non-equilibrium dynamics (Brown & Lomolino 2000; Cook *et al.* 2002; Heaney 2000; Laurance 2008). However, the basic ideas of the equilibrium theory of island biogeography provided a basis for further theoretical development and still clearly shape the current perspective on population and community dynamics in fragmented landscapes.

The application of spatial colonization-extinction dynamics at the population level led to the development of the metapopulation concept (Levins 1969; Levins & Culver 1971; Hanski 1999). Accordingly, a metapopulation has been defined as a set of local populations in spatially isolated habitat patches, which are partially connected by dispersal (Hanski 1999). The key idea of the metapopulation concept suggests that a species in a fragmented landscape can persist as a "metapopulation" even if each local population carries a significant risk of local extinction. The mechanism that allows persistence at the landscape scale is the (re)colonization of empty habitat patches by propagule input from occupied patches (Hanski 1999). In comparison to the theory of island biogeography, the metapopulation concept demonstrated that connectivity among habitat patches by propagule exchange can facilitate species persistence in fragmented landscapes, even if there is no mainland with indefinite species persistence.

Based on the ideas of the equilibrium theory of island biogeography, Bell (2000) and Hubbell (2001) independently developed the neutral theory of biodiversity and biogeography. This theory was built on the premises that all species share equal *per-capita* demographic rates of birth, death, and dispersal and that community dynamics are entirely governed by ecological drift, including random speciation and extinction events. Therefore, according to the neutral theory, also ecological key patterns, such as species richness, relative abundance distributions and species-area relationships emerge from pure ecological drift and dispersal limitation (Hubbell 2001). Due to its claim for generality and due to the radical assumption of species per-capita equivalence, the neutral theory has arguably initiated the most prominent controversial debate in community ecology during the last decades (e.g. McGill 2003; Chave 2004; Chase 2005; Hubbell 2005; Clark 2009). However, it has generally been acknowledged that the neutral theory provides a comprehensive null-model for highly diverse communities (Alonso *et al.* 2006; Rosindell *et al.* 2011). In comparison to the theory of island biogeography, which considers immigration and extinction rates in the unit of "number of species per time", the major conceptual advance of the neutral theory has been the specification of birth, death and dispersal rates on a *per-capita* level (Hubbell 2001; Rosindell *et al.* 2011). In this way, the neutral theory consistently links demographic processes at the individual level to patterns at the community level and thus provides an important conceptual basis for process-based and mechanistic understanding of biodiversity and biogeography.

The most recent conceptual development with respect to community dynamics in fragmented and heterogeneous landscapes is the metacommunity concept (Leibold *et al.* 2004; Holyoak *et al.* 2005). Leibold *et al.* (2004) defined a metacommunity as *" . . . a set of local communities that are linked by dispersal of multiple potentially interacting species"*. Accordingly, the metacommunity concept rather provides an ecological framework, which embraces many previously existing ideas, than a closed theory with specific assumptions and predictions. For instance, the theory of island biogeography and the neutral theory are included in the metacommunity concept as special cases with extreme assumptions on the asymmetry of dispersal – from the mainland to islands only – or on species *per-capita* equivalence, respectively. The theory of island biogeography and the metapopulation concept primarily focus on the regional processes of dispersal and patch connectivity, but considered local processes within habitat patches only in a highly simplified way. In contrast, the metacommunity concept explicitly aims at considering local community dynamics *and* the influence of dispersal and migration (Leibold *et al.* 2004). Thereby, the metacommunity concept highlights the importance of feedbacks between local and regional scales for dynamics at the landscape scale (Leibold *et al.* 2004; Holyoak *et al.* 2005).

Leibold *et al.* (2004) identified four perspectives on metacommunities: the patch-dynamics, the species-sorting, the mass-effects and the neutral perspective. Two of these – the species-sorting and the mass effects perspectives – stress the importance of species' niche differentiation along environmental gradients. From these perspectives, species with different functional trait attributes are adapted to distinct environmental conditions. During community assembly, these trait and niche differences translate into spatially segregated species distributions. This process, which is known as "habitat filtering", thus drives the relationship between species' traits and the environment they occupy (Ackerly & Cornwell 2007; Weiher *et al.* 2011). Considering the species-sorting and mass-effects perspectives, the metacommunity concept acknowledges the relationship between functional traits and species' niches as a general principle of community ecology (Schimper 1898; Whittaker 1975; McGill *et al.* 2006).

In this context, the analysis of plant functional traits has been suggested as a promising approach, first, to gain an improved understanding of the processes that drive community assembly in heterogeneous landscapes (Cornwell & Ackerly 2009; Kraft & Ackerly 2010; Weiher *et al.* 2011) and second, to gain knowledge of plant communities' responses to environmental drivers that can be generalized over specific locations and floral compositions (Westoby *et al.* 2002; Westoby & Wright 2006). Ultimately, functional trait research is motivated by the idea that a thorough understanding of current trait distributions within and among plant communities facilitates robust and transferable predictions of community responses to environmental changes (Díaz & Cabido 1997; Lavorel & Garnier 2002; McGill *et al.* 2006).

1.3 Research questions and objectives

The overall aims of this thesis are to improve our understanding of plant community dynamics in fragmented landscapes and to improve our ability to project communities' responses to current and future habitat fragmentation. In order to approach these general aims systematically, in this section I identify essential and specific research questions. These questions are then addressed consecutively in the chapters of this thesis.

All theories and concepts introduced above include the assumption that dispersal among habitat patches is an important process for population and community dynamics in fragmented landscapes. In particular, the neutral theory highlights dispersal limitation as a key determinant of species diversity (Hubbell 2001; Chave *et al.* 2002). A crucial issue in this context is the scale-dependence of the relationship between diversity and species' dispersal capabilities. Previous metacommunity models, including implementations of the neutral theory, predicted that increasing dispersal capability increases diversity at the local scale by increasing the rate of species immigrations, but reduces diversity at the regional (or metacommunity) scale by reducing species' spatial segregation and thus increasing the intensity of interspecific competition (Hubbell 2001; Levine & Murrell 2003). However, this conclusion was derived from spatially implicit models that use a dichotomous distinction between local and regional scales and completely neglect dispersal limitation at the local scale (Hubbell 2001; Economo & Keitt 2008). This artificial separation of scales and the spatially unrealistic representation of dispersal might impede general conclusions on the scale-dependent relationship between diversity and dispersal capability. Therefore, in this thesis I address the question how dispersal capability will affect species diversity along a continuous set of scales, if dispersal is modelled in a spatially explicit way.

In plant ecology, different perspectives on the role of seed dispersal for connectivity among habitat patches have led to an intensive debate, if and how metapopulation and metacommunity concepts can be applied to plants (Eriksson 1996; Bullock *et al.* 2002; Freckleton & Watkinson 2002, 2003; Ehrlén & Eriksson 2003; Alexander *et al.* 2012). On the one hand, seed dispersal is usually restricted to relatively short distances (Willson 1993; Venable *et al.* 2008), while on the other hand, even rare long-distance dispersal events can have important consequences for population and community dynamics at the landscape scale (Nathan 2006). Therefore, different types of regional plant population and community dynamics have been suggested, ranging from completely isolated populations and communities to well-connected metapopulations and metacommunities (Freckleton & Watkinson 2002; Alexander *et al.* 2012). This issue also concerns differences between the theory of island biogeography and the metacommunity concept. For fragmented landscapes it is a highly relevant question, whether (i) species diversity depends on propagule exchange among small habitat fragments, or (ii) species diversity is maintained by propagule immigration from a mainland species pool, or (iii) local communities can persist without propagule input (Freckleton & Watkinson 2002). For this reason, I developed a modelling approach to assess the type of regional community dynamics in fragmented landscapes. I applied this approach using field data from species-rich plant communities in Israel.

The theory of island biogeography and the neutral theory have been usually applied to provide predictions of species diversity or abundance distributions in a dynamic equilibrium between immigrations and extinctions (MacArthur & Wilson 1967) or speciation and extinction events (Hubbell 2001). However, in real landscapes there is a time lag between environmental perturbations, for instance habitat fragmentation, and the response of plant communities. Especially in recently fragmented landscapes, community dynamics are more likely to be in a transient phase than in dynamic equilibrium (Jackson & Sax 2009). Time lags can cause a significant decline of species diversity, even in periods without further fragmentation or changes of other environmental drivers. This phenomenon is known as the "extinction debt", which specifies the number of species going extinct during the period of transient dynamics following an environmental perturbation (Tilman *et al.* 1994).

For plant communities in fragmented landscapes, several studies assessed the evidence for an extinction debt from field observations of species distributions and past as well as present habitat configurations (reviewed in Cousins 2009). While these observational approaches are an important first step, they are not able to project future extinction rates with or without certain conservation measures. The projection of transient community dynamics following environmental changes currently poses a major challenge in conservation biology (Jackson & Sax 2009). Especially for species-rich plant communities there is a lack of approaches that link a dynamic community model to field data from fragmented landscapes. Therefore, I also applied the dynamic simulation model, which I used to assess the type of regional community dynamics, to derive projections and uncertainty estimates of the extinction debt in a fragmented landscape in Israel.

In contrast to the theory of island biogeography and the neutral theory, the metacommunity concept acknowledges the importance of functional traits for species distributions in heterogeneous landscapes (Leibold *et al.* 2004). In this context, several studies addressed the relationship between plant functional traits and habitat fragmentation (Dupré & Ehrlén 2002; Kolb & Diekmann 2005; Hérault & Honnay 2005; Lindborg 2007; Schleicher *et al.* 2011; Lindborg *et al.* 2012). However, all of these studies were conducted in plant communities located in the temperate region of Europe. As plant communities are expected to be driven by multiple interacting factors, particularly climate change and habitat fragmentation, there is a lack of studies analysing fragmentation effects on plant functional trait distributions in different climate zones or along climatic gradients (De Bello *et al.* 2005; Chust *et al.* 2006). Therefore, I address the questions: (i) Which community assembly processes drive the distribution of plant functional traits among and within communities? (ii) If and how does the association between plant functional traits and habitat fragmentation change along a precipitation gradient at the transition zone between Mediterranean and desert ecosystems?

In order to consecutively address these research questions, I chose different methodological approaches, depending on the scope of the question, the limitations of previous approaches and the availability of data. All approaches used in this thesis have in common that they aim at considering the key processes of dispersal and habitat connectivity in a spatially realistic way. The research questions outlined above can be summarized and specified as the following objectives of this thesis:

1. Assessment of the scale-dependent relationship between plant species diversity and dispersal capability (chapter 2).
2. Assessment of the type of regional community dynamics (metacommunity, mainland-island system or island communities) in a fragmented, species-rich landscape (chapter 3).
3. Estimation of the extinction debt in this landscape (chapter 3).
4. Assessment of the effects of community assembly processes, such as habitat filtering and interspecific competition, on plant functional trait distributions at different spatial scales (chapter 4).
5. Assessment of the association between plant functional traits and habitat fragmentation and the change of this association along a precipitation and productivity gradient (chapter 4).

1.4 Study system

The Mediterranean basin has been highlighted as a global biodiversity hot-spot due to its high proportion of endemic plant species and as a region with high priority for conservation due to an intensive rate of habitat fragmentation (Myers *et al.* 2000). According to model projections, regions with Mediterranean climate are expected to experience the highest losses of biodiversity world-wide, especially if habitat fragmentation and climate change show synergistic effects on biodiversity (Sala *et al.* 2000). Therefore, thorough understanding of plant community dynamics as prerequisite for conservation is urgently needed in the Mediterranean.

In this thesis, I focus on species-rich plant communities in the Southern Judean Lowlands (SJL) in Israel. This landscape is located at the transition zone between the Negev desert and the Mediterranean region and is characterized by a steep south-north precipitation and productivity gradient with an increase from ca. 300 mm/year in the south to ca. 400 mm/year in the north over a S-N distance of 30 km only (Giladi *et al.* 2011). The natural vegetation consists of scrubland and grassland and comprises 400 – 500 vascular plant species in an area of 30 km (S-N) × 5 km (E-W).

The study area in the Southern Judean Lowlands can be characterized as a mosaic of natural vegetation patches embedded in an agricultural matrix (Yaacobi *et al.* 2007; Giladi *et al.* 2011). Due to agriculture practices, including ploughing, the natural vegetation patches feature distinct boundaries and the matrix can be considered as hostile and unsuitable for the plant species occurring in the natural vegetation patches. Therefore, the study area closely resembles a patch-matrix system as postulated in the theory of island-biogeography and in the metapopulation concept. The sizes of the patches range from very small (ca. $100\,\mathrm{m}^2$) up to continuous habitat areas of more than 100 ha. Habitat patches of different sizes and of different degrees of isolation can be found everywhere along the S-N precipitation gradient. For these reasons, this study area is well suited to study the interacting effects of habitat fragmentation and precipitation on plant diversity (Giladi *et al.* 2011) and on plant species functional traits (chapter 4).

1.5 Habitat fragmentation – terminology

The term “habitat fragmentation” has been used in different ways, which has lead to partly inefficient debates on the relationship between fragmentation, diversity and community composition (Lindenmayer & Fischer 2007). In this thesis, using the term habitat fragmentation I distinguish the two processes habitat loss and fragmentation “per se” (Fahrig 2003; Ewers & Didham 2006). Habitat loss refers to the conversion of suitable habitat into matrix, which is unsuitable for the target species or target community under consideration. An example for habitat loss is the conversion of natural scrub- and grassland into intensively used cropland. Habitat loss is specified in changes of the area of suitable habitat vs. unsuitable matrix without considering the spatial configuration of the remaining habitat. In contrast, fragmentation "per se" refers to the spatial configuration of a given total habitat area. Increasing fragmentation "per se" is indicated by increasing patch isolation or reduced patch connectivity, respectively, without variation of the total habitat area.

In real landscapes, habitat loss and fragmentation "per se" tend to be highly correlated, as the conversion of suitable habitat into matrix usually results in higher isolation of the remaining habitat fragments (Fahrig 2003). Despite this close correlation, habitat loss and fragmentation "per se" are expected to have distinct ecological consequences. According to the theory of island biogeography and the metapopulation concept, habitat loss primarily drives (local) species extinctions, while fragmentation "per se" limits propagule exchange and thus the connectivity between habitat patches (Hanski 1999). Therefore, in the models and analyses presented in this thesis, I aim at separating the effects of habitat loss and fragmentation "per se" in order to assess their implications for different ecological processes and thus for community dynamics. Throughout this thesis, I focus on species-rich communities of vascular plants. Therefore, the use of the terms "habitat fragmentation" and "suitable habitat" vs. "unsuitable matrix" refers to the habitat requirements of the whole community and distinguishes natural scrub- and grassland from agricultural cropland if not specified further.

1.6 Outline of the thesis

The outline of this thesis corresponds to the questions and objectives described in section 1.3. The five objectives are addressed in three separate chapters, as the objectives 2 and 3 are approached using the same simulation model and the objectives 4 and 5 are approached using the same data set of plant functional traits.

In chapter 2, I analyse scale-dependent relationships between plant species richness and dispersal capability (objective 1). For this purpose, I used a general, spatially explicit neutral model that allows assessing a wide range of spatial scales and testing a broad parameter space of dispersal capabilities, speciation rates and landscape sizes. This conceptual modelling study unifies previous work on dispersal-diversity relationships and provides important general insights into the effects of dispersal capability on species diversity at different spatial scales.

In chapter 3, I investigate the landscape-scale community dynamics in the study area in Israel. Using a multi-species, spatially explicit incidence-function model (IFM) in combination with extensive vegetation data, I answer the question, which of the three types of regional dynamics (i) the metacommunity, (ii) the mainland-island or (iii) the island communities type, best reflects community dynamics in the study area (objective 2). For the estimation of model parameters, I used recently developed techniques of Approximate Bayesian Computation (ABC). With model simulations, I provided projections of the long-term extinction debt in the landscape including an assessment of the uncertainty of these projections (objective 3).

Changing the focus to plant functional traits in chapter 4, I first assess the effects of the community assembly processes habitat filtering and interspecific competition on plant functional trait distributions (objective 4). Second, I analyse the association of plant functional traits with habitat fragmentation along the S-N precipitation gradient in our study area (objective 5). These analyses are based on extensive field data of species' distributions and functional traits collected in the SJL. I used a comprehensive set of community-level trait indices and several null-models of random community assembly for the first part of chapter 4. In the second part, I used an improved connectivity index that considers patch shapes, as well as linear mixed-effect models to account for the spatially nested structure of the data, when testing for associations between plant traits, fragmentation indices and the position along the S-N gradient.

In the last chapter, I summarize and synthesize the main findings from the single chapters and discuss their implications within the context of plant community ecology and conservation biology. Finally, I reflect the limitations of the approaches used and propose directions for further research on plant community dynamics in fragmented landscapes.

Chapter 2

Dispersal and diversity – unifying scale-dependent relationships within the neutral theory [1]

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[1] An article with equivalent content was published as:
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Abstract

The response of species diversity to dispersal capability is inherently scale-dependent: Increasing dispersal capability is expected to increase diversity at the local scale, while decreasing diversity at the metacommunity scale. However, these expectations are based on model formulations that neglect dispersal limitation and species segregation at the local scale.

We developed a unifying framework of dispersal-diversity relationships and tested the generality of these expectations. For this purpose we used a spatially explicit neutral model with various combinations of survey area (local scale) and landscape size (metacommunity scale). Simulations were conducted using landscapes of finite and of conceptually infinite size. We analysed the scale-dependence of dispersal-diversity relationships for exponentially-bounded vs. fat-tailed dispersal kernels, several levels of speciation rate and contrasting assumptions on recruitment at short dispersal distances.

We found that the ratio of survey area to landscape size is a major determinant of dispersal-diversity relationships. With increasing survey-to-landscape area ratio the dispersal-diversity relationship switches from monotonically increasing through a U-shaped pattern (with a local minimum) to a monotonically decreasing pattern. Therefore, we provide a continuous set of dispersal-diversity relationships, which contains the response shapes reported previously as extreme cases. We suggest the mean dispersal distance with the minimum of species diversity (minimizing dispersal distance) for a certain scenario as a key characteristic of dispersal-diversity relationships. We show that not only increasing mean dispersal distances, but also increasing variances of dispersal can enhance diversity at the local scale, given a diverse species pool at the metacommunity scale.

In conclusion, the response of diversity to variations of dispersal capability at spatial scales of interest, e.g. conservation areas, can differ more widely than expected previously. Therefore, manipulations of dispersal capability need to consider the landscape context and potential species pools carefully.

2.1 Introduction

Studies of plant communities incorporating spatial aspects in species interactions identified dispersal as an important determinant of species diversity (Chave *et al.* 2002; Bolker *et al.* 2003; Levine & Murrell 2003; Mouquet & Loreau 2003). One theory that gained remarkable prominence in this context is the neutral theory of biodiversity and biogeography (UNTB) (Bell 2001; Hubbell 2001). In addition to the radical assumption of species per-capita ecological equivalence, the UNTB highlights dispersal limitation as a key factor affecting community diversity and species relative abundances (Hubbell 2001) and acknowledges that the effect of dispersal capability on diversity is inherently scale dependent. Hubbell used a simple spatial simulation model to show that diversity at the scale of the local community (α-diversity) increases, but diversity at the metacommunity scale (γ-diversity) decreases with increasing dispersal capability (Hubbell 2001, pg. 218). Recently Economo & Keitt (2008) and Vanpeteghem & Haegeman (2010) confirmed these results using an analytical approach for neutral metacommunities that are represented as networks of habitat patches.

The positive response of α-diversity to an increasing dispersal capability can be explained from a metacommunity perspective (Leibold *et al.* 2004). If local communities within a metacommunity are linked by dispersal, spatial mass effects can establish source-sink relationships between these communities. Sink populations maintained by immigration can substantially increase α-diversity, for instance by contributing to a higher number of locally rare species (Shmida & Ellner 1984; Loreau & Mouquet 1999; Pulliam 1988, 2000; Esther *et al.* 2008; Gardner & Engelhardt 2008). This argumentation is supported by many experiments where seed introduction, which mimics dispersal among local communities, leads to an increase of local diversity (Tilman 1997; Hubbell *et al.* 1999; Turnbull *et al.* 2000; Ehrlén *et al.* 2006; Cadotte 2006a; Stein *et al.* 2008).

The negative response of γ-diversity to increasing dispersal capability can be explained considering spatially limited dispersal and local competitive interactions (Weiner & Conte 1981; Pacala 1997; Bolker & Pacala 1999; Murrell & Law 2003). Low dispersal capability leads to aggregation of conspecific individuals and consequently to the spatial segregation of species. If individuals are restricted to interact locally, there will be a relative increase of intraspecific interactions compared to interspecific ones. Therefore, low dispersal capability is expected to slow down competitive exclusion and ecological drift and thus favours high species diversity (Chave *et al.* 2002; Levine

& Murrell 2003). This mechanism of species coexistence was called the "spatial segregation hypothesis" by Pacala (1997). Empirical evidence for the negative response of γ-diversity to increasing dispersal in plant communities is scarce, as it is extremely difficult to manipulate dispersal capability and trace the community response at the metacommunity scale (Cadotte 2006a). However, experiments of plant-plant competition confirmed that the spatial aggregation of conspecific individuals, which is consistent with low dispersal capability, can indeed influence species performance and therefore community diversity (Stoll & Prati 2001).

Consequently, in order to understand the scale-dependent response of diversity to dispersal one must consider the spatial scales of dispersal and of local interactions. In that context, it is important to note that the neutral models mentioned above, use a dichotomous, conceptual distinction between local and metacommunity scales and consider dispersal limitation and species segregation only between, but not within local communities (Hubbell 2001; Economo & Keitt 2008; Vanpeteghem & Haegeman 2010). When contrasted with real data, the distinction made by such models between local and metacommunity is usually related to the sampling design, rather than to the scales at which important ecological processes operate. Since in reality, dispersal operates in a continuous space, it remains unclear whether neutral, spatially implicit models can provide realistic predictions for the relationship between diversity and dispersal capability at the local scale.

Spatially explicit extensions of the neutral model provide the possibility to overcome this limitation. So far such models have been used to analyse the response of γ-diversity to variations in dispersal capability (Chave & Leigh 2002; Condit *et al.* 2002) or to study species-area curves (Rosindell & Cornell 2007, 2009; O'Dwyer & Green 2010). However, to the best of our knowledge there has been no study, which relaxes the conceptual distinction between local- and metacommunity and addresses the effect of dispersal capability on α-diversity in detail.

Here we strive to fill this gap and present a framework that can accommodate several response types of diversity to dispersal (hereafter called "dispersal-diversity relationships") at several spatial scales. For this purpose, we used a spatially explicit neutral model with one individual per grid cell and simulated metacommunities within landscapes of different extents. Within these landscapes we analysed species richness in survey areas of different sizes, avoiding an ad hoc definition of a "local community" of fixed size. With this approach we will answer the following questions: (i) What are the combinations of survey area and landscape size, where increasing or decreasing dispersal-diversity relationships emerge? (ii) Are there combinations of survey area and landscape size, where both positive and negative effects of dispersal on local diversity emerge and the dispersal-diversity relationship features a local minimum or maximum? (iii) If yes, what is the characteristic scale of dispersal where local diversity is minimized or maximized?

2.2 Methods

2.2.1 The model

The model used for this study is a spatially explicit version of the neutral theory (Chave *et al.* 2002). The landscape is represented as a square lattice, where sessile individuals compete for space. The landscape is saturated with individuals, i.e. each grid cell is occupied by one individual at any given time according to the assumption of zero-sum dynamics (Hubbell 2001; Chave & Leigh 2002; Chave *et al.* 2002). Each time step, one individual dies at random irrespective of species identity or location and the evacuated microsite is immediately colonized by a new individual. The new individual can be either an offspring of another individual within the landscape, or it may originate from a speciation event, thus introducing a novel species to the community.

In the first case the parent individual is assigned by randomly choosing direction and distance from the vacant cell as follows: A random point within the focal cell is chosen. Then a random draw from a given dispersal kernel (see below) determines the distance to the parent cell and the direction is drawn from a circular uniform distribution in the interval $[0, 2\pi]$ assuming isotropic dispersal. The choice of a random point within the focal cell, rather than assuming that an individual is located in the cell centre, was implemented in order to minimize the effect of the discrete cell size.

For each single birth-death event the possibility of speciation is considered. The parameter speciation rate ν provides the probability that the newborn individual belongs to a novel species that has not been in the community before, corresponding to the case of speciation by point mutation (Hubbell 2001; Rosindell & Cornell 2007). For the choice of parent individuals within the landscape, we use two different dispersal kernels (i) the negative exponential kernel (Eq. 2.1), where the mean and the standard deviation of dispersal distance (r) are given by the parameter α (Clark *et al.* 1998, 1999) or (ii) the log-normal kernel (Eq. 2.2), where the mean and the standard deviation of the log-transformed dispersal distance are given by the parameters μ and σ, respectively. The log-normal kernel allows us to study the effect of “fat-tailed” dispersal, i.e. a higher probability of long-distance dispersal events compared to the negative-exponential kernel (Nathan & Muller-Landau 2000; Stoyan & Wagner 2001).

$$k_{\text{NExp}}(r) = \frac{1}{\alpha} \cdot \exp\left(-\frac{r}{\alpha}\right) \tag{2.1}$$

$$k_{\text{LNorm}}(r) = \frac{1}{\sqrt{2\pi}\sigma r} \cdot \exp\left(-\frac{(\ln(r)-\mu)^2}{2\sigma^2}\right) \tag{2.2}$$

Furthermore, we use two different model versions to distinguish the effects of very short dispersal distances. In the first version we allow “within-cell recruitment” whenever the random location of the parent individual lies within the vacant cell. This assumption mimics the in-situ replacement of the mother plant by its own offspring (Willson 1993; Clark *et al.* 1998; Venable *et al.* 2008). In the second model version we do not allow “within-cell recruitment”. In this case we discard draws that positioned the parent within the vacant cell and repeat drawing from the dispersal kernel until a parent individual outside of the vacant cell is found.

As an output, the model derives species richness of a square survey area with ${N_{Survey}}^2$ grid cells and thus ${N_{Survey}}^2$ individuals. This survey area is located in a landscape that is a square grid as well, but with a side length of $N_{Landscape}$ grid cells. In order to simulate the equilibrium species richness of the survey area, we make use of the coalescence approach to neutral ecology, which is described in detail in Rosindell *et al.* (2008). Instead of starting from an arbitrary initial state and simulating forward in time until any criteria for convergence to equilibrium are fulfilled, simulations proceed backwards in time constructing the ancestry (or phylogeny) of all individuals in the survey area. The sequence of ancestors belonging to each microsite is considered as one lineage. A common ancestry of two lineages implies that they belong to the same species. Following all lineages until the most recent speciation event in their ancestry directly leads to a realization of the equilibrium state without additional assumptions about convergence criteria and decay rates of transient system states (Rosindell *et al.* 2008).

Computational efficiency and the direct derivation of realizations of the equilibrium state constitute two main advantages of the coalescence approach. Furthermore, it enables the analysis of diversity patterns in landscapes of infinite size (Rosindell &

Cornell 2007, 2009).

In nature, even the largest metacommunity is essentially located in a landscape of a finite size. In contrast to several previous studies, we conducted model simulations and compared results of both finite and infinite landscapes. In the case of a finite landscape, we used periodic boundary conditions and treated the landscape as a torus.

2.2.2 Simulation scenarios and analysis

We conducted simulations in landscapes of finite sizes with $N_{Landscape}$ in {100, 200, 300, ..., 1000}. We recorded species richness in several survey areas that comprise defined fractions of the landscape. For each landscape size we used 12 different survey areas corresponding to the ratios $N_{Survey}/N_{Landscape}$ in {0.01, 0.05, 0.1, 0.2, ..., 1.0}. In addition we simulated species richness in infinite landscapes for survey areas with N_{Survey} in {10, 20, 50, 100, 200, ..., 1000}. As speciation rates, we considered the values ν in $\{1 \times 10^{-6}, 1 \times 10^{-5}, 1 \times 10^{-5}\}$, which corresponds to the lower range of speciation rates used in previous simulation studies (Chave *et al.* 2002; Rosindell & Cornell 2007). In the reference scenario we modelled dispersal using a negative exponential kernel, where mean and variance of dispersal distance are equal. In order to study the effect of a different shape of the kernel, we conducted additional simulations with a log-normal dispersal kernel with mean values (at the linear scale) equal to the reference scenario. For the two parameter log-normal kernel it is possible to define the variance independently of the mean dispersal distance. For this purpose, we set the coefficient of variation (cv = standard deviation/mean dispersal distance) to 0.5, 1, 2 (at the linear scale). All simulations were carried out for the case when "within-cell-recruitment" was allowed and when it was disallowed.

For each combination of survey area, landscape area and dispersal kernel, we evaluated species richness for 20 values of mean dispersal distance, which were equally spaced (at log-scale) and covered the range of 0.1 – 50 grid cells. From these we constructed the dispersal-diversity relationship by plotting species richness as a function of mean dispersal distance.

The dispersal-diversity relationship can feature four different general shapes: (i) monotonically increasing (ii) monotonically decreasing (iii) hump-shaped with a local maximum (iv) U-shaped with a local minimum of species richness. Therefore, we searched for a local extremum of species richness within the interval of mean dispersal distances used. As we never found a hump-shaped response with a local maximum, we will describe our approach for searching a local minimum only.

The shape of the dispersal-diversity relationship is highly non-linear and species richness is provided as a random variable by the stochastic neutral model. Therefore, we used a generalized additive model (GAM) of log(species richness) vs. log(mean dispersal distance) to provide a smooth dispersal-diversity relationship (Wood 2008). The model fit was carried out with mean values for species richness of 30 replicate simulations. We tested if the minimum species richness of the smoothed curve was significantly smaller (based on standard confidence intervals with 30 replicates) than species richness at the minimum and the maximum of the dispersal distance interval. If there was a significant minimum of species richness within the dispersal interval, the corresponding mean dispersal distance is defined as "minimizing dispersal distance" (MDD). Otherwise the end of the interval with the lower species richness was defined as MDD. Therefore our results provide three general cases (i) The MDD equals 0.1 grid cells, which indicates a monotonically increasing dispersal-diversity relationship with a positive slope. (ii) The minimizing dispersal distance is larger than 0.1 but smaller than 50 grid cells, which characterizes a U-shaped dispersal-diversity relationship with a local minimum and a switch from a negative to a positive slope. (iii) The minimizing dispersal distance equals 50 grid cells, indicating a monotonically decreasing dispersal-diversity relationship with a negative slope.

2.3 Results

As expected, species richness always decreases with increasing dispersal distance, if the entire landscape is sampled (Fig. 2.1d, h). However, if only parts of the landscape are sampled a continuous spectrum of dispersal-diversity relationships is observed, ranging from positive to negative responses of diversity to an increasing mean dispersal distance. The shape of the dispersal-diversity relationship is determined, to a large degree, by the ratio of survey to landscape area. For small ratios the positive (increasing) branch is dominant (Fig. 2.1a, b, e, f), while at large ratios the negative (decreasing) branch of the relationship is dominant (Fig. 2.1c, d, h). At intermediate survey to landscape area ratios U-shaped dispersal-diversity relationships emerge (Fig. 2.1b, g). For infinite landscapes the ratio between survey and landscape area mathematically equals zero, but we still found a negative response of species richness at low dispersal distances, and thus a local minimum in the response curve, at least for relatively large survey areas (Fig. 2.1a, e).

Excluding within-cell recruitment does not change these general patterns, but clearly affects dispersal-diversity relationships at low dispersal distances. For any mean dispersal distances below five grid cells, species richness was higher with within-cell recruitment than without. This reduction in species richness implies changes in the shape of the dispersal-diversity relationship. At low ratios of survey to landscape area, the negative branch at low dispersal distances disappears (Fig. 2.1b, f). At intermediate ratios the negative branch is still present, but features lower species richness (Fig. 2.1c, g). Species richness at mean dispersal distances larger than five grid cells does not differ between scenarios with and without within-cell recruitment.

The type of the dispersal kernel did not affect the dispersal-diversity relationship, as results for the negative exponential and the log-normal kernel with equal mean and variance do not differ substantially. In contrast, the variance of dispersal did have an effect on species richness and thus on dispersal-diversity relationships. In scenarios with within-cell recruitment and finite landscapes, species richness increased with dispersal variance at intermediate values of mean dispersal distance, but this effect disappears at low and high mean dispersal distances (Fig. 2.1b, c, d). In infinite landscapes, the increasing branches of dispersal-diversity relationships for different dispersal variances are parallel (Fig. 2.1a, e). This indicates that increasing dispersal variance always increased species richness by the same factor (note the logarithmic scaling in Fig. 2.1). Scenarios excluding within-cell recruitment again showed a different pattern at the negative branch of the dispersal-diversity relationship. There, higher dispersal variance rather reduced species richness (Fig. 2.1g, h).

In addition to the ratio of survey to landscape area, the absolute value of landscape area, as well as the speciation rate, influence the dispersal-diversity relationship. Speciation rate and landscape area had an analogous effect on local species richness and on dispersal-diversity relationships (compare Fig. 2.2, left vs. right panels). Both, increasing speciation rate and larger landscape sizes result in higher species richness at all sampling scales. This change in species richness feeds back into the dispersal-diversity relationship. At a ratio of $N_{Survey}/N_{Landscape} = 0.2$, we found a decreasing dispersal-diversity relationship at low speciation or small landscape size, but a clear U-shaped pattern for high speciation or large landscape size (Fig. 2.2a, b). In general this means, the lower species richness, either due to low speciation or small landscape area, the weaker are the positive effects of dispersal on species richness.

For scenarios excluding within-cell recruitment these findings hold as well, but as

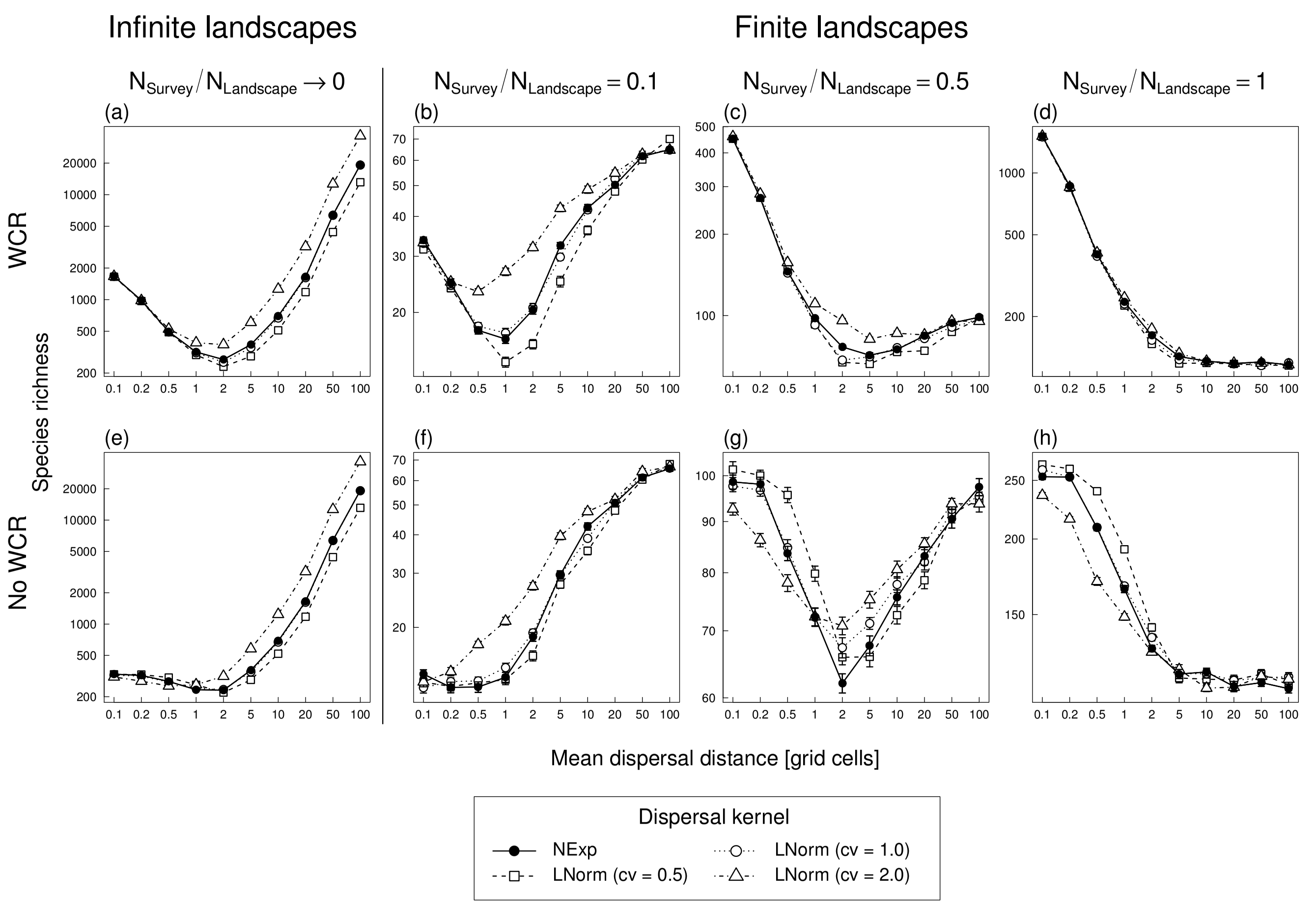

Figure 2.1. Dispersal-diversity relationships for different combinations of survey and landscape area. For scenarios with infinite landscapes (a, e) a survey area with $N_{Survey} = 1000$ was used. Finite landscapes were simulated with $N_{Landscape} = 1000$ (b–d, f–g). The speciation rate was 1×10^{-5}. in all scenarios shown. The top row of panels (a-d) shows results when "within-cell recruitment" (WCR) was allowed, while the bottom row (e-g) shows results when within-cell recruitment was excluded. Different symbols correspond to different dispersal kernels (NExp = negative exponential, LNorm = log-normal) and different variances of dispersal, measured by the coefficient of variation (cv). Points and error bars show mean and standard error of 30 replicates.

shown earlier at low mean dispersal distances the decreasing branch of the dispersal-diversity relationship disappears. For low speciation rates and/or small landscape areas, this reduction in species richness at short mean dispersal distances, leads to the result, that there is no response of species richness to dispersal at all (Fig. 2.2c, d).

In order to further explore the effects of various parameter combinations on the dispersal-diversity relationships we used, for any given scenario, the dispersal distance that minimizes species richness as a new response variable. We found that in general the minimizing dispersal distance (MDD) increases with the survey-to-landscape area ratio (Fig. 2.3a, c). In landscapes of infinite size, the same increase of the MDD is observed with increasing absolute survey area (Fig. 2.3b, d). For most values of the survey-to-landscape area ratio, MDD was lower when within-cell recruitment was excluded than when it was allowed. This was especially apparent at small survey-to-landscape area ratios when the exclusion of within-cell recruitment resulted in a MDD that equalled the lowest mean dispersal distance simulated (0.1 grid cells), indicating the lack of the negative branch of dispersal-diversity relationships at low mean dispersal distances (Fig. 2.3, compare top and bottoms rows).

Much of the variation in the MDD that is not explained by the survey-to-landscape area ratio can be attributed to speciation rate and landscape area. In finite landscapes, the MDD decreases with increasing speciation rate (Fig. 2.4a). This finding corresponds with the results mentioned above, that a lower speciation rate reduces the positive branch of the dispersal-diversity relationship and more likely leads to a monotonically decreasing relationship (compare Fig. 2.2). Interestingly, we found the opposite result for infinite landscapes. There, a higher speciation rate, lead to an increase in the MDD (Fig. 2.4b). According to our findings for single dispersal-diversity relationships, the response to absolute landscape size is analogous to our findings for speciation rate (compare Fig. 2.2). In finite landscapes, the MDD decreases with an increase in landscape area (results not shown).

The influence of the dispersal variance on the MDD is much weaker than the one of speciation rate and landscape size. Significant effects of dispersal variance were only found when combined with high speciation rate (1×10^{-4}) and relatively large landscape areas ($N_{Landscape} \geq 500$). In finite landscapes and low ratios of $N_{Survey}/N_{Landscape}$, the MDD is lower with high variance of dispersal. However, at $N_{Survey}/N_{Landscape} = 0.4$, there is a switch and at higher ratios, higher dispersal variance increases the MDD (Fig. 2.5a). In infinite landscapes the effect of dispersal variance is relatively weak, but there is a tendency for a lower MDD with high variance

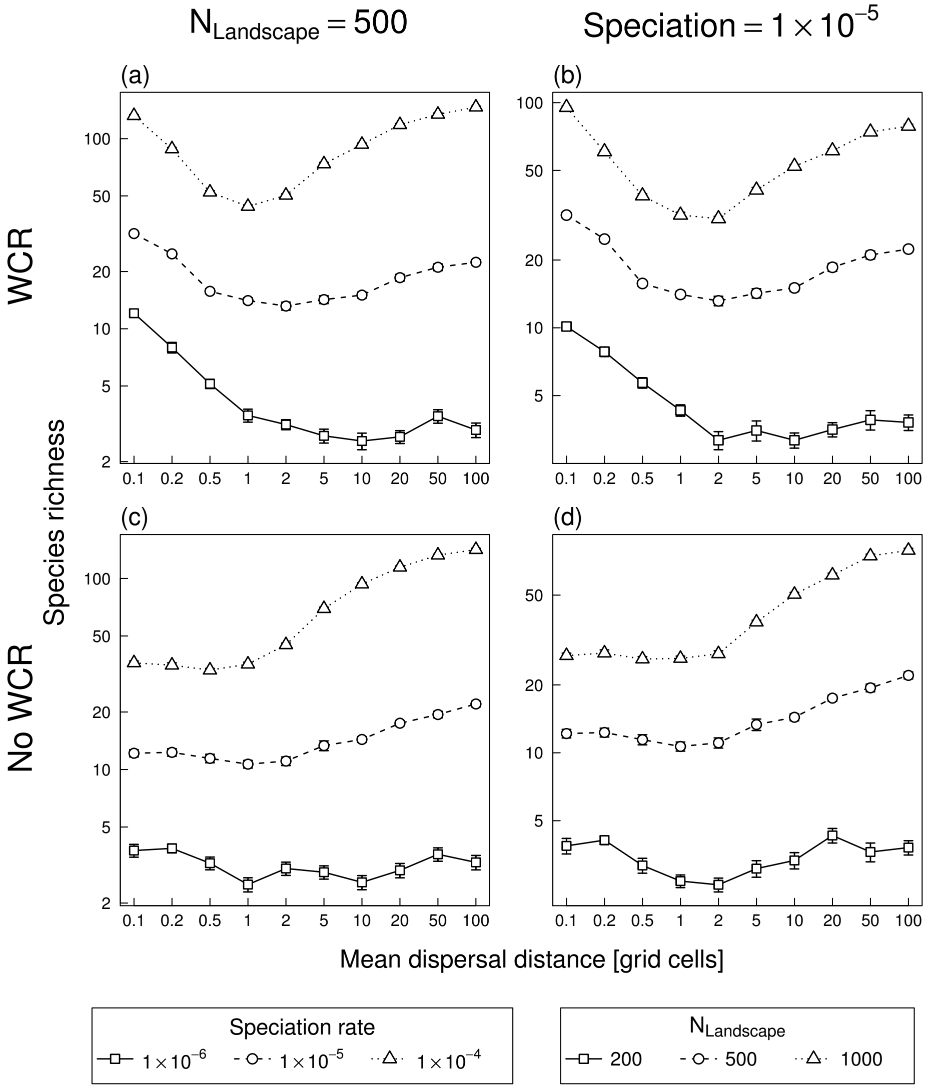

Figure 2.2. Dispersal-diversity relationships with equal ratio of survey to landscape area ($N_{Survey}/N_{Landscape} = 0.2$). In the panels on the left, landscape area was constant, but speciation rate varied (a, c). In the panels on the right, speciation rate was constant, but landscape area varied (b, d). Speciation rates and landscape sizes ($N_{Landscape}$) are indicated by different symbols and line types, as shown in panel legends.

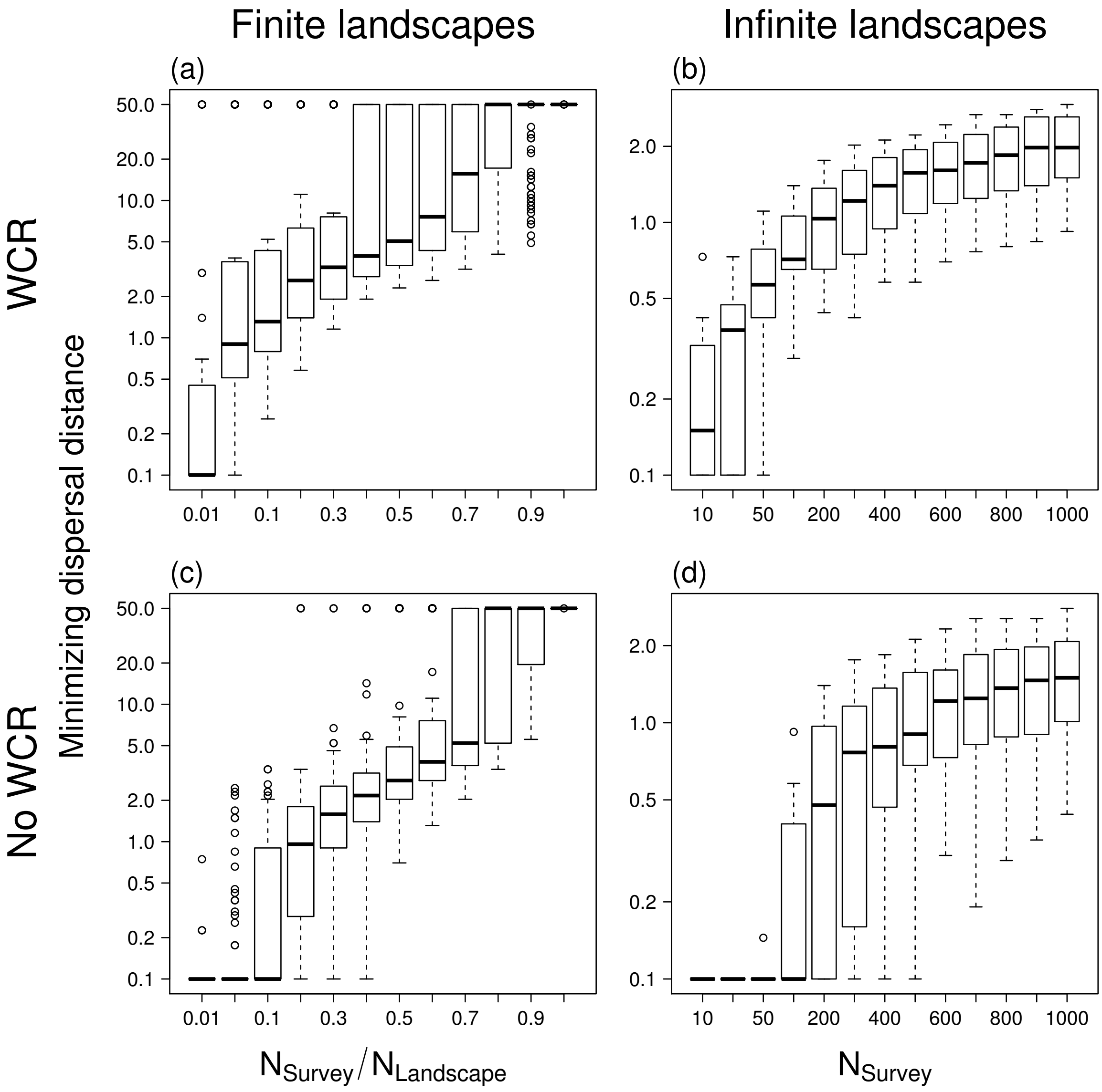

Figure 2.3. The dispersal distance, where the minimum species richness was found (= minimizing dispersal distance, MDD) as a function of the ratio of survey area and landscape area (finite landscapes, a, c), or survey area only (infinite landscapes, b, d). The boxplots summarize results for all different speciation rates, dispersal kernels and absolute values of survey and landscape area. The panels at the top show results including within-cell recruitment (WCR) and at the bottom excluding WCR.

of dispersal independently of absolute survey area (Fig. 2.5b). Excluding within-cell recruitment does not change the results concerning speciation rate, landscape area and dispersal variance qualitatively.

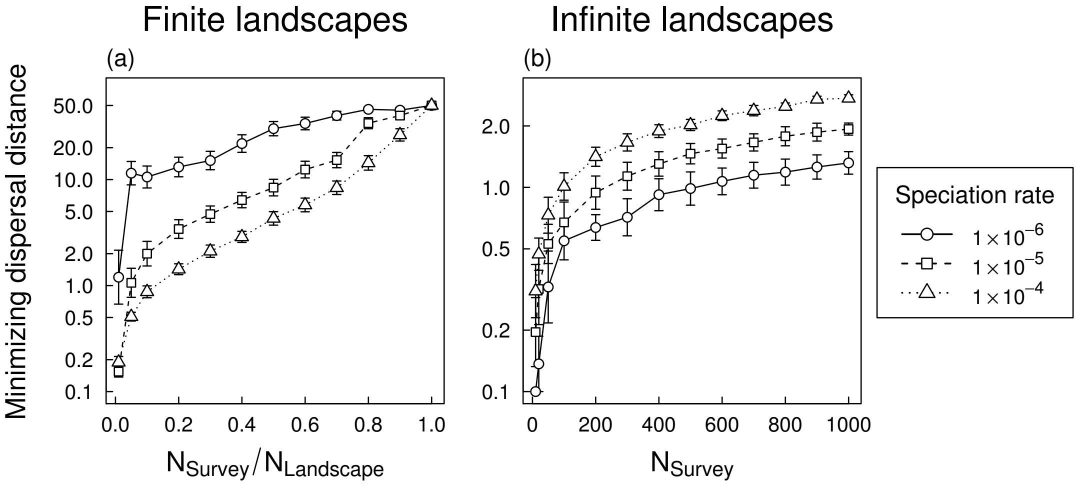

Figure 2.4. The minimizing dispersal distance (MDD) vs. the ratio survey area to landscape area for finite landscapes (a) or vs. survey area only for infinite landscapes (b). The results are separated by speciation rate, indicated by different symbols. The points and error bars show mean and standard error, averaged over different dispersal kernels and absolute values of survey and landscape areas (for finite landscapes).

2.4 Discussion

The scale-dependent effects of dispersal capability on species diversity, reported in previous studies, can be generalized with the following statement: Higher dispersal capability increases diversity at the local scale, but reduces diversity at the metacommunity scale (Hubbell 2001; Mouquet & Loreau 2003; Cadotte 2006a; Economo & Keitt 2008). Our study fully agrees with that statement for the metacommunity scale, but it provides a much more detailed analysis, yielding partly contrasting conclusions, for the local scale. We found that at the local scale diversity may increase with dispersal capability due to species immigrations (Loreau & Mouquet 1999), but it may also decrease with dispersal due to increased mixing and reduced species segregation (Pacala 1997). The balance between these contrasting effects leads to various distinct dispersal-diversity relationships at the local scale, ranging from monotonically

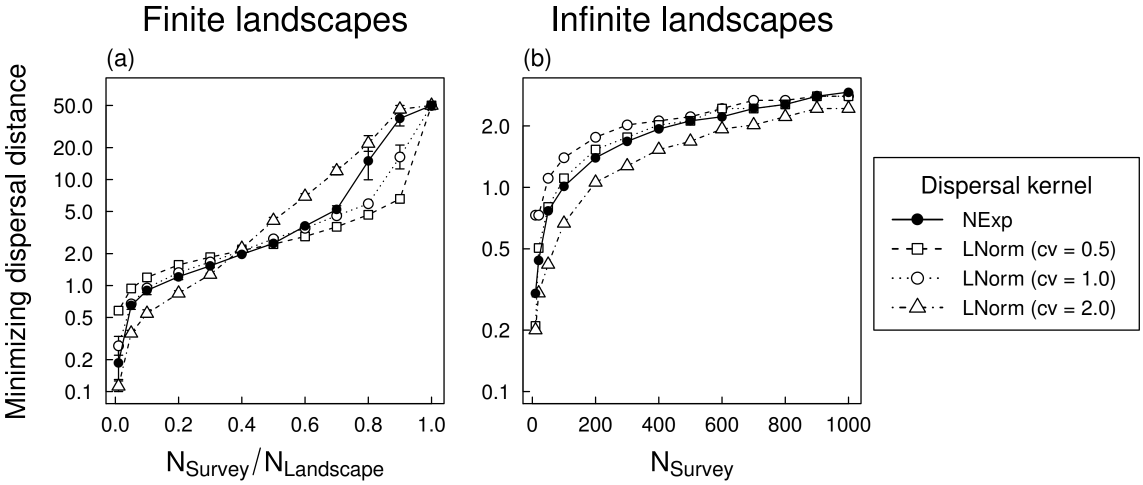

Figure 2.5. The minimizing dispersal distance (MDD) vs. the ratio survey area to landscape area for finite landscapes (a) or vs. survey area only for infinite landscapes (b). The results are separated by dispersal kernel and dispersal variance. Only results with $N_{Landscape} >= 500$ and a speciation rate of 1×10^{-4} are shown. Symbols indicate the dispersal kernel and the coefficient of variation (cv) of dispersal (NExp = negative exponential, LNorm = log-normal). For finite landscapes the results were averaged over different absolute values of survey and landscape area. Points and error bars show mean and standard error (for finite landscapes only)

increasing, via U-shaped to monotonically decreasing response patterns. We suggest that the mean dispersal distance at which species richness for a given community is minimized (MDD), provides a comprehensive aggregated measure of the dispersal-diversity relationship. A low MDD implies dominance of spatial mass effects while a high MDD indicates importance of interspecific interactions.

2.4.1 Ratio of survey area and landscape area

In a given local community the response of diversity to dispersal capability strongly depends on the definition of the "local" scale. Our results demonstrate that the ratio of the survey area (i.e. the “local” community) to the total landscape area is an important determinant of dispersal-diversity relationships. When the survey area is much smaller than the landscape, species richness is minimized at short dispersal distances (short MDD) and our results agree with the results of previous studies regarding local diversity (Loreau & Mouquet 1999; Esther *et al.* 2008). When the survey area approaches the landscape area, species richness is maximized at long dispersal distances (long MDD) and our results agree with dispersal-diversity relationships as predicted for the metacommunity scale (Chave *et al.* 2002; Levine & Murrell 2003).

2.4.2 Speciation rate and absolute landscape area

Recognizing that both speciation rate and the absolute size of the landscape influence diversity in a similar manner, Hubbell (2001) lumped these into the “fundamental biodiversity number”. Following that insight, we suggest an analogous explanation for the effects of both factors. Both, speciation rate and landscape area determine species richness at the landscape scale and thus the size of the species pool, which provides potential immigrants to any “local” scale. Therefore, the higher speciation rate and/or landscape area, the more important is the increasing branch of the dispersal-diversity relationship and the lower the MDD in any survey area.

When the species pool is small, due to low speciation rate and/or small landscape area, diversity monotonically decreased with dispersal capability, even at small ratios of survey to landscape. This result contradicts the general finding of increasing local diversity with increasing dispersal capability (Hubbell 2001; Economo & Keitt 2008). In species-poor metacommunities, the limited potential of the species pool to contribute to local diversity is insufficient to balance the negative effect of dispersal due to reduced segregation.

Rosindell *et al.* (2010) suggest that protracted speciation provides a much better fit to species abundance distributions and species life times than speciation by point mutation. Protracted speciation leads to less rare species and thus to a lower species richness at the metacommunity scale compared to point mutation (Rosindell *et al.* 2010). Therefore, we expect that protracted speciation will show similar effects on dispersal-diversity relationships as those of a lower speciation rate in the case of point mutation. In principal protracted speciation could easily by included into our approach, but a comparison between different modes of speciation is beyond the scope of this study.

2.4.3 Dispersal variance and kernel type

Higher moments of the dispersal kernel as variance and kurtosis determine the frequency of both short- and long-distance dispersal events (Nathan & Muller-Landau 2000). In our simulations increasing dispersal variance did not significantly affect the negative branch, but it increased species richness at the positive branch. In finite landscapes, this positive effect of high dispersal variance disappears at higher dispersal distances, as the community approaches complete mixing (Fig. 2.1b). In contrast, the positive effect remains visible in infinite landscapes (Fig. 2.1a), where increasing dispersal variance always causes a higher frequency of species immigrations over long-distances and thus from regions, which likely provide new species to the survey area (Rosindell & Cornell 2009).

Comparing negative-exponential and log-normal dispersal kernels with equal mean and standard deviation, we found no significant differences of the dispersal-diversity relationship between both kernels. This is surprising, as these kernels differ in their higher moments. For instance the kurtosis, which is often used to quantify the "fatness" of the tail of dispersal kernels equals 6.0 and 34.0 for negative-exponential and log-normal kernel (both with mean = standard deviation), respectively (Clark *et al.* 1999). Rosindell & Cornell (2009) found that the "fatness" parameter of the dispersal kernel they used, clearly influences species richness and species-area-relationships. However, they did not provide a link of their dispersal parameters to the moments of the distribution and thus did likely not vary variance and kurtosis independently.

In general our results provide some evidence that interspecific segregation is mainly governed by the mean of dispersal distance, while mass effects are influenced by the variance of dispersal as well (Clark 1998; Rosindell & Cornell 2009). Still, this finding is only based on a few scenarios and the comparison of two kernel types only. Therefore, we suggest that the link between the higher moments of dispersal kernels and species diversity requires further and more detailed investigations.

2.4.4 Within-cell recruitment

Excluding the possibility of within-cell recruitment (WCR) did not influence our findings qualitatively. Nevertheless, species richness at low dispersal distances differs clearly between model versions with and without WCR. Allowing WCR means, that recruitment events follow exactly the same distance kernel as dispersal events. The probability that a seedling establishes at the microsite of its parent equals the probability of being dispersed to this site. We argue that this assumption is reasonable for most plant species, where seedlings can emerge below the canopy or fill the gap that was opened by the death of their mother plant (Clark *et al.* 1999; Venable *et al.* 2008).

Without WCR, recruitment is impossible within the microsite of the parent and therefore short distance dispersal (within microsite) cannot be realized as recruitment. As the distribution of recruitment probabilities (recruitment kernel) has to sum to one across space, the probability of recruitment events at distances of about half a cell size is drastically reduced, while at the same time the probability of recruitment at distances of about one cell size is increased, relative to the dispersal kernel. This corresponds to the case, where mother plants have strong inhibiting effects on their direct offspring (Nathan & Casagrandi 2004).

Comparing scenarios with and without WCR, but with equal mean dispersal distances reveals that the average distance of recruitment events is higher without WCR. This implies lower species segregation and therefore leads to reduced species richness. However, this difference vanishes for higher mean dispersal distances as recruitment kernel and dispersal kernel get more and more similar for both assumptions.

2.4.5 Comparison with other neutral modelling approaches

Previous neutral- as well as non-neutral metacommunity models usually used a dichotomous distinction between local and regional scales and at the same time they did ignore dispersal limitations at the local scale (Hubbell 2001; Kadmon & Allouche

2007; Economo & Keitt 2008). These models by definition exclude the possibility of species segregation at the scale defined as "local" and therefore ignore the mechanism which generates the negative branch and the local minimum of the dispersal-diversity relationship at the local scale.

Rosindell & Cornell (2007) were the first who analysed species-area relationships (SARs) for finite survey areas within an infinite landscape. They reported a monotonic increase of species richness with increasing dispersal capability at irrespective of survey area (compare Fig. 2a in Rosindell & Cornell (2007)). They missed the local minimum of species richness, as they only used mean dispersal-distances larger than 5 grid cells, while we found a minimizing dispersal distance of about 2 grid cells for a survey area of 1000 × 1000 grid cells in an infinite landscape.

Recently, O'Dwyer & Green (2010) provided an approximate analytical solution for SARs based on a spatially explicit neutral model. In contrast to our findings their approach predicts monotonously increasing dispersal-diversity relationships irrespective of sampling area (compare eqn 10 in O'Dwyer & Green (2010)). This qualitative mismatch arises because their model ignores species competitive interactions, which are responsible for the decreasing branch of the dispersal-diversity relationship. Our simulation model explicitly includes competition for space by considering the assumption of zero-sum dynamics. We expect that solving a spatially explicit neutral model including species competition is mathematically very challenging, but this analytical solution would provide an interesting test of our simulation results.

2.5 Conclusions

To our knowledge this is the first study which presents U-shaped dispersal-diversity relationships. This pattern fills a gap between the dispersal-diversity relationships reported previously for the local and the metacommunity scale. Our study does not contradict the general findings of increasing local, and decreasing metacommunity diversity, but unifies both patterns, by incorporating them as extremes of a continuous spectrum of dispersal-diversity relationships. Manipulating dispersal and recording the communities' response is challenging at the metacommunity scale, but experimental validation of results could be done using microbial communities (Cadotte 2006b). Empirical test of our theoretical findings will shed new light on the scale-dependent dispersal-diversity relationships. Increasing species richness by manipulating dispersal capability or landscape connectivity is the aim of many conservation programs. Our findings of complex dispersal-diversity relationships at the local scale ask for careful consideration of such measures and highlight the need to define the scale(s) at which an increase of species richness is desired.

Link to the next chapter

In the previous chapter, I investigated scale-dependent dispersal-diversity relationships using a grid-based neutral model. Thereby, I focused on the general consequences of species' dispersal capabilities for diversity at different spatial scales and thus analysed theoretical model simulations for broad parameter ranges of survey areas, landscape sizes and mean dispersal distances. While this approach provided interesting new insights into the scale-dependence of dispersal-diversity relationships in general, it did not provide predictions for specific real-world applications in fragmented landscapes.

One key question of regional plant community dynamics in fragmented landscapes concerns the connectivity between local communities by seed dispersal. Accordingly, in the following chapter, I proceed to an assessment of the connectivity between local communities in discrete habitat patches and a classification of the type of regional community dynamics in the Southern Judean Lowlands (SJL) in Israel.

The natural vegetation patches in this landscape contain thousands to millions of plant individuals, which cannot be simulated with an individual based neutral model due to computational limitations. Therefore, I chose an incidence-function modelling approach, which predicts species presences/absences based on patch connectivities and patch sizes. In order to model patch connectivity in a spatially realistic manner, I implemented an advanced connectivity index, which takes into consideration the shapes and orientations of habitat patches. The parameters of the incidence-function model (IFM) were estimated from vegetation data collected in 40 habitat patches in the SJL. I considered three different scenarios of regional community dynamics (metacommunity, mainland-island and island communities), which are primarily differentiated by the connectivity between local communities. Based on the model parameterisations for each scenario, I discuss the role of dispersal and connectivity in the SJL. Finally, I apply the model to predict the "extinction debt", i.e. the number of species going extinct during the transient phase of community dynamics, for each of the three scenarios.

Chapter 3

Metacommunity, mainland-island system or island communities? – Assessing the regional dynamics of plant communities in a fragmented landscape [1]

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Abstract

Understanding the regional dynamics of plant communities is crucial for predicting the response of plant diversity to habitat fragmentation. However, for fragmented landscapes the importance of regional processes, such as seed dispersal among isolated habitat patches, has been controversially debated. Due to the stochasticity and rarity of among-patch dispersal and colonization events, we still lack a quantitative understanding of the consequences of these processes at the landscape scale.

In this study, we used extensive field data from a fragmented, semi-arid landscape in Israel to parameterize a multi-species incidence-function model. This model simulates species occupancy pattern based on patch areas and habitat configuration and explicitly considers the locations and the shapes of habitat patches for the derivation of patch connectivity. We implemented an approximate Bayesian computation approach for parameter inference and uncertainty assessment. We tested which of the three types of regional dynamics – the metacommunity, the mainland-island, or the island communities type – best represents the community dynamics in the study area and applied the simulation model to estimate the extinction debt in the investigated landscape.

We found that the regional dynamics in the patch-matrix study landscape is best represented as a system of highly isolated “island communities” with low rates of propagule exchange among habitat patches and consequently low colonization rates in local communities. Accordingly, the extinction rates in the local communities are the main drivers of community dynamics. Our findings indicate that the landscape carries a significant extinction debt and in model projections 33% – 60% of all species went extinct within 1000 years.

Our study demonstrates that the combination of dynamic simulation models with field data provides a promising approach for understanding regional community dynamics and for projecting community responses to habitat fragmentation. The approach bears the potential for efficient tests of conservation activities aimed at mitigating future losses of biodiversity.

3.1 Introduction

Understanding the regional dynamics of plant populations and communities in fragmented landscapes is a key challenge in spatial ecology (Leibold *et al.* 2004; Alexander *et al.* 2012). From a conservation biology perspective, this issue is pivotal for projecting community responses to habitat fragmentation, in particular to mitigate time-delayed extinctions, which are known as the "extinction debt" of fragmented landscapes (Tilman *et al.* 1994; Cousins 2009; Jackson & Sax 2009; Kuussaari *et al.* 2009). One major obstacle for the assessment of regional plant community dynamics is the difficulty of quantifying and predicting regional processes, such as seed dispersal and colonization (Freckleton & Watkinson 2002; Alexander *et al.* 2012). Especially seed dispersal among spatially isolated habitat patches and the establishment of new populations in previously unoccupied patches are typically rare events, highly stochastic and difficult to measure (Clark *et al.* 1999; Nathan & Muller-Landau 2000). However, these regional processes are crucial for landscape connectivity and thus for regional community dynamics (Hanski 1999; Leibold *et al.* 2004) . Furthermore, for many plant species it is difficult to assess the availability of suitable vs. unsuitable habitat in a landscape due to limited knowledge of plant species habitat requirements (Freckleton & Watkinson 2002). These two issues - the difficulty of quantifying regional processes and uncertainties concerning the spatial distribution of suitable habitat - contributed to an intensive and on-going debate regarding the prevalence of various types of regional plant population and community dynamics in the real world (Eriksson 1996; Freckleton & Watkinson 2002, 2003; Ehrlén & Eriksson 2003; Alexander *et al.* 2012).

Although molecular markers and genetic techniques enable the quantification of regional processes, such as dispersal and colonization (Broquet & Petit 2009), these approaches are limited to single species and are hardly feasible for species rich plant communities. An alternative approach for a mechanistic understanding of plant community dynamics is provided by linking process-based models with species distribution and/or seed-trap data (Clark *et al.* 1999). Techniques of "inverse modelling" or "model calibration" allow the estimation of model parameters and the quantification of uncertainties in parameter estimation and in model predictions within a statistically rigorous framework (Clark 2005; Hartig *et al.* 2011). However, so far studies of regional dynamics that link process-based models with empirical data were either limited to a single or a few species (e.g. Cabral & Schurr 2010; Körner *et al.* 2010), or did not treat space and habitat fragmentation explicitly (e.g. Etienne 2007; Jabot &

Chave 2009).

The existence of an extinction debt in plant communities has been tested several times by correlating current species richness with past as well as present landscape configurations (reviewed in Cousins 2009; Kuussaari *et al.* 2009). While this approach allows assessing whether the landscape carries an extinction debt or not, it rarely provides predictions for the number of species that are expected to go extinct during the transient phase of regional community dynamics (Kuussaari *et al.* 2009, but see Helm *et al.* 2006). Empirically based, spatially explicit population modelling has been advocated as a promising approach to quantify extinction debts (Hanski 1999; Kuussaari *et al.* 2009). However, this approach has only been applied so far for single species, but not for plant communities (e.g. Herben *et al.* 2006; Bulman *et al.* 2007).

In this study we combine an extensive data set of species-rich plant communities in a fragmented, semi-arid landscape with a spatially explicit multi-species simulation model. In contrast to previous metacommunity studies, our model explicitly considers the location, shape and orientation of suitable habitat patches in a real landscape. We use the empirical data on species distributions and recently developed techniques of Bayesian inference to estimate model parameters that describe key processes such as extinction, dispersal and colonization (ter Braak & Etienne 2003; Hartig *et al.* 2011). In particular, we aim at detecting the role of connectivity by seed dispersal among habitat patches in determining the regional dynamics of the community and provide estimates for the extinction debt in the investigated landscape.

In our study area, the Southern Judean Lowlands (SJL), the species rich natural scrub and grassland vegetation is restricted to discrete habitat patches that are embedded in a hostile agricultural matrix (Yaacobi *et al.* 2007; Giladi *et al.* 2011). We compare parameter estimates and model predictions with respect to the extinction debt for three different types of regional community dynamics, namely the metacommunity, the mainland-island, and the island communities types. These types are primarily differentiated by assumptions regarding the role of landscape connectivity for regional scale dynamics. These three types were derived by expanding the population-scale concepts of Freckleton & Watkinson (2002) to the community-scale. Accordingly, these three types can be differentiated as follows: In a metacommunity (MC) all habitat patches are considered as potential sources and recipients of propagules and seed dispersal among patches plays a crucial role for regional dynamics. In a mainland-island system (ML-IL) seed dispersal is directional, where smaller patches (islands) receive propagules from large patches (mainlands), while the propagule output of smaller patches is negligible. In a system of island communities (IC) propagule exchange among local communities is negligible so that each habitat patch contains an essentially independent local community and the regional dynamics are fully determined by processes at the local patch scale.

The simulation model we implement is derived from a multi-species version of the well-known incidence-function model (IFM Hanski 1994; Hanski & Gyllenberg 1997). Previous studies applied the multi-species IFM for theoretical analysis of species-area curves, distribution-abundance curves or spatial pattern formation (Hanski & Gyllenberg 1997; Hovestadt & Poethke 2005). However, to our knowledge a multi-species IFM has never been combined with extensive field data so far. We develop three different model versions, corresponding to the three types of regional dynamics. Each model version is then parameterized using vegetation survey data and techniques of approximate Bayesian computation (ABC) (Hartig *et al.* 2011). The ABC approach provides the possibility for statistical inference on model parameters, even when a formal likelihood cannot be derived (Jabot & Chave 2009). The ABC approach produces probability distributions for parameter values, which include parameter estimates and the quantification of parameters uncertainty. Furthermore, by propagating parameter values and their uncertainty into the simulation model, we are able to provide model predictions and uncertainty estimates for the extinction debt in our study area (Clark 2005).

3.2 Methods

3.2.1 Study area

The study area is located in the Southern Judean Lowlands, Israel (31° 31’ 20” – 31° 33’ 40” N, 34° 46’ 50” – 34° 50’ 20” E) close to the village of Lachish (Fig. 3.1). This landscape is characterized by a typical semi-arid climate, with short mild winters and long, dry and hot summers. Mean annual temperature is 19°C (12°C in January and 26°C in August) and mean annual precipitation is 376 mm (average for 1998-2009) (Giladi *et al.* 2011). Soil types in the study area are mainly loessial light-brown soils and light-brown Rendzina (Dan *et al.* 1976).

For thousands of years the landscape has been used for sheep and goat grazing and for small scale agriculture (Naveh & Dan 1973). Today the landscape forms a mosaic composed of natural scrub- and grassland vegetation patches that are embedded in a matrix used for intensive agriculture (Fig. 3.1; Yaacobi *et al.* 2007; Giladi *et al.* 2011). Farming practices of the last decades resulted in discrete boundaries between natural vegetation patches and the agricultural matrix. Examination of historical aerial photographs indicated that the area and the configuration of natural vegetation patches changed only slightly during the last 65 years.

The main natural vegetation types are semi-steppe batha (Mediterranean scrubland) and grassland (Giladi *et al.* 2011). The most dominant perennial species are the dwarf shrub *Sarcopoterium spinosum* in the batha vegetation and the tussock grasses *Hyparrhenia hirta* and *Hordeum bulbosum* in the grassland. The region has a rich flora, with 406 vascular plant species observed within the study area.

Our study area includes 77 natural vegetation patches of different sizes ranging from continuous ($> 100ha$) to very small patches ($< 100m^2$). We used rectified aerial photographs (pixel size $= 1m^2$) to identify and digitize all the patches of natural vegetation (Fig. 3.1). The digitized map was used for calculation of patch areas and connectivities.

3.2.2 Vegetation sampling

Vegetation sampling was conducted in 40 patches that were chosen to represent wide ranges of patch size and patch isolation. All 40 sampled patches were thoroughly scanned for plant species by experienced botanists well familiar with the local flora (M. R. and I. G.). The time spent in each patch was adjusted in relation to its size and varied from approximately half an hour for the smallest patches to a full day for the largest. All vascular plant species within each patch were recorded during the height of the growing season between early March and early April, in either 2010 or 2011. Plant identification followed Feinbrun-Dothan & Danin (1991).

3.2.3 The model

The stochastic simulation model used here is an adapted multi-species version of Hanski's well-known incidence-function model (IFM Hanski 1994). This model does not include species interactions, but describes each species independently (Hanski & Gyllenberg 1997; Hovestadt & Poethke 2005). The model predicts the probability $P_{i,j}(t)$ that species i will occupy habitat patch j at time t, depending on the species occupancy at time t-1 and the habitat configuration in the landscape. Occupancy

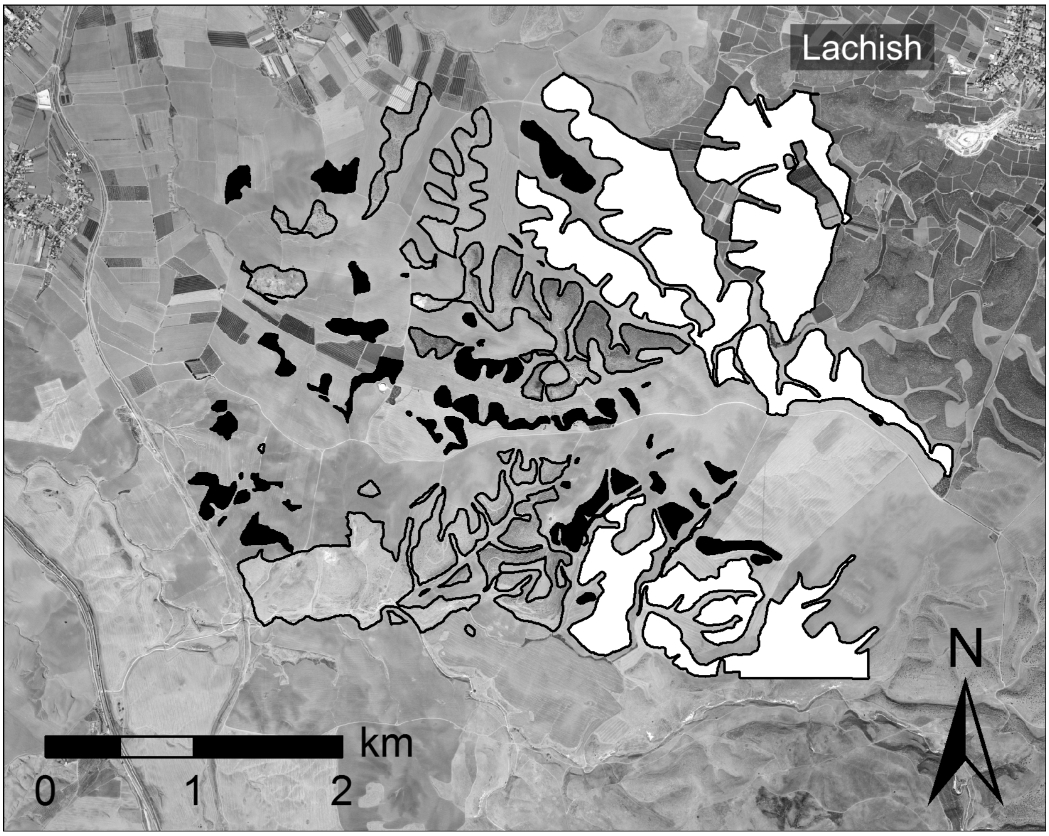

Figure 3.1. Map of natural habitat patches next to the village of Lachish. Natural habitat patches are indicated by black boundary lines. Patches that were surveyed are indicated in black. Large patches that are considered as mainlands in the mainland-island scenario are filled in white.

$O_{i,j}(t)$ is defined as a binary variable that can only take the values unoccupied (0) or occupied (1). Patches that are currently not occupied by species i are colonized with probability $C_{i,j}(t)$, which is defined as

$$C_{i,j}(t) = \frac{M_{i,j}(t)^2}{M_{i,j}(t)^2 + Y^2}, \tag{3.1}$$

where $M_{i,j}(t)$ is the number of immigrants of species i into patch j and Y is a model parameter that specifies how many immigrants are needed for a 50% chance of colonization. The colonization rate $C_{i,j}(t)$ depends on two consecutive processes: The immigration of propagules into a patch ($M_{i,j}(t)$), which is defined below, and the establishment of a population from these immigrants as specified by Eq. 3.1. Increasing values of Y thus indicate a decreasing chance of establishment, given a constant number of immigrants, and $1/Y$ can be interpreted as "power of establishment" (Hovestadt & Poethke 2005).

Populations of species i in patch j can go extinct with probability $E_{i,j}(t)$, defined as

$$E_{i,j}(t) = [1 - C_{i,j}(t)] \times \min\left[1, \left(\frac{K_0}{K_{i,j}}^{X}\right)\right], \tag{3.2}$$

where $K_{i,j}$ is the carrying capacity of species i in patch j and K_0 is a model parameter specifying the threshold population size with extinction probability of one, as long as the rescue-effect is ignored (see below). This formulation mirrors an Allee effect where K_0 represents a "minimum viable population size" (Cabral & Schurr 2010). Parameter X describes the scaling of extinction risk with patch carrying capacity. Increasing values of X indicate a decreasing risk of extinction, given a constant carrying capacity. According to Hanski (1994) low values of X indicate high demographic stochasticity and thus low species persistence. The carrying capacity $K_{i,j}$ is derived as patch area A_j times the species-specific population density n_i, which is assumed to be equal in all patches occupied by a certain species (Hanski & Gyllenberg 1997; Hovestadt & Poethke 2005). The first term in 3.2 considers the rescue-effect, i.e. the reduction of the "intrinsic" extinction probability by propagule immigration from neighbouring patches (Brown & Kodric-Brown 1977).

The probability for patch occupancy $P_{i,j}(t)$ is then defined by Eqs. 3.1 and 3.2 as

$$P_{i,j}(t) = \begin{cases} C_{i,j}(t) & \text{if} \quad O_{i,j}(t-1) = 0, \\ 1 - E_{i,j}(t) & \text{if} \quad O_{i,j}(t-1) = 1. \end{cases} \tag{3.3}$$

In order to produce time series of species occupancy, the occupancy of the current time step $O_{i,j}(t)$ is determined by randomly drawing from a Bernoulli-distribution with $P_{i,j}(t)$ as probability for patch occupancy (Hovestadt & Poethke 2005).

One crucial issue in the incidence-function model is the link between habitat configuration and the propagule immigration into a patch (Eq. 3.1). The number of immigrants $M_{i,j}(t)$ depends on the connectivities of the target patch j to the source patches k and the occupancy of the source patches in the time step $t-1$.

$$M_{i,j}(t) = \sum_{k=1, j \neq k}^{N_{Patch}} S_{j,k} \cdot O_{i,k}(t-1), \tag{3.4}$$

where $S_{j,k}$ is the species- and time-independent connectivity between target patch j and source patch k, and $O_{i,k}(t-1)$ is the occupancy of species i in patch k at $t-1$. We assumed that patch connectivity $S_{j,k}$ decreases with patch-to-patch distance (Hovestadt & Poethke 2005). In previous studies patch-to-patch distances were usually measured between patch centroids or between patch edges (reviewed in Moilanen & Nieminen 2002). These may be reasonable approximations if the distances between patches are much larger than the patch extents. However, if patch extents and inter-patch distances are of similar order of magnitude, as in our landscape (Fig. 3.1), considering patch shapes and orientations may much better reflect the functional connectivity (i.e. the probabilities of seed dispersal) among patches. Therefore, we developed and used a connectivity index that considers patch shapes and orientations explicitly and corresponds to area-to-area dispersal as suggested by Chipperfield *et al.* (2011).

For the calculation of patch connectivities, we projected the habitat map onto a raster grid with grain size of $5m \times 5m$. In this raster representation each patch is represented by a set of contiguous grid cells, labelled with the same patch ID number. The connectivity $J_{m,k}$ of one single grid cell m in target patch j to source patch k is defined by assuming a negative-exponential 2D-kernel (Clark *et al.* 1999; Hovestadt & Poethke 2005) and summing up the grid-cell connectivities between the cell m in target patch j and all grid cells n belonging to source patch k:

$$J_{m,k} = \frac{1}{2\pi\alpha^2} \sum_{n=1}^{N_k} \exp\left(-\frac{d_{m,n}}{\alpha}\right), \tag{3.5}$$

where $d_{m,n}$ is the distance between grid cells m (in patch j) and n (in patch k) and N_k is the number of grid cells that constitute patch k. The model parameter α provides the mean distance of patch-to-patch dispersal events and the normalization constant in front of the summation assures that the connectivity kernel properly integrates to one, which means in an ecological sense that every propagule is dispersed somewhere, either to matrix habitat, where it is lost, or to suitable habitat, where it contributes to patch connectivity and thus to colonization probability. An implicit assumption of our model is that there is no dispersal limitation within patches.

Finally, the total connectivity of patch j to patch k ($S_{j,k}$) is calculated as the sum of all grid-cell connectivities $J_{m,k}$ belonging to patch j:

$$S_{j,k} = \sum_{m=1}^{N_j} J_{m,k}, \tag{3.6}$$

where N_j is the number of grid cells that constitute patch j. With this definition of patch-to-patch connectivity the shapes of target and source patches are considered, as source-patch grid cells that are close to the target patch contribute more to its connectivity than distant source-patch grid cells. Furthermore, our connectivity index depends on the areas of target and source patches, considering that larger source patches provide more emigrants and larger target patches sample more immigrants from any propagule rain (Moilanen & Nieminen 2002; Hovestadt & Poethke 2005; Chipperfield *et al.* 2011).

As patch connectivities do not vary in time, the computationally demanding calculation of $S_{j,k}$ on a large raster grid (Eqs. 3.5 and 3.6) needs to be done only once for a specific landscape. Based on the patch-to-patch connectivity matrix, iterating equations 1 – 4 provides stochastic realizations of species occupancy in the landscape. Species composition or species richness of habitat patches can then be simply evaluated by considering which species or which number of species occupies a certain patch at the same time.

3.2.4 Model scenarios and parameterization

We implemented three different model scenarios with the multi-species IFM, which correspond to the three different types of regional scale community dynamics (i) the metacommunity (MC), (ii) the mainland-island (ML-IL) and (iii) the island communities (IC) types. These three scenarios primarily differ in the calculation of propagule immigration into habitat patches. In the metacommunity scenario we assumed that all patches provide potential sources of propagules if they are occupied and therefore all patches are considered for the summation in Eq. 3.4. Furthermore, all species in all patches bear a certain risk of extinction according to Eq. 3.2 (Hovestadt & Poethke 2005).

In the mainland-island scenario we assume that only very large patches that were classified as “mainlands” provide propagules to smaller patches, while the propagule rain provided by “island” patches is considered negligible in this scenario. As mainlands we classified all patches that are larger than 150 hectares and are currently covered with undisturbed natural vegetation, which lead to six mainlands in our landscape (Fig. 3.1). Only these six mainlands are considered as sources contributing to patch connectivity, which means the summation in Eq. 3.4 is only applied to these six mainlands. Furthermore, we assume that all species build up stable populations in the mainlands and thus extinction risk equals zero there for all species.

In the island communities scenario (IC) we consider the extreme assumption that there is no propagule exchange among patches and thus the probability of colonization (Eq. 3.1) equals zero for all species in all patches. Accordingly, regional community dynamics are only driven by species extinctions, according to Eq. 3.2. This assumption implies that there is no stable dynamic equilibrium in species occupancy patterns, but that an extreme equilibrium is expected, where – in the absence of colonization – all species will ultimately go extinct (Hanski 1994). The IC scenario can be considered as a special case of the MC and ML-IL scenarios with colonization rates equal to zero.

As initial condition for all three scenarios we assume that all species are present in all patches. We do not have sufficient information to determine whether regional dynamics in our system already approached a dynamic equilibrium or are still in a transient phase. Furthermore, the only possible stable equilibrium for the island communities scenario includes only unoccupied patches. Therefore, as a reference parameterization, we started from the initial condition and simulated regional dynamics for 100 years in each scenario. In order to test the sensitivity of our results to simulation time, we additionally tested simulation times of 50 and 200 years. This range broadly covers our uncertainty on the onset of intensive land use and habitat fragmentation in the Southern Judean Lowlands.

The size of the species pool in the system is provided by the total species number found in the vegetation surveys and equalled 406 species. The distribution of species population densities was estimated from vegetation surveys in hierarchically nested sampling plots carried out in 2009 (Giladi *et al.* 2011). These data include species presences/absences at 3 different sampling scales – $15m \times 15m$, $5m \times 5m$, $1m \times 1m$ – and counts of individuals at the sampling scale of $0.25m \times 0.25m$. If a species was present at the smallest sampling scale, we used the count data to estimate the population density in the respective patch. If there were only presence-absence data for a species, we used data from the smallest sampling scale where it occurred and calculated the species' density by counting each presence in a sampling plot as one individual. We acknowledge that this method is likely to underestimate population densities of the less common species (i.e. those for which only presence/absence data are available), but nevertheless follows pretty well the ranking of species by population densities. As population density estimates from hierarchically nested sampling plots were available for only a subset of the 40 patches with complete species surveys (Giladi *et al.* 2011), we used the plot data to calculate the average population density for each species and used these averages as species-specific constant (n_i) in our model. Using maximum-likelihood estimation we fitted a log-normal distribution to species average population densities (Hanski & Gyllenberg 1997; Hovestadt & Poethke 2005). The distribution of species-specific populations densities (n_i) could be well approximated by a lognormal distribution with the parameters $\mu = -0.8$ and $\sigma = 2.5$. For model simulations a population density randomly drawn from this distribution was assigned to each species.

3.2.5 The approximate Bayesian computation (ABC) approach

In the framework of Bayesian data analysis, model parameters are considered as random variables and can thus be described by probability distributions. The basic idea of Bayesian inference is to update our existing, or "prior" knowledge on model parameters with the information provided by the data, according to Bayes' rule

$$P(\Theta|D) = \frac{P(D|\Theta) \cdot P(\Theta)}{P(D)}, \tag{3.7}$$

where Θ indicates the model parameters, D the data, and every term is described as a probability distribution P. In Bayesian terminology $P(\Theta)$ is called the "prior distribution" of the parameters, i.e. our estimates of model parameters and their uncertainty expressed as probability distributions prior to any data collection, $P(D|\Theta)$ is called the likelihood of the data given the model, while the term on the left hand side of Eq. 3.7 is called the "posterior distribution" of the parameters. The posterior distribution is an updated estimate of model parameters and their uncertainty after considering the information in the data. It can be used as a final result or as the basis for further analyses and forecasting. $P(D)$ provides a normalization constant to convert the numerator of the right-hand side into a proper probability density (Gelman *et al.* 2004). One important advantage of Bayesian inference compared to "classical" likelihood optimisation is that the Bayesian framework directly provides estimates of parameter uncertainty by describing model parameters as probability distributions. Propagating parameter uncertainty, as specified in the posterior distribution, into the model, directly allows analysing uncertainty of higher level model predictions (ter Braak & Etienne 2003; Clark 2005).

In this study we aimed at estimating posterior distributions for all model parameters (K_0, X, Y, and α) and using these estimates for generating predictions of the extinction debt and the uncertainty of these predictions. Considering the three model scenarios, all four parameters are relevant for the metacommunity and the mainland-island scenarios, while only the extinction parameters ($K0$ and X) are relevant for the island communities scenario. Similar to previous studies, we assumed that species differ mainly in their population densities, but share similar traits of dispersal, establishment and persistence (Hanski & Gyllenberg 1997; Hovestadt & Poethke 2005). Accordingly, we did not estimate species-specific parameters, but estimated one joint posterior distribution including K_0, X, Y, and α for the whole community within each scenario.

For the incidence-function model, a real likelihood can only be defined if temporally longitudinal data are available, while only approximations are possible when the data consist of only one snapshot (ter Braak & Etienne 2003). As our data includes only one temporal snapshot, we adopted recently developed methods of approximate Bayesian computation (ABC) (Csilléry *et al.* 2010; Hartig *et al.* 2011). So far the approach of ABC has been commonly applied in population genetics and evolutionary biology, but seldom in ecological studies (but see Jabot & Chave 2009). The approach of ABC differs from classical Bayesian inference in two important points. First, as the likelihood of the data cannot be evaluated directly, it is approximated by a large number of stochastic simulations. Second, instead of comparing model predictions and data directly, ABC uses summary statistics that are derived from the data as well as from simulation results, using a wide range of parameter values (Jabot & Chave 2009; Hartig *et al.* 2011). In order to derive posterior distributions of model parameters, the general idea behind the ABC approach is to consider only parameter combinations that yield summary statistics close to the value derived from the real data (Hartig *et al.* 2011).

Here, we used two different summary statistics for comparing data and simulation results: (i) The patch-level species richness (SR) and (ii) the patch-to-patch Sørensen-similarity indices for all the pair-wise combinations of the 40 habitat patches sampled. The simulated summary statistics were derived from species occupancy pattern at the end of the simulation time. As distance metric between simulated and observed summary statistics, we used the sum of squared errors (Van Oijen *et al.* 2005).

$$d(S_{obs}, S_{sim}) = \sum_{j=1}^{N} (S_{j,obs} - S_{j,sim})^2 \tag{3.8}$$

where $S_{j,obs}$ is the observed summary statistic (species richness or Sørensen-similarity), $S_{j,sim}$ is the simulated summary statistic for patch or patch pair j, respectively and N is the number of patches (for species richness) or the number of patch pairs (for Sørensen-similarity). We constructed posterior distributions from 10000 parameter samples for each model scenario. Details on the prior distributions and the Markov Chain Monte Carlo algorithm used for generating posterior samples are provided in Appendix A.1.

We tested the convergence and performance of the ABC algorithm in providing reliable and unbiased parameter estimation by applying this approach to simulated "data" with known parameter values (Jabot & Chave 2009). This method for testing an optimisation algorithm is known as the "virtual ecologist approach", which includes stochastic simulations of ecological processes as well as of the sampling process (Zurell *et al.* 2010). In our case we did assume perfect detection of species composition and richness and thus did not include observation errors. For each model scenario, we chose parameter values for simulating "data", which yield an average patch species richness of about 150 species, corresponding to the field data (Appendix A, Figs. A.1, A.2). Evaluating the posterior distributions of the model parameters, we found that parameter estimates for the extinction parameters K_0 and X are closely correlated.

Due to this correlation it is impossible to simultaneously estimate both parameters without serious bias of parameter estimates (Fig. A1). Therefore, we set K_0 to a constant biologically plausible reference value of 100 individuals. In this case the remaining three parameters (X, Y, α) can be estimated from the simulated data without bias (Fig. A.2). Due to this constraint that K_0 and X cannot be jointly estimated, we additionally tested the sensitivity of parameter estimates for X, Y, and α to variations in the constant value of K_0 by repeating the analysis for the real data with $K_0 = 20$ and $K_0 = 500$ (Fig. A.3).

3.2.6 Extinction debt

As an application of the model parameterization derived by the ABC approach, we predicted the long-term extinction debt for each model scenario. Extinction debt is defined here as the difference between the current total species richness observed in the 40 patches (406 species) and the total species richness in these 40 patches after 1000 time steps of simulation. For each model scenario we simulated long-term species richness with each of the 10,000 samples from the respective posterior distribution to assess how parameter uncertainty translates into uncertainty in predictions of species richness and the extinction debt.

3.3 Results

Our general findings with respect to regional community dynamics were very similar whether we used species richness or Sørensen-similarity as a summary statistic for model-data comparisons and parameter inference. Therefore, in the following we present results based on using species richness as a summary statistics. Parameter estimates and uncertainties based on Sørensen-similarity indices are shown in Appendix A, Fig. A.5.

The approximate posterior distributions estimated from the field data indicated that the persistence parameter X was well defined by the data in all three scenarios (Fig. 3.2). The establishment parameter Y (number of immigrants needed for 50% chance of colonization) was estimated with high uncertainty, as indicated by the wide posterior distributions for the metacommunity and mainland-island scenarios. Furthermore, posterior densities of Y were high at the upper limit of the prior range of 1000 immigrants, which lead to a truncated shape of the posterior distribution

(Fig. 3.2). However, we decided not to extend the prior range beyond 1000 individuals, as it is biologically implausible that more than 1000 immigrants are needed for a 50% chance of successful colonization. Estimated values for the connectivity parameter α were restricted to the range below 20 m in the metacommunity, as well as in the mainland-island scenario. The posterior densities for the connectivity parameter α were relatively high at the prior minimum (5 m) and thus the posterior distribution showed a truncated shape at the lower limit (Fig. 3.2). Lowering the prior minimum for the connectivity parameter α will not earn us any additional insight, as it would essentially exclude propagule migration among patches, an extreme case already captured by the island communities scenario.

The posterior mean values of the persistence parameter X increased gradually from the metacommunity, via the mainland-island to the island communities scenario. At the same time the range of the credible intervals slightly decreased, yet the credible intervals clearly overlapped among all three scenarios (Fig. 3.3). This indicates that the relationship between carrying capacities and species extinction risks, as captured by X, was very similar in all three model scenarios.

The credible intervals for the establishment parameter Y estimated from the metacommunity scenario overlapped almost completely those estimated from the mainland-island scenarios, and the same was found for the connectivity parameter α (Fig. 3.3). In the metacommunity scenario the posterior mean values of both Y and a were slightly higher than those in the mainland-island scenario. Considering the structure of our model, parameter Y is negatively associated with establishment and thus with colonization (Eq. 3.1), while parameter α is positively associated with connectivity and colonization (Eq. 3.5). Accordingly, the high posterior means of Y and the low posterior means of α indicated that colonization rates were low in both scenarios.

Varying K_0 and/or the simulation time lead to changes in the parameter estimates for X, while estimates for Y and α did not change significantly (Appendix A, Figs. A.3, A.4). The changes in estimates for X were consistent with our expectations, considering that overall extinction probabilities (Eq. 3.2) need to remain constant, if the values for K_0 or the simulation time were changed. Therefore, our general finding of low colonization rate and dynamics that are primarily driven by extinction rates were not sensitive to changes in K_0 and the simulation time.

Model predictions for patch species richness based on the metacommunity scenario captured a reasonable amount of variation in the data (Fig. 3.4a). Comparing species richness predicted by the metacommunity scenario to the corresponding predictions

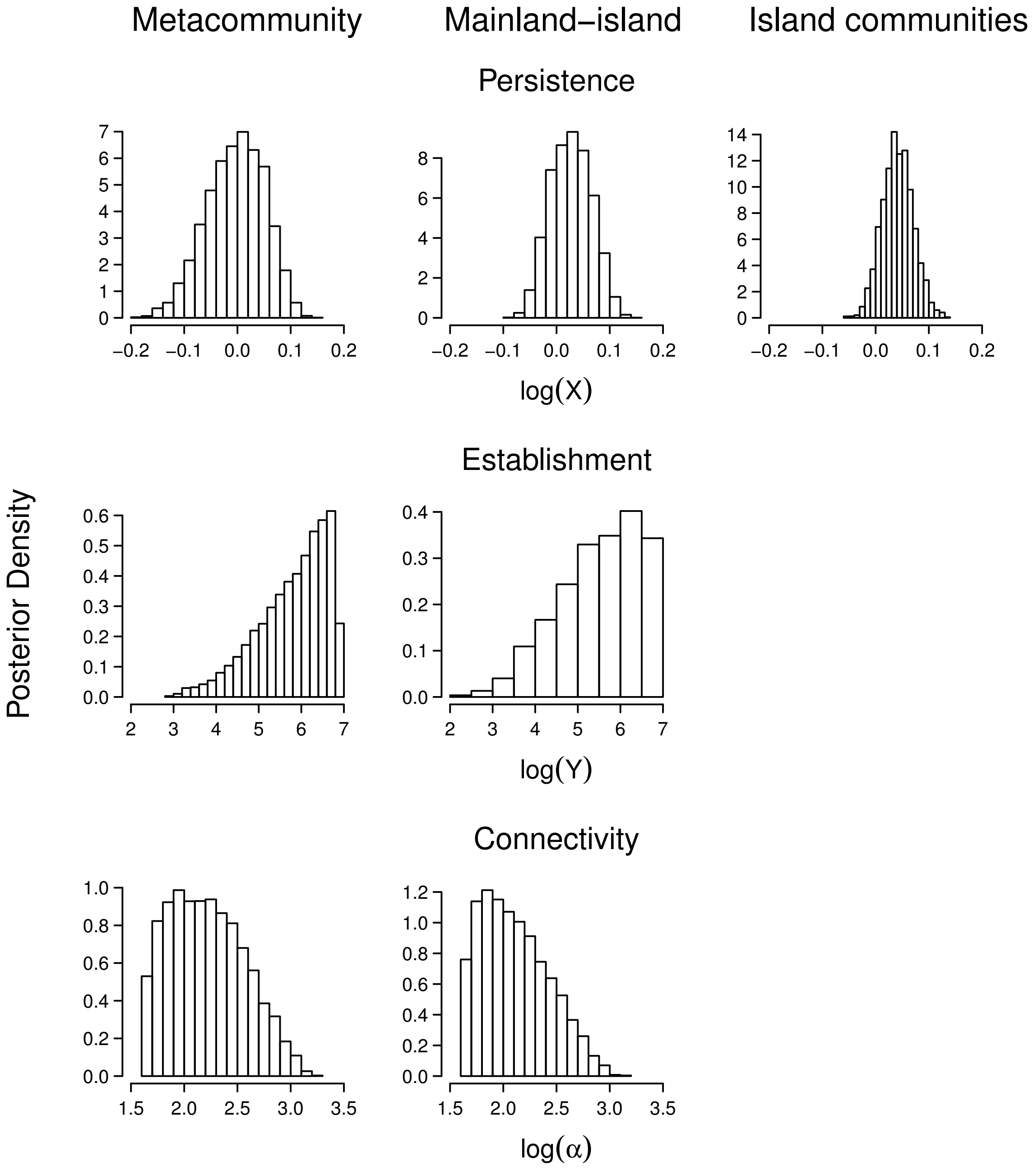

Figure 3.2. Approximated posterior distributions for model parameters X, Y and α (at the log-scale, using the natural logarithm). The left panels portray approximations for the metacommunity scenario, the panels in the middle column correspond with the mainland-island scenario and the panel on the right represent the island communities scenario. The histograms were constructed based on 10,000 samples (2000 samples from 5 replicate chains).

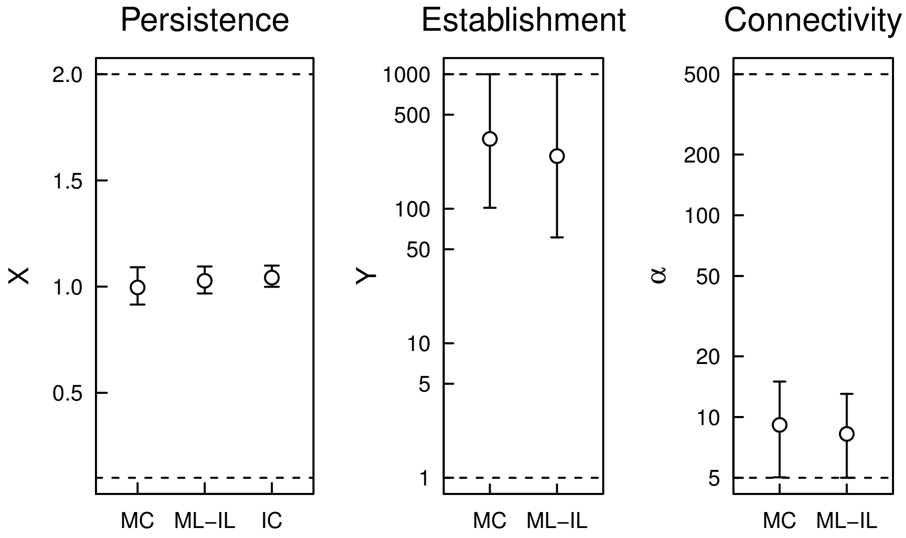

Figure 3.3. Posterior mean values and 90% credible intervals for model parameters for the metacommunity scenario (MC), the mainland-island scenario (ML-IL) and the island communities scenario (IC). The dashed horizontal lines indicate the range of uniform prior distributions for each parameter. Posterior means and credible intervals were calculated based on the samples shown in Fig. 3.2. Parameter X is dimensionless; Y conceptually refers to the number of immigrants for a 50% chance of establishment and α specifies the mean distance of among-patch dispersal events in meters.

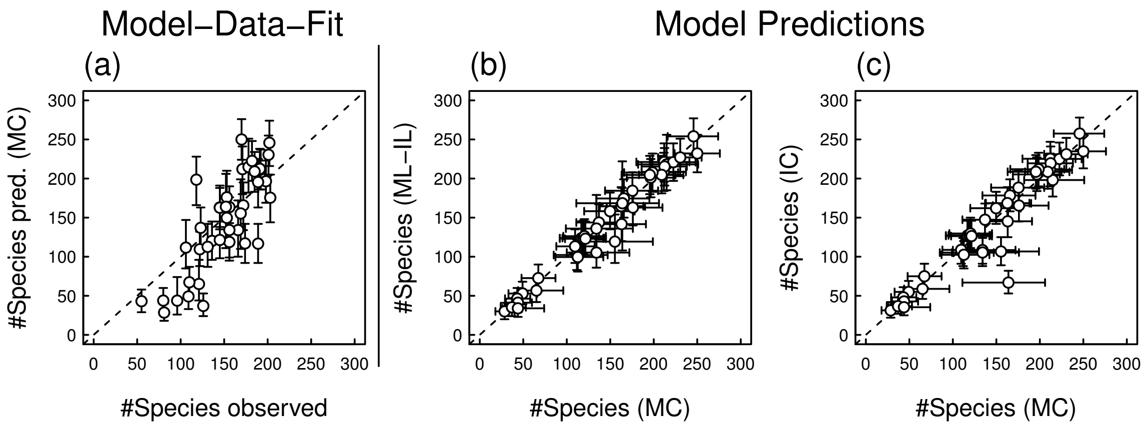

Figure 3.4. (a) Predicted vs. observed species richness for 40 habitat patches. Predictions are based on the metacommunity scenario. (b, c) Correlation between patch species richness predicted by different model scenarios. Species numbers were predicted for the same 40 patches as in (a). Points and error bars show mean values and 90% credible intervals based on 10,000 simulations with parameter sets from the respective posterior distribution. The dashed line indicates the line of perfect agreement between model and data (a), or different model scenarios (b, c). Scenario abbreviations: metacommunity – MC, mainland-island – ML-IL, island communities – IC.

of the mainland-island and the island communities scenario, we found that species richness predictions were remarkably similar among all the three scenarios (Fig. 3.4b, c). Patch species richness predicted by the metacommunity and the mainland-island scenario matched almost perfectly (Fig. 3.4b). Predictions of the metacommunity and island communities scenarios also matched closely and there were only a few patches, where the island communities scenario predicted substantially lower species richness than the metacommunity scenario (Fig. 3.4c).

In order to evaluate the long-term extinction debt for each of the three model scenarios, we projected community dynamics for 1000 time steps in each scenario. Thereby, the parameter uncertainty included in the posterior distributions was propagated into model predictions by conducting simulations with each of the 10,000 posterior samples.

After 1000 time steps the metacommunity and mainland-island scenario predicted, on average, higher species richness and thus lower extinction debts than the island communities scenario. However, even after 1000 time steps the 90% credible intervals for species richness still overlapped among all three scenarios (Fig. 3.5). The upper and lower bounds of the credible intervals of the species richness after 1000 time steps were [190; 270] in the metacommunity scenario, [182; 268] in the mainland-island scenario and [160; 207] in the island communities scenario. Defining the extinction debt as the percentage of species lost during 1000 time steps and with an initial species richness of 406 species, these predictions translated into estimates of the extinction debt of 33% – 53% in the metacommunity scenario, 34% – 55% in the mainland-island scenario and 49% – 60% in the island communities scenario.

3.4 Discussion

In this study we explored the regional dynamics of species rich plant communities by combining extensive field data with a spatially explicit simulation model. Specifically, we strived to distinguish between three different types of regional dynamics – the metacommunity, the mainland-island and the island communities type. Using the approach of approximate Bayesian computation (ABC) we were able to provide parameter estimates and to quantify parameter uncertainty for three different model scenarios that correspond to the three types of regional community dynamics. For each scenario the application of the dynamic simulation model provided estimates and uncertainties of the long-term extinction debt in the landscape investigated here.

All three model scenarios produced similar predictions for patch species richness, irrespective of the inclusion or exclusion of the regional processes of dispersal and colonization, and these predictions were similar to the observed values. In the model scenarios including colonization (metacommunity and mainland-island scenarios), our parameter estimates of low connectivity (low α) and low establishment (high Y) resulted in extremely low realized colonization rates and therefore the regional dynamics in all scenarios are primarily determined by the extinction rates within local communities. This means that the metacommunity and mainland-island scenario essentially converged to the island communities scenario. Accordingly, our study system corresponds best to a system of isolated “island” communities with negligible importance of regional processes. Such a system very likely features transient dynamics and carries a significant extinction debt. For the 40 patches surveyed here, our approach produced estimates of 33% – 60% species going extinct within 1000 years, even without further habitat fragmentation.

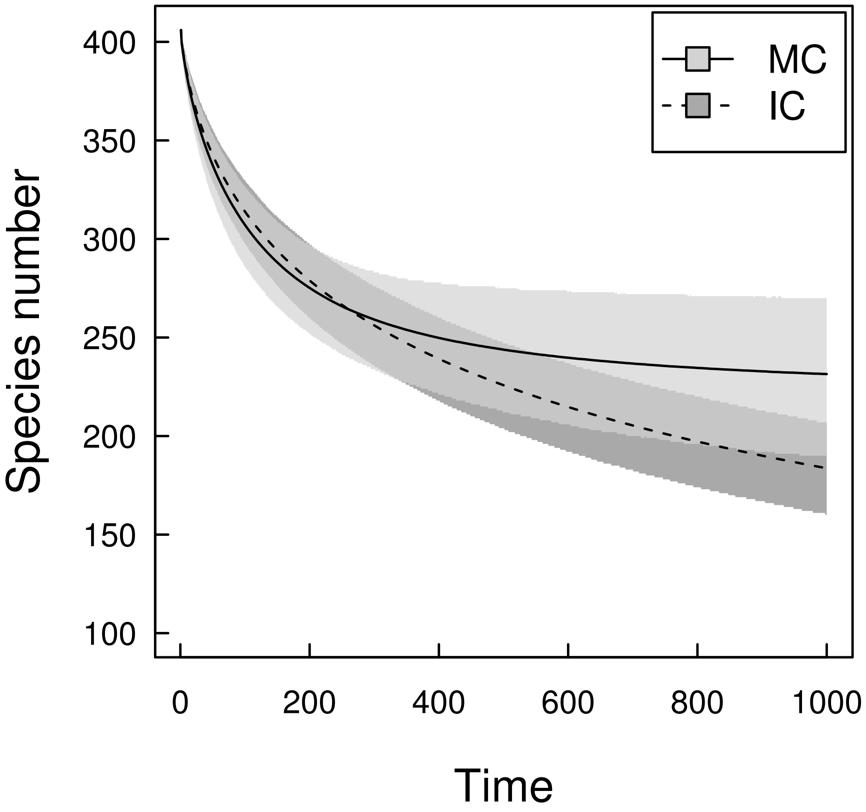

Figure 3.5. Predictions for the total patch species richness of 40 habitat patches over 1000 time steps. The lines indicate the average of 10,000 simulations using approximate posterior distribution samples for parameter values (Fig. 2). The shades of gray indicate 90% credibility intervals of the predictions for the metacommunity (MC, light gray) and island communities (IC, dark grey) scenarios. The third shade of grey represents overlap in prediction credibility intervals. Results for the mainland-island scenario were very similar to the metacommunity scenario and are not shown here for better readability.

3.4.1 Importance of regional processes

The central question for the regional dynamics of communities is the importance of regional processes, such as mass effects, source-sink and colonization-extinction dynamics (Leibold *et al.* 2004). In plant communities these regional processes are all driven by seed dispersal among habitat patches, which has been typically classified as long-distance dispersal (LDD) (Nathan & Muller-Landau 2000; Alexander *et al.* 2012). Our findings of high isolation among habitat patches and negligible colonization rates correspond well to existing data on seed dispersal from small-scale experimental studies in semi-arid and arid landscapes. Venable *et al.* (2008) showed that seed dispersal of desert annuals is usually restricted to very short distances, while Kadmon & Danin (1999) and Siewert & Tielbörger (2010) found that seed dispersal is rather unimportant for population persistence and recruitment at the local scale. However, methods for quantifying seed dispersal at small scales are not necessarily appropriate for assessing dispersal among patches (Nathan *et al.* 2008). Even rare events of among-patch dispersal of species with rather short mean dispersal distances might have important consequences for species dynamics at the landscape scale (Clark *et al.* 2001b). In our results the effects of rare among-patch dispersal events were evident in the differences between long-term predictions of species extinctions comparing the scenarios that included dispersal (metacommunity and mainland-island) and the scenario that excluded dispersal (island communities). Although the former scenarios included very low colonization rates – and thus very rare colonization events in the stochastic simulation – they predicted higher mean species richness compared to the scenario without any among-patch dispersal. However, due to parameter uncertainties the differences among the scenarios were not significant.

In addition to direct measurements of dispersal at rather small spatial scales, field observations can provide indirect evidence for the consequences of dispersal among habitat patches by analysing species distribution pattern at larger spatial scales (Clark *et al.* 2001b). In this context, observational studies in forest fragments in temperate Europe concluded that local environmental conditions are more important for species distributions and species diversity than habitat configuration and patch connectivity by seed dispersal (Dupré & Ehrlén 2002; Hérault & Honnay 2005). Our findings from a semi-arid ecosystem are in agreement with these studies in temperate Europe with respect to higher importance of local, compared to regional processes.

Another critical question in studies of regional dynamics is the role of the matrix and its effect on propagule migration among suitable habitat patches (Prevedello & Vieira 2010). Similar to previous metapopulation and metacommunity studies we assumed that the matrix is inhospitable for species occurring in the natural vegetation of suitable habitat patches. However, species survival in what is considered matrix habitat and colonization of suitable habitat patches from the matrix can have significant implications for species distributions (Cook *et al.* 2002; Laurance 2008). In our study landscape intensive agricultural practices result in a clear distinction between patch and matrix and according to our field observations hardly any species is able to complete its life cycle in the intensively cultivated matrix. Therefore, we are confident that the contribution of immigrants from the matrix to the habitat patches is negligible and does not confound our findings.

The interpretation of our results is somewhat limited due to a lack of detailed information on the fragmentation history of our landscape. We know that the habitat configuration changed little during the last 65 years, but we lack information on the land-use history before that time. Consequently, we tested a wide range of simulation times, which represents our uncertainty on the habitat fragmentation history of the Southern Judean Lowlands. We found that the results of low connectivity and the classification as system of island communities were robust to the variations in simulation time. The parameter space tested confidently includes the start of intensive agriculture in the Southern Judean Lowlands.

In our study landscape many species are known to build up seed banks that may contribute significantly to local recruitment (Osem *et al.* 2006; Siewert & Tielbörger 2010) and dormancy has been highlighted as a process that introduces difficulties for the application of metapopulation and metacommunity models to plants (Freckleton & Watkinson 2002; Alexander *et al.* 2012). When the presence of a species in a previously unoccupied patch is observed, without further inspection it is unclear whether the species was introduced by seed dispersal or if it emerged from the local seed bank (Vandvik & Goldberg 2006). Accordingly, ignoring dormancy in a model of metacommunity dynamics should result in overestimation of colonization rates, as “colonization events” from the seed bank are erroneously considered as colonization events by seed dispersal. However, an overestimation of colonization by excluding dormancy cannot affect our main conclusion, as our findings already provided support for low colonization rates.

3.4.2 Extinction debt

We used the parameter estimates derived from the ABC approach to project the long-term community dynamics within each model scenario. In this way, our study presents a novel approach of using data-based spatially explicit modelling to predict the extinction debt of a plant community (Jackson & Sax 2009; Kuussaari *et al.* 2009). Our projections indicated that the extinction debt in our study landscape is far from being paid. In our model, species are only differentiated by their population density, which is closely linked to species extinction rates. Therefore, the model predicts that species with low population densities go extinct first, while abundant species persist for longer time. Despite the relative constancy of landscape configuration for at least 65 years, we predicted that the total species richness of the patches surveyed will still decrease for several hundred years and that in the long-term between 33% – 60% of all species will go extinct.

The most common approach for assessing the extinction debt of plant communities is to correlate present species richness with past, as well as present habitat configuration (reviewed in Cousins 2009; an approach that rarely provides projections of future species extinctions (Kuussaari *et al.* 2009). However, Helm *et al.* (2006) empirically derived an estimate of the extinction debt for fragmented calcareous grasslands in Estonia of about 40% of species going extinct before the system reaches its equilibrium state. Their finding for a temperate grassland system matches surprisingly well with our estimation of the extinction debt for a Mediterranean shrub- and grassland. Furthermore, the slow response of species richness to habitat fragmentation in our projections is in agreement with findings for temperate grasslands or forest herb communities (Helm *et al.* 2006; Vellend *et al.* 2006). In a review of studies in fragmented temperate grasslands, Cousins (2009) found that landscapes that still contain more than 10% suitable habitat tend to carry a significant extinction debt, while landscapes with less than 10% suitable might habitat have already paid the debt. As our landscape still contains about 30% of suitable habitat, our findings from a semi-arid region fit well within this perspective.

Due to parameter uncertainty and due to the conceptual simplicity of the model used, our quantification of the extinction debt can only provide very rough first estimates. On a time scale of 1000 years, ecological drivers other than current habitat fragmentation, e.g. climate change, are expected to influence species persistence and species distributions. Climate change predictions for the Mediterranean include a decrease in precipitation and could thus become a major driver of vegetation changes in this region in general and in this fragmented landscape in particular (Sala *et al.* 2000; Brook *et al.* 2008; Chenoweth *et al.* 2011). Although the local adaptation of plant species might buffer climate-driven extinctions, the slow rate at which such evolutionary changes occur may not be sufficient to have any discernible buffering effect (Parmesan 2006).

3.4.3 Methodological issues

In analogy to previous multi-species incidence-function models we assumed that for any given species all patches are of similar habitat quality and thus support equal population densities once they get occupied (Hanski & Gyllenberg 1997; Hovestadt & Poethke 2005). However, as in our approach population density is closely related to extinction probability, variations in patch quality might significantly influence the species' regional dynamics. Variations in patch quality could be incorporated into the incidence-function modelling by parameterizing relationships between environmental variables, e.g. soil properties, and species extinctions and/or colonizations (Moilanen & Hanski 1998; ter Braak & Etienne 2003). The identification and parameterization of species' environmental requirements provides a challenging task in itself (e.g. Guisan & Thuiller 2005), but if significant species-environment relationships could be identified, the consideration of environmental data in the incidence-function modelling approach might shed additional light on the plant community dynamics in the Southern Judean Lowlands.

In our model, species only differ in their population densities, but not in their parameters for persistence, establishment and connectivity (Hovestadt & Poethke 2005). However, species responses to habitat fragmentation might differ depending on their functional traits (Lindborg *et al.* 2012). While our approach of using one snapshot of species presence/absence data was successful in estimating one parameter set for the plant community, preliminary analysis indicated that it is impossible to reliably estimate species-specific parameter sets from our data. For a highly diverse community as the one investigated here, we suggest that the identification of plant functional groups followed by the estimation of functional group-specific parameter sets can further improve our understanding of regional community dynamics (Hérault & Honnay 2005; Lindborg *et al.* 2012). However, similar to previous applications of the incidence-function model to single species this approach will require several years of species occupancy data (ter Braak & Etienne 2003; Risk *et al.* 2011).

In this study we did not account for observation errors with respect to species richness, as robust estimation of observation error requires several samples of the same location (Zurell *et al.* 2010; Risk *et al.* 2011). Although patch surveys were thoroughly conducted by experienced botanists, we might have missed a few species and might have thus slightly underestimated patch species richness. This might lead to slight biases in parameter estimates, but given the clear evidence for low colonization rates found, we do not expect that observation errors would affect our main findings and conclusions.

In accordance with previous versions of the incidence-function model we used an exponential kernel to describe patch connectivity (Hovestadt & Poethke 2005). We expect that our findings with respect to the type of regional community dynamics will be robust to differences in the shapes of the connectivity kernel, but we suggest that an interesting issue would be to investigate the implications of a more leptokurtic (or "fat-tailed") connectivity kernel on the long-term species richness in the system. Parameterizing more complex connectivity kernels will require substantially more data than a one-parameter kernel, but might shed more light on the consequences of low rates of among-patch dispersal for community dynamics (Clark *et al.* 1999).

3.5 Conclusions

Despite a wealth of theoretical studies using dynamic (meta)community models (e.g. Chave *et al.* 2002; Mouquet & Loreau 2003; Hovestadt & Poethke 2005), there have been very few studies that combined a dynamic simulation model with data of species rich plant communities at the landscape scale (but see Condit *et al.* 2002 for an example in a continuous landscape). Therefore, the study presented here provides a novel approach for combining a dynamic simulation model with field data to gain general insights into regional community dynamics in fragmented landscapes and to derive projections that are relevant for conservation biology. From the methodological perspective, our approach provides two main advances compared to previous (meta)community models: First, the explicit consideration of patch shapes and relative locations for the definition of patch connectivities and second, the inference of model parameters and parameter uncertainty from field data within a statistically rigorous framework (Clark 2005).

From the perspective of conservation biology our finding of high isolation among patches and the close link between patch area and species diversity stresses the need to preserve existing habitat or even establish new suitable habitat area for natural vegetation to reduce extinction risks and maintain the high diversity of this system. The question whether and to which degree an increase in habitat connectivity, e.g. by establishing corridors or “stepping stones” of suitable habitat, would improve the maintenance of plant species diversity in the landscape could in principle be investigated within our modelling framework by simulation experiments with additional natural habitat patches and/or corridors. Such analysis is beyond the scope of this study presented here, but could provide an interesting follow-up investigation.

Link to the next chapter

In the previous chapters, I focused on plant species diversity and its relationship to species' dispersal capabilities (chapter 2) as well as to patch sizes and patch connectivities (chapter 3). The diversity of plant communities and its relationship to environmental drivers is of high interest, in particular for biodiversity conservation. However, diversity indices, e.g. species richness, provide highly aggregated descriptions of communities and might thus convey only a limited amount of information on the processes that drive community dynamics.

Beyond species diversity, the distribution of functional traits in plant communities is expected to be indicative of community assembly processes, such as abiotic habitat filtering and interspecific competition. Furthermore, the analysis of plant functional traits along environmental gradients has been suggested as a promising approach to predict species' and communities' responses to environmental changes. For these reasons, in the following chapter, I change the focus from species diversity to plant functional traits in the SJL.

Previous studies of trait-environment relationships usually analysed the implications of single environmental drivers. However, it has been predicted that fragmentation and climate change may have synergistic adverse effects on plant species and communities. In the following chapter, I provide the first analysis of the interactive effects of climate and fragmentation on community-mean plant functional traits. The study area in the SJL is well-suited for this analysis due to the steep south-north precipitation gradient and the occurrence of patches of varying size and isolation everywhere along the precipitation gradient. In the statistical models, I included the spatially explicit connectivity index, which has been already applied in chapter 3, as an potential explanatory variable of community-mean plant functional traits.

Chapter 4

Plant functional traits and community assembly along interacting gradients of productivity and fragmentation[1]

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[1] An article with similar content was published as:
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Abstract

Quantifying the association of plant functional traits to environmental gradients is a promising approach for understanding and projecting community responses to land use and climatic changes. Although habitat fragmentation and climate are expected to affect plant communities interactively, there is a lack of empirical studies addressing trait associations to fragmentation in different climatic regimes.

In this study, we analyse data on the key functional traits: specific leaf area (SLA), plant height, seed mass and seed number. First, we assess the evidence for the community assembly mechanisms habitat filtering and competition at different spatial scales, using several null-models of random community assembly and a comprehensive set of community-level trait indices, which quantify trait convergence and divergence. Second, we analyse the association of community-mean traits with patch area and connectivity along a south-north productivity gradient.

We found clear evidence for trait convergence due to habitat filtering. In contrast, the evidence for trait divergence due to competition fundamentally depended on the null-model used. When the null-model controlled for trait convergence by habitat filtering, there was no evidence for trait divergence. All traits varied significantly along the S-N productivity gradient. While plant height and SLA were consistently associated with fragmentation, the association of seed mass and seed number with fragmentation changed along the S-N gradient.

Our findings indicate trait convergence due to drought stress in the arid sites and due to higher productivity in the mesic sites. The association of plant traits to fragmentation is likely driven by increased colonization ability in small and/or isolated patches (plant height, seed number) or increased persistence ability in isolated patches (seed mass).

Our study provides the first empirical test of trait associations with fragmentation along a productivity gradient. We conclude that it is crucial to study the interactive effects of different ecological drivers on plant functional traits.

4.1 Introduction

Habitat fragmentation, climate change and their interactive effects have been highlighted as the most important drivers of diversity loss and of shifts in species composition in plant communities (Sala *et al.* 2000; Fahrig 2003; Travis 2003; Opdam & Wascher 2004; Thuiller *et al.* 2005; Parmesan 2006; Jeltsch *et al.* 2011). Drastic shifts in community composition and structure were especially predicted for species range margins and ecotones that represent transition zones between different ecosystems and different climatic regimes (Allen & Breshears 1998; Hampe & Petit 2005; Thuiller *et al.* 2008).

A promising approach for understanding and for ultimately projecting community responses to environmental changes is the quantification of the association between plant functional traits and environmental conditions (Lavorel & Garnier 2002; McGill *et al.* 2006; Jeltsch *et al.* 2008). So far, numerous studies adopted the framework of trait-based ecology to address community assembly processes and changes of plant functional traits along climatic gradients in different continents and at scales ranging from regional to global (Díaz & Cabido 1997; Fonseca *et al.* 2000; Wright *et al.* 2004; Westoby *et al.* 2002; Cornwell & Ackerly 2009). The link between plant functional traits and habitat fragmentation was primarily studied in temperate European ecosystems focusing on forest herbs (Dupré & Ehrlén 2002; Kolb & Diekmann 2005; Hérault & Honnay 2005), semi-natural grasslands (Lindborg 2007; Lindborg *et al.* 2012; Marini *et al.* 2012; Purschke *et al.* 2012) and urban ruderal communities (Schleicher *et al.* 2011). However, little is known on the response of plant functional traits to habitat fragmentation in other climatic regimes (Chust *et al.* 2006) and on the interacting effects of climate and fragmentation of functional trait distributions in plant communities.

Classical community assembly theory encompasses two potentially opposing processes that affect the distribution of functional traits within and among communities. First, as species distributions are often shaped by environmental conditions, co-occurring species are likely to experience and to be functionally adapted to the same abiotic environment. This process is known as "“habitat filtering” and is expected to result in trait convergence among coexisting species (Cornwell & Ackerly 2009). Second, as species with similar functional traits are assumed to experience substantial niche overlap, interspecific competition is expected to preferentially exclude species with high trait similarity and thus results in trait divergence within communities (MacArthur & Levins 1967; Stubbs & Wilson 2004; Kraft *et al.* 2008). The effects of these opposing processes may vary with the spatial scale, with habitat filtering being predominant on comparably large spatial scales with substantial environmental variation, while interspecific competition might be more important at small spatial scales, where plants actually compete for resources (Kraft & Ackerly 2010). In addition to its influence on trait distributions within communities, habitat filtering may also cause shifts in community-mean trait values along environmental gradients (Ackerly & Cornwell 2007; Cornwell & Ackerly 2009).

In this study, we investigate plant functional trait distributions in a fragmented landscape that encompasses a steep south-north environmental gradient at the transition zone between desert and Mediterranean ecosystems (Giladi *et al.* 2011). We approach the crucial issue of functional trait responses to interacting gradients of fragmentation and environmental conditions in two conceptual steps: First, we assess if there is evidence for assembly processes, such as habitat filtering and interspecific competition, in the functional trait distributions of plant communities. Second we investigate specific shifts in community-mean trait values along fragmentation and environmental gradients (Cornwell & Ackerly 2009).

Our study area in the Southern Judean Lowlands (SJL), Israel, consists of discrete habitat patches of natural vegetation embedded in a matrix that is used for intensive agriculture (Yaacobi *et al.* 2007; Gavish *et al.* 2011; Giladi *et al.* 2011). The natural scrubland and grassland vegetation features high species richness and a high proportion of annual plant species. Natural habitat patches of different sizes and degrees of isolation occur everywhere along the S-N gradient, such that habitat fragmentation is not confounded with the environmental gradient. Therefore, this landscape is well suited to study the interacting effects of fragmentation and environmental conditions on plant functional traits. In previous studies conducted in the same landscape, we found that the relative importance of fragmentation and the position along the S-N gradient for species richness varies with spatial scale (Giladi *et al.* 2011) and we assessed the role of habitat connectivity for regional community dynamics (chapter 3; May *et al.* 2013). Here we focus on the interactive effects of fragmentation and environmental gradients on the distribution of plant functional traits within and among communities.

Hypotheses on the association of plant functional traits with fragmentation are based on island biogeography and metapopulation theories (MacArthur & Wilson 1967; Hanski 1999). The presence of a species in a given patch within a fragmented landscape depends on its ability to (a) colonize the patch, and (b) persist in a patch once present. Persistence can be either assured by positive long-term population growth in the focal patch or by the input of sufficient propagules from neighbouring patches, which is known as rescue effect (Brown & Kodric-Brown 1977). As the challenge of colonization increases with patch isolation, we expect that plants with traits that favour colonization will be disproportionally represented in isolated patches (Dupré & Ehrlén 2002). As the rescue-effect will be most important for small populations in small patches, we additionally expect that plants with traits that favour colonization will be disproportionally represented in small patches as well (Hanski 1999; Dupré & Ehrlén 2002). Analogously, as extinction risk increases with a decreasing patch size, the challenge of persistence also increases and therefore we expect that plants with traits favoring persistence will be disproportionally represented in smaller patches.

The importance of various functional traits for species persistence may vary along environmental gradients. In our study area, increasing precipitation and increasing plant density from south to north indicates that there is a shift from high drought-stress in the south to higher productivity and thus higher intensity of above-ground competition in the north (Giladi *et al.* 2011). Therefore, our hypotheses on the response of plant functional traits to patch area rely on the premise that species persistence in the south will mainly depend on a species' ability to cope with drought-stress, while in the north it will depend on the ability to avoid competitive exclusion (Grime 2001). Considering the interactive effects of patch area and the position along the S-N gradient we therefore predict that in the arid sites adaptation to drought-stress is higher in small than in large patches, while in the mesic sites adaptation to competition is higher in small than in large patches.

For this study we sampled five key plant functional traits – specific leaf area (SLA), canopy height, seed-release height, seed mass and seed number (Westoby *et al.* 2002; Cornelissen *et al.* 2003). Our specific predictions for the response of these functional traits to the interacting gradients investigated here are summarized in Table 4.1. This study is organized in two main parts: In the first one we assess trait convergence and trait divergence within plant communities to answer the following specific questions with respect to community assembly processes: (1a) Are plant communities in the SJL structure by habitat filtering? (1b) Is there evidence for reduced niche-overlap among coexisting species due to interspecific competition? (1c) Does the evidence for habitat filtering and/or competition in trait distributions vary with spatial scale? In the second part we focus on the issue of plant traits distributions along the S-N and fragmentation and gradients. More specifically we investigate: (2a) How do community-mean traits values change along the S-N gradient? (2b) Are community-mean traits values associated with fragmentation? (2c) Does the association of community-mean traits with fragmentation change along the S-N gradient?

Table 4.1. Specific predictions of plant functional trait responses to climate, fragmentation and the interactive effects of climate and fragmentation. The predictions always refer to the expected response of community-mean traits to environmental drivers. General theory and hypotheses on trait-environment relationships are provided in the main text.

Environmental driver	**Prediction**	**Rationale**	**References**
Climate			
	Arid sites: Low SLA Low seed mass High seed number	Adaptation to drought-stress and bet-hedging	Venable & Brown (1988); Leishman *et al.* (2000); Westoby *et al.* (2002)
	Mesic sites: High SLA High plants High seed mass	Adaptation to above-ground and seedling competition	Westoby *et al.* (2002); Grime (2006); Metz *et al.* (2010)
Fragmentation			
	Small and isolated patches: High seed release height High seed number	Dispersal distance and colonization ability increase with seed release height and seed number	Clark *et al.* (1999); Dupré & Ehrlén (2002); Tackenberg *et al.* (2003); Thomson *et al.* (2011)
Climate × Fragmentation			
	Small and arid patches: Very low SLA Very low seed mass Very high seed number	High extinction risk in small patches requires high degree of adaptation to drought-stress	
	Small and mesic patches: Very high SLA Very high seed mass Very high plants	High extinction risk in small patches requires high degree of adaptation to competition	

4.2 Methods

4.2.1 Study area

The study area is located in the Southern Judean Lowlands (SJL), Israel (31°24′ – 31°41′ N; 34°46′ – 34°52′ E) (Fig. 4.1). This region represents a transition zone between desert and Mediterranean ecosystems with a sharp increase in precipitation from south to north. The study area is characterized by a typical semi-arid climate, with short mild winters and long, dry and hot summers. Mean annual temperature is 19 °C (12 °C in January and 26 °C in August) throughout the study area. Mean annual precipitation, which is almost exclusively restricted to October until March, increases from 300 mm in the south to 450 mm in the north over a distance of 30 kilometres only (Table 4.2). This increase in precipitation results in substantial increases in plant density, plant species richness (Giladi *et al.* 2011), vegetation biomass (Schmidt & Gitelson 2000) and in considerable changes in floral community composition (Kadmon & Danin 1997, 1999).

For thousands of years the landscape has been used for sheep and goat grazing and small scale subsistence farming (Naveh & Dan 1973; Ackermann *et al.* 2008). Intensified agriculture in the last decades reshaped the landscape into a patch-matrix mosaic, with clear boundaries between semi-natural habitat and agricultural matrix (Fig. 4.1; Yaacobi *et al.* 2007; Gavish *et al.* 2011; Giladi *et al.* 2011). Historical aerial photographs showed that the distribution of natural habitat patches in the landscape has remained relatively constant during the last 60 years (I. Giladi, unpublished data). Today the natural vegetation patches experience sheep grazing on the south and cattle grazing in the north of the SJL (Rotem 2012).

The main vegetation types are characterized as semi-steppe batha (Mediterranean scrubland) and grassland (Giladi *et al.* 2011). The most dominant perennial species are the dwarf shrub *Sarcopoterium spinosum* in the batha vegetation and the tussock grasses *Hyparrhenia hirta* and *Hordeum bulbosum* in the grassland. Plant communities are characterized by a high species richness of 83 ± 17 species (mean ± standard deviation, n = 81) at the 15 m × 15 m plot scale, and by a high proportion of annual species throughout the study region, accounting for 67% of all species. The most common annual species are *Avena sterilis*, *Anagallis arvensis*, *Linum strictum*, *Urospermum picriodes*, and *Plantago afra* (Giladi *et al.* 2011).

In this study we exclusively focus on annual plant species in order to control for a potentially varying representation of plant species' life forms in the sampled communities. We sampled plant traits and conducted vegetation surveys in three land units, called Dvir, Lachish and Galon (from S to N) that are arranged along a S-N gradient (Fig. 4.1, Table 4.2). Due to the substantial increase in mean annual precipitation, we will refer to Dvir as the "arid" and to Galon as the "mesic" end of the S-N gradient. Each land unit (4 km × 6 km) includes 70 – 170 natural vegetation patches of different sizes ranging from continuous (> 100 ha) to very small patches ($< 100\,\mathrm{m}^2$). We used rectified aerial photographs (pixel size = $1\,\mathrm{m}^2$) to identify and digitize all the patches of natural vegetation within each of the three land units. The digitized map was stored as vector-based format in a Geographical Information System (GIS) platform (ArcGIS$^{\mathrm{TM}}$; ESRI) and used for the calculations of patch area and connectivity.

4.2.2 Patch connectivity

The connectivity of a patch correlates with the probability of seed dispersal into that patch from other patches in the landscape (Moilanen & Nieminen 2002). According to previous studies, we assumed that patch connectivity increases with the number and area of neighbouring patches and decreases with patch-to-patch distances (Hanski 1999; Hovestadt & Poethke 2005). However, in previous studies patch-to-patch distances were usually measured between patch centroids or between patch edges (reviewed in Moilanen & Nieminen 2002). These may be reasonable approximations if the distances between patches are much larger than the patch extents, but if patch extents and inter-patch distances are of similar order of magnitude, as in our landscape (Fig. 4.1, considering patch shapes and orientations may much better reflect the functional connectivity (i.e. the probabilities of seed dispersal) among patches. Therefore, we develop and use a connectivity index that considers patch shapes and orientations explicitly and corresponds to area-to-area dispersal as suggested by Chipperfield *et al.* (2011).

For the calculation of patch connectivities, we projected the habitat map onto a raster grid with grain size of 5 m × 5 m. In this raster representation each patch is represented by a set of contiguous grid cells. The connectivity c_i of one single grid cell i in a target patch K is calculated by assuming a negative-exponential 2D-kernel (Clark *et al.* 1999; Hovestadt & Poethke 2005) and summing up the grid-cell connectivities between the focal cell i in target patch K and all grid cells j in all source patches M in the same land unit:

$$c_i = \frac{\alpha^2}{2\pi} \sum_{M \neq K}^{N_P} \sum_{j=1}^{N_M} \exp\left(-\alpha \cdot d_{i,j}\right), \tag{4.1}$$

where $d_{i,j}$ is the distance between grid cells i (in patch K) and j (in patch M), N_P is the number of patches in the land unit, and N_M is the number of grid cells that constitute source patch M. Accordingly, the outer summation is applied over all source patches, and the inner summation over all grid cells of the source patch M. The model parameter α [1/m] provides the decay rate of connectivity with distance and the normalization constant in front of the summation assures that the connectivity kernel properly integrates to one. Finally, the total connectivity of patch K (C_K) is calculated as the mean of all grid-cell connectivities belonging to patch K:

$$C_K = \frac{1}{N_K} \sum_{i=1}^{N_K} c_i, \tag{4.2}$$

where NK is the number of grid cells that constitute patch K. Using the mean connectivity of all target patch grid cells instead of their sum assures that the new index is independent of target patch area. With this definition of patch connectivity the shapes and the relative positions of target and source patches are considered, as source-patch grid cells that are close to the target patch contribute more to its connectivity than distant source-patch grid cells. As connectivity parameter value for the annual plant community we used $\alpha = 0.002$ [1/m] following Verheyen *et al.* (2004) and Hérault & Honnay (2005). In order to test the sensitivity of our findings, we additionally used $\alpha = 0.01$ and $\alpha = 0.001$. As this did not change our results, we only present results using $\alpha = 0.002$ in the following. The correlation of our connectivity index with previously used connectivity/isolation indices is presented in the supplementary material (Fig. B.1).

4.2.3 Vegetation sampling

We established 80 vegetation sampling plots of the size 15 m × 15 m within 40 patches of natural vegetation (26, 29 and 25 plots in 12, 16 and 12 patches within Dvir, Lachish and Galon, respectively). Each 15 m × 15 m plot included 3, 6 and 12 subplots of the sizes 5 m × 5 m, 1 m × 1 m and 0.25 m × 0.25 m, respectively (Giladi *et al.* 2011). In our study landscape habitat fragmentation and patch sizes are confounded with an east to west gradient. However, by a careful choice of patches to be sampled, we were able to avoid these confounding effects in our sampling (Fig. 4.1).

The number of plots placed within each patch varied according to patch area and ranged between one and seven plots. All annual plant species within each sampling plot were recorded during the peak of the growing season between early March and early April in 2008 and 2009. In 2009 we recorded plant density as well by counting all individuals within 12 small sampling plots of the size $0.25\,\mathrm{m} \times 0.25\,\mathrm{m}$ in each $15\,\mathrm{m} \times 15\,\mathrm{m}$ plot (Giladi *et al.* 2011).

In 77 of the plots we collected soil samples. Each soil sample consisted of a mixture of three 300 g sub-samples taken at a depth of 10 cm from three positions within a plot. These samples were later used for measurements of field capacity and organic matter content using standard soil analysis methods (Carter & Gregorich 2007). Organic matter content was determined by the loss of ignition procedure (LOI). Field capacity was determined used by simple a simple gravimetric procedure.

The 40 patches sampled include five patches of continuous habitat, each with an area of more than 35 ha, while all other patches are smaller than 5 ha. We do not expect that large areas of continuous natural habitat depend on propagule immigration from much smaller neighbouring patches (Giladi *et al.* 2011). Therefore, connectivity indices were only calculated for patches smaller than 5 ha.

4.2.4 Trait measurements

From a “core list” of plant functional traits we chose two vegetative and three regenerative traits, which were proposed to reflect plant strategies along environmental gradients (Weiher *et al.* 1999; Westoby *et al.* 2002). As vegetative traits we measured canopy height (CH) [cm] and specific leaf area (SLA) [$\mathrm{mm}^2\,\mathrm{mg}^{-1}$], which was derived by dividing fresh leaf area by leaf dry mass. As regenerative traits we recorded seed release height (SRH) [cm], the seed mass of one seed (SM) [mg] and the seed number (fecundity) of one individual (SN). Seed mass was measured after removing any seed appendages (Cornelissen *et al.* 2003).

Trait sampling was conducted in March and April 2009 and 2010, and measurements followed the standard protocols suggested by Cornelissen *et al.* (2003) and Kleyer *et al.* (2008). Accordingly, CH and SRH were measured for 25 individuals and SLA, SM and SN for 10 individuals per species. For SLA measurements we sampled two fresh, healthy and light exposed leaves per plant. If a species has different types of leaves, we collected two leaves from each type. For seed mass we used at least 10 ripe seeds of each plant and 10 seeds per type, if the species produces different types of seeds. In order to estimate the seed number (fecundity), we counted the number of fruits or infructescences of 10 plant individuals. Then, we collected two fruits or infructescences per plant prior to any dispersal and counted the number of seeds per fruit or infructescence in the lab. Seed number was then determined as the product of the number of fruits/infructescences per individual and the average number of seeds per fruit/infructescence.

Usually, trait measurements were conducted in one, well-established population. However, for rare species and species with very low population density, we pooled data from several populations to attain the sample sizes mentioned above. Accordingly, our results always refer to interspecific trait variation and we do not address intraspecific trait variation in this study. For 12 species we supplemented our data for seed mass with measurements taken in a site adjacent to our study area by Osem *et al.* (2006). In total, we gathered trait data for the following numbers of annual plant species: SLA - 134 species, CH and SRH - 137 species, SM - 115 species, SN - 110 species. A complete list of species, their functional trait values and their occupancies in the three land units is provided in the supplementary material (Table B.3).

Based on the species survey data, we calculated that our trait data set accounts for 60 - 75% of annual species and for 80 - 95% of annual plant individuals in the $15\,\mathrm{m} \times 15\,\mathrm{m}$ plots and therefore provides a reliable representation of community-level trait indices (Pakeman & Quested 2007).

4.2.5 Data analysis and statistics

Prior to the calculation and analysis of community-level trait indices, we assessed the univariate distribution and bivariate correlations of species' mean trait values. Species' trait values for CH, SRH, SN and SM showed a right-skewed distribution. Therefore, we used a $\log_{10}$-transformation to normalize these traits (Westoby 1998; Fonseca *et al.* 2000). Species' SLA values were normally distributed. We analysed pair-wise correlation between species-level traits by non-parametric Spearman rank correlation of untransformed trait data.

Null-model tests for community assembly processes

In order to test for convergence and divergence in trait values, as predicted by habitat filtering and interspecific competition, respectively, we calculated several community-level trait indices for each sampling plot and contrasted these values with indices derived from null-models based on random community assembly.

Trait convergence was assessed by measuring the range and variance of trait values in a community, both of which are expected to be reduced by habitat filtering. We combine these indices, as each of them has its advantages and shortcomings. Trait range closely represents the concept of habitat filtering and is independent of trait divergence within communities, but it is sensitive to extreme trait values. In contrast, trait variance is simultaneously determined by convergence due to filtering and divergence due to competition, but it is more robust to extreme trait values (Cornwell & Ackerly 2009).

Interspecific competition is expected to result in a limiting similarity and/or an even spacing among species trait values and thus in a platykurtic distribution of trait values in communities (Stubbs & Wilson 2004; Kraft & Ackerly 2010; Götzenberger *et al.* 2012). Accordingly, we used the kurtosis of the community-level trait distribution as well as three indices based on distances along trait axes to test for trait divergence. First, we used the standard deviation of nearest neighbour distances (sdNN), which directly mirrors the idea of limiting similarity, and second we calculated the standard deviation of the consecutive neighbour distances (sdND) of species trait values ordered along the respective trait axis, which quantifies the evenness of trait spacing (Cornwell & Ackerly 2009; Kraft & Ackerly 2010). In order to control for habitat filtering while testing for trait divergence, we followed the recommendation by Kraft & Ackerly (2010) and used range-standardized indices sdNNr and sdNDr, which were obtained by dividing sdNN and sdND by the observed trait range in the community. As the neighbour distances sum up to the trait range and are thus, by definition, related to the trait range of a plot, we only used the range- standardized version of this index (sdNDr).

We implemented three different null-models that reflect different levels of randomness in community assembly and account for habitat filtering in different ways. All three null-models maintained the observed species richness of sampling plots and the probability of assembling a species into a null-community was proportional to its plot-level incidence in the survey data (Gotelli & Graves 1996; Kraft *et al.* 2008; Kraft &

Ackerly 2010). In null-model 1 we used the same regional species pool for all plots, irrespective of their position along the S-N gradient, thus testing for habitat filtering in sampling plots relative to the regional species pool. In null-model 2 species occurrences were only randomized within land units by using specific species pools for each land unit. In this way, null-model 2 was used to test for habitat filtering in sampling plots relative to land unit specific species pools.

In null-model 3 we adopted the two-step approach of Cornwell & Ackerly (2009). For each 15 m × 15 m plot sampling plot we first derived a specific species pool, which includes only those species with trait values that are within the observed trait range of this sampling plot. Then, null communities for this plot were randomly assembled from this plot-specific species pool only. This null-model strictly controls for trait convergence at the sampling plot scale and is therefore only used for tests of trait divergence.

We calculated community trait indices and tested for community assembly processes at three different scales: 15 m × 15 m, 5 m × 5 m and 1 m × 1 m. In null-model 3 we used the trait range observed at the 15 m × 15 m scale to derive plot-specific species pools for the scales of 5 m × 5 m and 1 m × 1 m. Accordingly, null-model 3 assumes that habitat filtering mainly operates at the 15 m × 15 m, while testing for competition at the scales of 5 m × 5 m and 1 m × 1 m.

For each null-model and each scale, we simulated 1999 random permutations to generate expected trait indices under random assembly. We tested the deviation of observed values vs. null expectations using paired Wilcoxon signed rank tests (Kraft *et al.* 2008). All tests were one-tailed with the expectation of lower trait ranges and variances due to habitat filtering and lower kurtosis and standard deviations of nearest neighbour and neighbour distances due to competition. Standard effect sizes (SES) for each plot and each trait index (T) were calculated as:

$$SES = \frac{T_{obs} - T_{exp}}{\mathrm{sd}(T_{exp})}, \tag{4.3}$$

where T_{obs} is the observed trait index and T_{exp} the expected trait index. The standard deviation in the denominator of T_{exp} was calculated from the 1999 null-model simulations (Kraft *et al.* 2008; Cornwell & Ackerly 2009; Kraft & Ackerly 2010).

Shifts of plant strategies along the south-north gradient and with fragmentation

After testing the effects of habitat filtering and competition on community trait distributions, we assessed the effects of fragmentation and position along the S-N gradient on community-level traits. For this purpose we calculated community-mean trait values by averaging trait values of all annual species present at the 15 m × 15 m plot scale using equal weights for all species (Cornwell & Ackerly 2009; Golodets *et al.* 2009).

The position along the S-N gradient was used as a categorical factor, called land unit, with the three levels Dvir, Lachish and Galon. Habitat fragmentation was represented by patch area ($\log_{10}$-transformed) and by patch connectivity, as described above. We analysed collinearity between explanatory variables using robust Spearman-correlation analysis for testing patch area vs. patch connectivity and Kruskal-Wallis tests for testing land unit vs. both continuous patch variables.

Due to the nested structure of our sampling design with 1–3 plots in one patch, we used linear-mixed effects models (lme) with patch ID as a random factor and with land unit, $\log_{10}$(patch area) and patch connectivity as fixed-effect explanatory variables (Pinheiro & Bates 2000). In addition, we included all three two-way interactions (land unit × $\log_{10}$(patch area), land unit × connectivity, $\log_{10}$(patch area) × connectivity). The inclusion and exclusion of the three main effects and the interaction terms lead to 18 possible models for each community-mean trait value. We calculated the AIC_c (AIC for small sampling sizes) for each of these models and used the AIC_c values for model selection and to assess the importance of the explanatory variables on community-mean trait values (Burnham & Anderson 2001; Burnham *et al.* 2011). First, we selected the best model with the lowest AIC_c and all models whose difference in AIC_c with the best model was less than two. In addition, we calculated the Akaike weights for all the a priori chosen 18 models and, for each explanatory variable we used the sum of these weights as a measure of the relative importance of this variable (Burnham & Anderson 2001).

Finally, we checked whether our models might be biased by spatial autocorrelation. For this purpose, we first tested the model residuals for differences of among land units using Kruskal-Wallis tests and second, we calculated correlograms of the model residuals based on Moran's I for each land unit (Dormann *et al.* 2007). Model fitting and analysis was carried out using R (R Core Team 2012) and the packages `nlme`, `AICmodavg` and `ncf`.

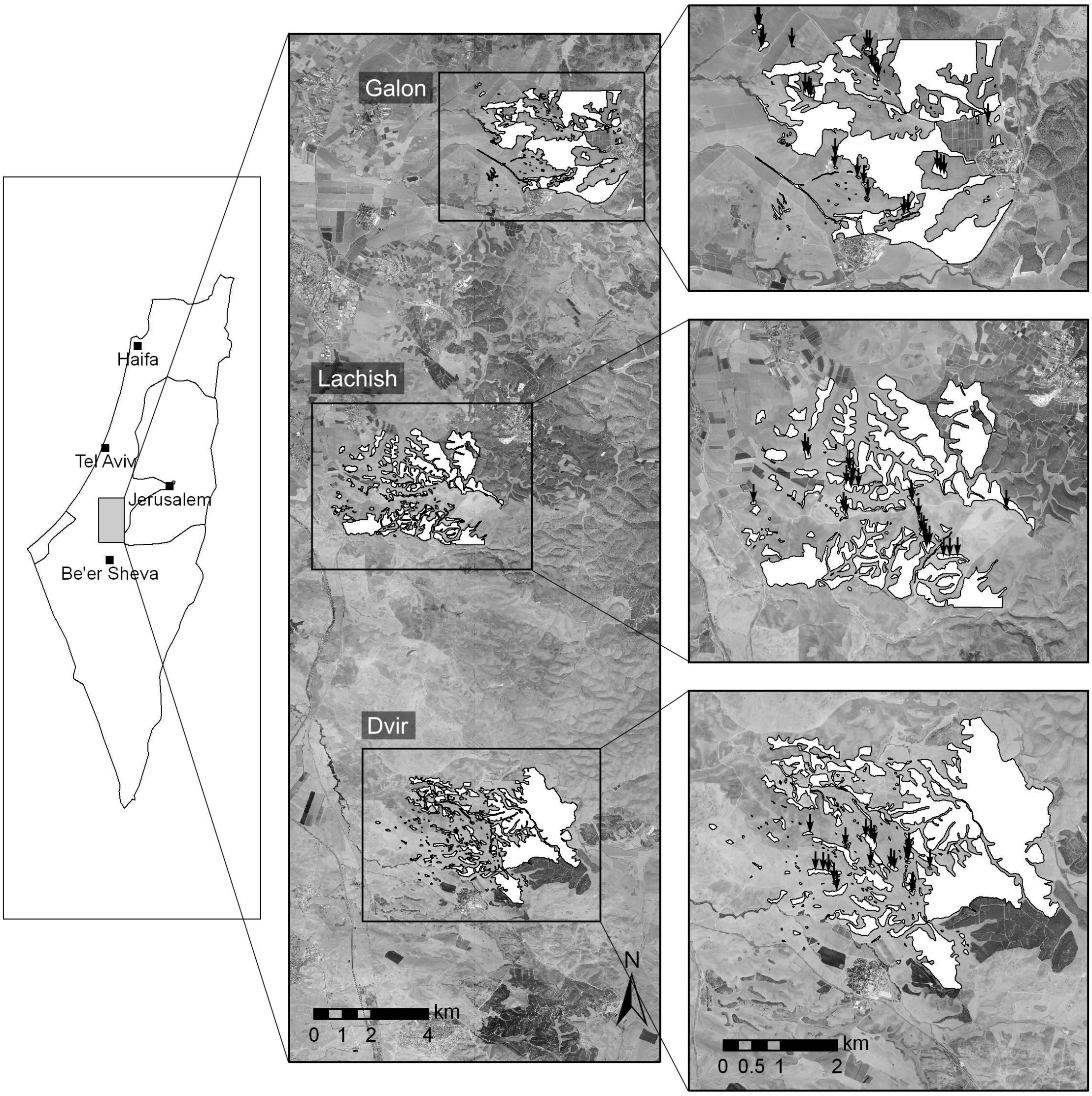

Figure 4.1. Maps of the Southern Judean Lowlands. The left panel shows the location of the study area in Israel. The middle panel shows the arrangement of the land units along the south-north gradient. The three panels on the right show all digitized patches with natural vegetation in each land unit (in white). Arrows indicate patches where vegetation surveys were conducted and for which community-level trait indices were derived.

Table 4.2. Climate and soil data for each land unit in the Southern Judean Lowlands. Precipitation data are from the Israeli Meteorological service data base for the years 1975–2009. Data were collected from weather stations that are within 5 km of the field sites. Temperature data are long-term averages from Goldreich (2003). The wettest month was December, January or February (with 2 exceptions where November was the wettest)

Land unit	**Precipitation [mm]**			**Temperature [°C]**			**Soil properties**	
	Annual mean	**Mean driest month**	**Mean wettest month**	**Annual mean**	**Mean coldest month**	**Mean hottest month**	**Field capacity [% volumetric water content]**	**Soil organice matter [mol C/kg soil]**
Galon	430 ± 149	0	154 ± 64	19	10	25	74.6 ± 5.3	7.8 ± 1.2
Lachish	395 ± 136	0	146 ± 60	19	10	25	63.8 ± 6.6	6.3 ± 1.0
Dvir	291 ± 118	0	110 ± 47	19	11	26	55.1 ± 4.1	6.0 ± 1.0

4.3 Results

4.3.1 Correlations among explanatory variables and species' trait values

In our study landscape field capacity as well as soil organic matter content increased along with precipitation from south to north (Table 4.2, supplementary material Fig. B.2). In contrast, neither patch area nor connectivity was correlated with any soil variable or with the position along the S-N gradient (supplementary material Figs. B.2, B.3).

Interspecific trait correlations, which reflect morphological associations between certain trait attributes, were explored prior to any analysis of community-level trait indices (Table 4.3). Seed release height and canopy height were strongly and positively correlated. Seed mass and seed number were negatively correlated, reflecting a seed size-seed number trade-off among annual plant species. A relatively weak, but significant positive correlation was found between height measurements (CH and SRH) and seed mass. Interestingly, SLA was not correlated with any other trait.

Significant correlations among traits at the species level imply that the potential response of these traits to habitat filtering and competition cannot be considered statistically independent. Therefore, we only used one of the closely correlated plant height measurements (canopy height) for any further analyses at the community-level. Seed mass and seed number were analysed independently, but we consider the seed size-seed number trade-off and the association between plant height and seed mass while discussing our results.

Table 4.3. Spearman rank correlation coefficients (ρ) for species' trait values. Correlations were calculated with untransformed species' trait values using species ranks. Significant correlations ($p < 0.05$) are shown in bold. Trait abbreviations: SLA – specific leaf area, CH – canopy height, SRH – seed release height, SM – seed mass, SN – seed number.

	SLA	**CH**	**SRH**	**SM**
CH	0.11			
SRH	0.12	**0.90**		
SM	–0.15	**0.42**	**0.36**	
SN	0.07	0.15	0.17	**–0.55**

4.3.2 Community assembly at different hierarchical scales

We tested for non-random patterns in community assembly using three null-models, four traits, three sampling scales and six community-level trait indices, two of which reflect trait convergence (trait range and variance) and four reflect trait divergence (trait kurtosis, sdNN, sdNNr, sdNDr). The tests provided similar results at the 15 m × 15 m and 5 m × 5 m sampling scales. Therefore, we present the results for the largest (15 m × 15 m) and smallest (1 m × 1 m) scales here (Table 4.4), while the test statistics and effect-sizes for all sampling scales are presented in the supplementary material (Tables B.1, B.2). In the following, we will first consider the evidence for trait convergence by habitat filtering and second the evidence for trait divergence by competition.

When we tested for habitat filtering in sampling plots relative to the regional species pool (null-model1), we found a significant reduction of trait ranges and variances for canopy height and seed mass at both sampling scales. For SLA the evidence varied with trait index and sampling scale, with significantly lower trait range at the large scale and significantly lower trait variance at the small scale. For seed number we only found a significant reduction of trait range at the small scale (Table 4.4a).

Using null-model 2, which tests for habitat filtering in sampling plots relative to land unit specific species pools, there was again strong evidence for trait convergence of canopy height and seed mass, irrespective of trait index and sampling scale. However for SLA there was only a significant reduction of trait variance at the small scale and for seed number we only found a significant reduction of trait range at the large scale (Table 4.4b).

With respect to trait divergence, the evidence for limiting similarity and even spacing of species trait values also varied among traits, scales and trait indices, but we found the most striking result considering the different null-models. When we did not restrict the trait range of simulated communities (null-models 1 and 2) our results indicate evidence for trait divergence for all four traits and at all sampling scales (Table 4.4a, b). However, when the trait ranges of simulated communities were restricted to the observed trait ranges at the 15 m × 15 m scale, nearly all significant effects disappeared (Table 4.4c).

Table 4.4. Wilcoxon signed rank tests of community assembly processes at the landscape level. Three different null-models were used to account for trait convergence due to habitat filtering at different scales. (a) Null-model 1 did not consider trait convergence. (b) Null-model 2 controls for trait convergence within land units and (c) null-model 3 for trait convergence at the sampling plot scale. In null-model 3 trait ranges observed at the 1 m × 1 m scale were used to restrict simulated trait ranges at the 1 m × 1 m sampling scale. P-values are reported for the one-tailed and paired test of the hypothesis that the observed trait index is lower than under the null-model. Significant deviations from the null-model ($p < 0.05$) are shown in bold. Abbreviations of trait divergence indices: sdNN - standard deviation of nearest-neighbour distance; sdNNr - sdNN divided by trait range; sdNDr - standard deviation of ordered neighbor distances divided by trait range. See text for further explanations of trait indices and the implementation of the null-models.

Trait & Scale	**Trait convergence**		**Trait divergence**			
	Range	**Variance**	**Kurtosis**	**sdNN**	**sdNNr**	**sdNDr**
(a) Null-model 1 – regional species pool						
SLA						
15 m	**0.008**	0.529	0.050	**<0.001**	**<0.001**	**<0.001**
1 m	0.164	**0.032**	0.106	**0.005**	**0.039**	0.106
CH						
15 m	**0.011**	**0.001**	**0.035**	**0.001**	**0.004**	**<0.001**
1 m	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SM						
15 m	**0.003**	**0.004**	**0.035**	**<0.001**	**0.001**	**<0.001**
1 m	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SN						
15 m	0.109	0.077	0.074	**0.007**	**0.041**	**0.017**
1 m	**0.033**	0.164	**<0.001**	**<0.001**	**<0.001**	0.103

Table 4.4. Continued.

Trait & Scale	Trait convergence		Trait divergence			
	Range	**Variance**	**Kurtosis**	**sdNN**	**sdNNr**	**sdNDr**
(b) Null-model 2 – land unit specific species pool						
SLA						
15 m	0.054	0.461	0.286	**<0.001**	**<0.001**	**0.024**
1 m	0.104	**0.020**	0.173	**0.006**	0.057	0.336
CH						
15 m	**0.009**	**0.001**	0.190	**<0.001**	**0.002**	**0.013**
1 m	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SM						
15 m	**0.007**	**0.009**	**0.024**	**0.002**	**0.009**	**<0.001**
1 m	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SN						
15 m	**0.036**	0.157	0.123	**0.003**	**0.015**	**0.009**
1 m	0.075	0.166	**<0.001**	**<0.001**	**<0.001**	0.087
(b) Null-model 3 – plot specific species pool						
SLA						
15 m			0.870	0.887	0.244	0.076
1 m			0.399	0.761	0.331	0.076
CH						
15 m			1.000	0.817	0.198	0.450
1 m			0.529	0.406	0.303	0.168
SM						
15 m			1.000	1.000	1.000	1.000
1 m			0.093	0.880	0.074	**0.019**
SN						
15 m			0.996	1.000	0.934	0.669
1 m			**0.014**	0.907	0.066	0.336

4.3.3 Shifts in community-mean trait values along the S-N gradient and with habitat fragmentation

The linear mixed-effects models revealed significant shifts of community-mean trait values with the S-N gradient and with habitat fragmentation (Table 4.5). Community-mean values of all traits were significantly associated with land unit and with patch area, while community means of canopy height and seed mass were additionally driven by patch connectivity. Especially for community-mean seed mass and seed number there is evidence for varying response to patch area and/or connectivity along the S-N gradient (Tables 4.5, 4.6; Fig. B.3). In the following we will only describe the effects of model terms with Akaike weights of at least 0.5 in order to focus on the associations with high statistical significance (Table 4.6). To improve readability, we will use simple trait names, but always refer to community-mean trait values.

SLA increased from south to north (Fig. 4.2a) and was negatively associated with patch area (Fig. 4.3b). Canopy height was higher in Galon, compared to Lachish and Dvir (Fig. 4.3b) and canopy height was negatively associated with patch connectivity and patch area (Fig. 4.3b). For SLA and canopy height there was little evidence for shifts in trait associations with fragmentation indices along the S-N gradient, indicated by low Akaike weights of the interaction terms (Table 4.6).

Seed mass increased from south to north when only the main effect of land unit was considered (Fig. 4.2c). The association of seed mass with fragmentation significantly varied along the S-N gradient (Tables 4.5, 4.6). Seed mass was negatively associated with patch connectivity and positively associated with patch area in the northernmost land unit – Galon – but we found no associations of seed mass with any fragmentation variable neither in Lachish nor in Dvir (4.3e, f).

Seed number tended to decrease along the S-N gradient (Fig. 4.2d). Seed number was not affected by patch connectivity (Fig. 4.3g), but the association with patch area varied along the S-N gradient. There was a negative association of seed number with patch area in the north (Galon), a weakly negative association in Lachish and no association at all in Dvir, at the southern end of the gradient (Fig. 4.3h).

We tested if our model results might be flawed by spatial autocorrelation. However there was no systematic variation of model residuals among land units and no indication of spatial autocorrelation within the land units (supplementary material, Figs. B.4, B.5).

Table 4.5. Linear mixed-effects models (lme's) of community-mean traits values. For each model the following information is provided: the number of parameters (K), the AIC value for low sample size (AIC_c), the difference in AIC_c to the best model (ΔAIC_c) and the Akaike weights (AIC_cwt). Only the models with $\Delta AIC_c < 2$ are shown. Community-mean traits were derived as equally-weighted average of species traits at 15 m × 15 m sampling plots. Trait abbreviations: SLA – specific leaf area, CH – canopy height, SM – seed mass, SN – seed number. Abbreviations of explanatory variables: LU – land unit, Area – $\log_{10}$(patch area), Con – patch connectivity.

Model	**K**	**AIC_c**	**ΔAIC_c**	**AIC_cwt**
SLA ~ LU + Area	6	122.07	0.0	0.34
SLA ~ LU + Area + LU×Area	8	122.44	0.36	0.29
CH ~ LU + Area + Con	7	-222.47	0.0	0.30
CH ~ LU + Area + Con + LU×Con	9	-221.12	1.35	0.16
SM ~ LU + Area + Con + LU×Area + LU×Con	11	-114.73	0.0	0.23
SM ~ LU + Area + Con + LU×Area + LU×Con + Area×Con	12	-114.34	0.39	0.19
SM ~ LU + Area + Con + LU×Area	9	-113.26	1.47	0.11
SN ~ LU + Area + LU×Area	8	-137.65	0.0	0.28
SN ~ LU + Area + Con + Area×Con	8	-136.36	1.29	0.15
SN ~ LU + Area	6	-136.28	1.37	0.14
SN ~ LU + Area + Con + LU×Area + Area×Con	10	-135.92	1.73	0.12

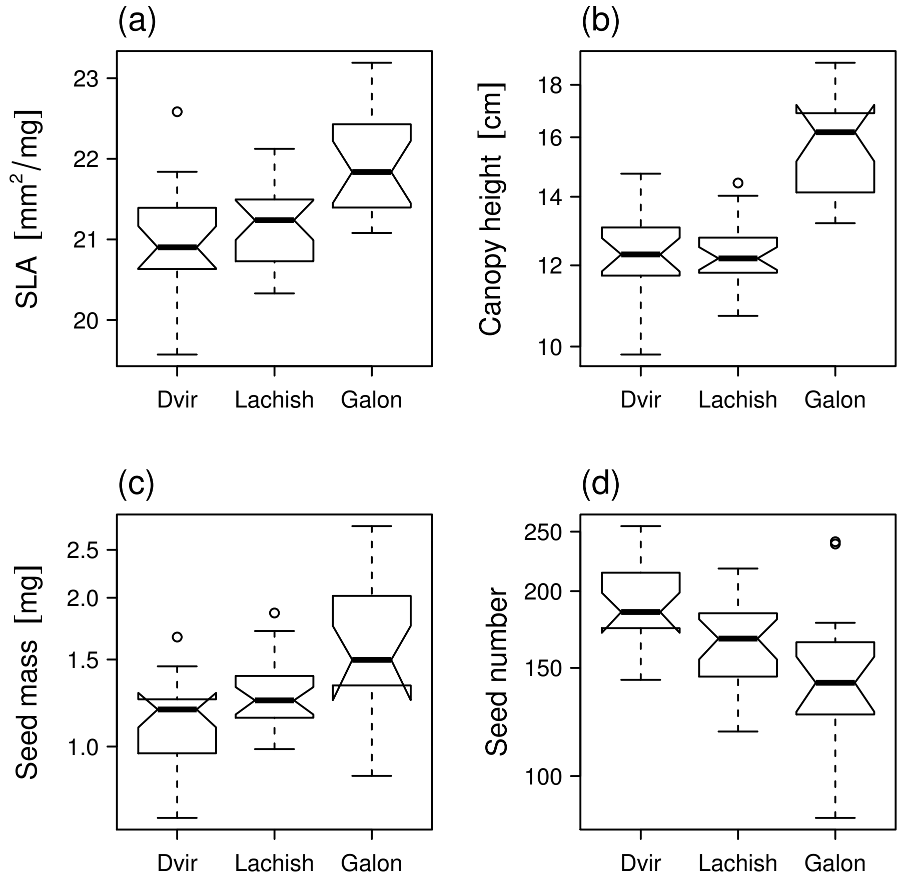

Figure 4.2. Distribution of community-mean traits along the S-N gradient, represented by the land units – Dvir, Lachish and Galon (from south to north). Species traits were averaged at 15 m × 15 m sampling plots. Boxes indicate median and quartiles (25% and 75% quantiles), and whiskers indicate minimum and maximum (if there are no outliers). Values, which are more extreme than the quartiles ± 1.5 × IQR (interquartile distance), are classified as outliers and shown as dots. The notches provide robust 95% confidence for the medians. If two notches do not overlap there is strong evidence that the two medians differ significantly

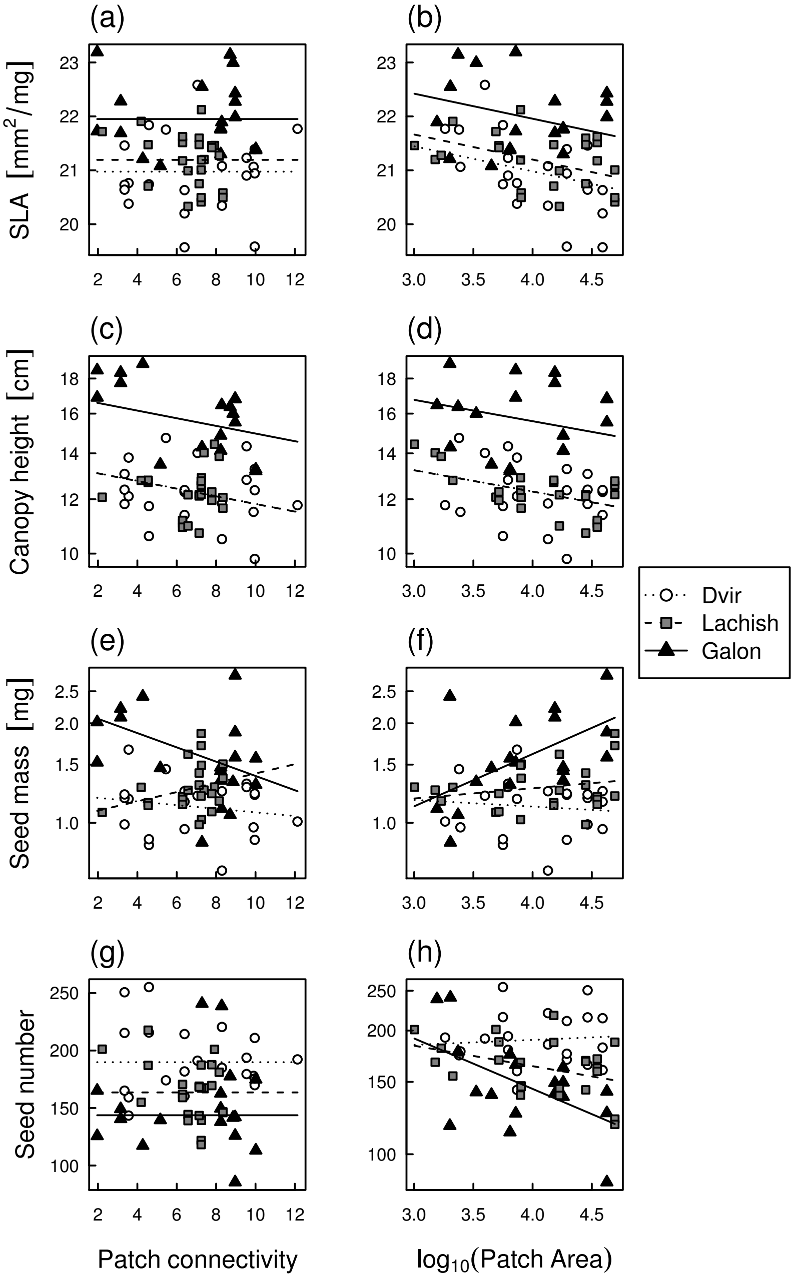

Figure 4.3. Association of community-mean trait values with patch connectivity (left column) and patch area (right column). The regression lines show predictions of mixed-effects models for each land unit (compare Table 4.5). The patch variable (area or connectivity) which is not shown in the respective panel was fixed at its mean value averaged over all patches. Within the panels, regression lines with different slopes indicate a significant interactive effect of land unit and the respective fragmentation index (patch area or connectivity)

Table 4.6. Sum of Akaike weights for all models that include a certain explanatory variables. The sum for each community-mean trait was derived from all 18 possible models. Trait abbreviations: SLA – specific leaf area, CH – canopy height, SM – seed mass, SN – seed number. Abbreviations of explanatory variables: LU – land unit, Area – $\log_{10}$(patch area), Con – patch connectivity.

Trait	**Model term**					
	LU	**Area**	**Con**	**LU×Area**	**LU×Con**	**Area×Con**
SLA	1.00	0.95	0.33	0.45	0.04	0.08
CH	1.00	0.87	0.83	0.18	0.28	0.16
SM	1.00	0.91	0.84	0.66	0.57	0.35
SN	1.00	0.97	0.56	0.55	0.16	0.39

4.4 Discussion

This study presents a detailed analysis of plant functional trait distributions of species rich annual plant communities along interacting gradients. First, we evaluated the evidence for community assembly processes, such as habitat filtering and interspecific competition, in the trait distributions of plant communities. We addressed this question at several spatial scales using a comprehensive set of community-level trait indices and different null-models of random community assembly. Second, we examined the association of community-mean trait values with habitat fragmentation along an environmental south-north gradient.

We found evidence for trait convergence by habitat filtering at different hierarchical scales. However, the evidence for trait divergence, as expected from interspecific competition, fundamentally depended on the specific null-model used and whether the effect of habitat filtering was controlled for. Furthermore, we found that community-mean trait values were significantly associated with the position along the S-N gradient and with habitat fragmentation. Thereby, the association of SLA and plant height with fragmentation remained consistent along the S-N gradient, but it varied for seed mass and seed number.

4.4.1 Evidence for community assembly processes

Our findings indicate that habitat filtering causes trait convergence within local communities compared to the regional species pool (null-model 1) for all functional traits studied here. When local communities were compared to land unit specific species pools, there was still strong evidence for trait convergence of plant height and seed mass (null-model 2). In contrast to Kraft & Ackerly (2010), we did not find systematic variations of trait convergence or divergence with sampling scale. This might be related to the fact that they investigated larger sampling scales (5 m × 5 m to 100 m × 100 m) than we did here (1 m × 1 m to 15 m × 15 m).

The Southern Judean Lowlands are characterized by a sharp productivity gradient that corresponds with substantial increases in precipitation, soil fertility (indicated by field capacity and organic matter content), plant density (Giladi *et al.* 2011) and vegetation biomass (Schmidt & Gitelson 2000) from south to north. As these productivity-related gradients are observed in an area with similar geology and temperatures (Table 4.2; Kloner & Tepper 1987; Goldreich 2003), we presume that precipitation is the main underlying driver of the trends in the other variables. Accordingly, we interpret the trait convergence in communities relative to the regional species pool as primarily reflecting trait adaptation to this productivity gradient (Cornwell & Ackerly 2009; Harel *et al.* 2011). In contrast, the trait convergence in local communities relative to the species pool a specific land unit might be related to differences in patch area and connectivity (Lindborg *et al.* 2012; Marini *et al.* 2012).

Habitat filtering and interspecific competition are expected to drive trait distributions simultaneously and therefore, testing for competition effects requires controlling for habitat filtering effects (Ackerly & Cornwell 2007; Cornwell & Ackerly 2009). For this purpose Kraft & Ackerly (2010) suggested using trait divergence indices, which are standardized by trait ranges (sdNNr, sdNDr). When we applied these indices, we found strong evidence for trait divergence across all traits and sampling scales (null-models 1 and 2). However, when we used the two-step procedure of Cornwell & Ackerly (2009), where the species pool for each local community was restricted by the observed trait range of this community, there was almost no evidence for trait divergence anymore (null-model 3). This finding underlines the importance and emphasizes the challenge of choosing an appropriate null-model and specifying an appropriate species pool for the question under study (De Bello 2012; De Bello *et al.* 2012).

Due to the evidence for habitat filtering, we presume that controlling for trait convergence while testing for trait divergence is most appropriate in our study area (null-model 3). This means with the null-model we consider to be most appropriate, we found no evidence for trait divergence. Such lack of evidence for trait divergence as an indication of competition and niche differentiation is common among studies of assembly mechanisms in plant communities (reviewed by Götzenberger *et al.* 2012. However, this lack of evidence does not necessarily mean that competition is unimportant in community assembly. First, the evidence of course depends on the investigated traits and it is possible that niche-differentiation is expressed in functional traits that were not measured and that might indeed be very difficult to measure (Silvertown 2004; Götzenberger *et al.* 2012). Second, the expectation of trait divergence as an outcome of interspecific competition might be misleading: Classical niche theory predicts that competition excludes species with similar traits and high niche-overlap, which results in a "limiting similarity" among co-occurring species and even spacing of species trait values (MacArthur & Levins 1967; Stubbs & Wilson 2004; Kraft *et al.* 2008). A more recent perspective on competition and traits challenges this prediction (Grime 2006; Mayfield & Levine 2010; De Bello *et al.* 2012; Spasojevic & Suding 2012). In general, coexistence is determined by the fitness differences and the niche differentiation among competing species (Chesson 2000). While stable coexistence is only possible with substantial niche differentiation, species can coexist over ecologically relevant timescales without any niche differentiation as long as they are equivalent in fitness and competitive ability (Hubbell 2001). On this conceptual basis, Mayfield & Levine (2010) suggested that competition could also results in trait convergence, when species trait differences translate into large fitness differences rather than into stabilizing niche differentiation. In this case species with high trait dissimilarity will be preferentially excluded by competition, which will thus result in trait convergence (De Bello *et al.* 2012).

For instance, in productive environments all species need to be adapted to high plant density and high competitive pressure. Accordingly, trait adaptation to productive environments has been also called a "productivity filter" (Grime 2006). This terminology can be confusing as the "productivity filter" essentially refers to consequences of competitive pressure, but it indicates that especially in productive habitats competition might also drive trait convergence analogously to abiotic habitat filtering in the strict sense.

4.4.2 Functional trait associations with the south-north gradient

Considering the increases in precipitation and soil fertility, we presume that the observed changes of community-level trait values along the S-N gradient are primarily driven by changes in productivity (Holzapfel *et al.* 2006; Harel *et al.* 2011). Accordingly, the positive association of SLA with the position along the S-N gradient found in our study closely corresponds to findings of previous studies of leaf morphology along precipitation and productivity gradients ranging from landscape to global scales (Fig. 4.2a; Fonseca *et al.* 2000; Ackerly *et al.* 2002; Wright *et al.* 2004). Low SLA is associated with thick and/or dense leaves and is known to reflect leaf adaptations to low water availability, high evapotranspiration and/or resource stress, while high SLA mirrors species adaptations to higher growth rates and higher competitive pressure within more productive communities (Reich *et al.* 1999; Westoby *et al.* 2002). Similarly, our finding of taller plant communities in the northern, mesic patches can be viewed as an adaptation for intensified competition for light in a more productive and competitive ecosystem (Fig. 4.2b; Grime 2001; Westoby *et al.* 2002).

The increase in plant density and productivity along the S-N gradient also provides an explanation, for the observed increase in community-level seed mass (Fig. 4.2c). High seed mass conveys a competitive advantage for seedlings, an advantage that might be most important in mesic and competitive environments (Leishman *et al.* 2000; Moles & Westoby 2004; Metz *et al.* 2010; Harel *et al.* 2011). However, as seed mass and plant height are weakly, but positively correlated at the species level, the increase in seed mass might be, at least partly, driven by selection for greater plant height. Overall the increase of community-mean SLA, plant height and seed mass along the S-N reflects increasing species adaptation to productivity and competitive pressure, or – using the terminology of Grime (2006) - an increasing importance of the “productivity filter”.

Our analysis provides evidence for a seed size-seed number trade-off among annual plant species (reviewed in Leishman *et al.* 2000), which implies that the response of community-level seed number is associated with the response of community-level seed mass. Therefore, the decrease in seed number along the S-N gradient may actually follow the selection for an increasing seed mass along that gradient (Fig. 4.2d). However, the increase in seed number with increasing aridity might also reflect an adaptation to the harsh and unpredictable conditions in arid environments, which select for high reproductive allocation as well as for bet-hedging strategies (Venable & Brown 1988; Aronson *et al.* 1990; Petru *et al.* 2006; Siewert & Tielbörger 2010). Venable & Brown (1988) suggested large seed size, dispersal and dormancy as three potential bet-hedging strategies. Considering the low community-level seed mass we found in the arid sites, we speculate that plant communities there do not rely on large seed size as a bet-hedging strategy, but rather on dispersal and or/dormancy. However, while seed dormancy has been suggested as an important bet-hedging strategy in arid and semi-arid environments (Venable 2007; Petru & Tielbörger 2008; Siewert & Tielbörger 2010), there is evidence that at least germination under optimal conditions is higher in arid than in Mediterranean environments (Harel *et al.* 2011). This mismatch between theoretical predictions and empirical evidence indicates the need for further research on the relationship between morphological seed traits and bet-hedging strategies of plant species.

In addition to habitat productivity, livestock grazing might be an important driver of plant functional traits in our study area. Along the S-N gradient studied here, there is a change from sheep and goat grazing in the southern, arid sites to cattle grazing in the northern, mesic sites (Rotem 2012). Grazing intensity is known to be negatively associated with community-level plant height (Osem *et al.* 2004; Díaz *et al.* 2007; Golodets *et al.* 2009). Accordingly, our finding of increasing plant height from south to north may reflect a decrease of grazing pressure in addition to the increase in productivity. Furthermore the increase in SLA might indicate a shift from grazing avoidance by mechanical or chemical defence, which is associated with low SLA, to grazing tolerance by high regrowth capacity after defoliation by herbivores, associated with high SLA (Bullock *et al.* 2001). Especially in landscapes with long grazing history plant functional traits are known to reflect convergent selection for grazing resistance and the specific environmental conditions in the landscape (Milchunas *et al.* 1988; Osem *et al.* 2004; De Bello *et al.* 2005). Therefore, we hypothesize that the community-level plant functional traits in our southern, arid sites mirror convergent adaptation to grazing and drought-stress. Separating grazing and habitat effects on plant functional traits by long-term grazing exclusion plots along the S-N gradient could provide an interesting follow up to the study presented here.

4.4.3 Functional trait associations with fragmentation along the S-N gradient

We predicted that isolated patches and, due to the rescue-effect also small patches, favour species with high colonization ability (Brown & Kodric-Brown 1977; Hanski 1999). In addition, small patches are expected to include a disproportionally high percentage of species with long persistence times (Lindborg *et al.* 2012). Furthermore, we hypothesized that trait attributes that convey high persistence vary along the

S-N gradient, which represents a shift from a stress-dominated system (arid) to a competition-dominated system (mesic). Therefore, we predicted that small patches will host communities with higher drought-adaptation (lower SLA, smaller seeds) in the arid sites and higher competitive ability (taller plants, higher SLA, larger seeds) in the mesic sites (compare Table 4.1).

We found that SLA was negatively associated with patch area, but this association did not significantly vary among the land units (Fig. 4.3b). This finding corresponds to our prediction for the mesic sites, but contrasts our expectation for the arid sites, which might indicate that fast growth is important for species persistence in small patches along the entire S-N gradient. Our predictions regarding negative associations between community-level plant height and patch connectivity, as well as between plant height and patch area, were both supported (Fig. 4.3c, d). Isolated and small patches might favour taller species, as these species release their seeds at greater height and therefore may achieve longer dispersal distances leading to higher colonization rates (Tackenberg *et al.* 2003; Thomson *et al.* 2011). Alternatively, the negative associations between plant height and fragmentation indices (patch area and connectivity) could also be explained by an association of grazing with fragmentation, for instance if small and isolated patches are less attractive for pastoralist. However, in a study that was conducted in the same landscape, which used counts of livestock faeces as a measure of grazing intensity, there was no evidence for such an association (Rotem 2012).

In contrast to plant height, the response of seed mass to patch connectivity changed along the S-N gradient, but in a different way than expected. Considering the higher colonization ability of species producing many seeds, we predicted decreasing seed number and - due to the seed size-seed number trade-off - increasing seed mass with increasing patch connectivity. However, we found the contrasting pattern of a negative association between seed mass and patch connectivity in the mesic sites and no association in the more arid sites (Fig. 4.3e). We suggest that the pattern observed in the mesic sites might emerge from a closer association of seed mass to seedling survival (Metz *et al.* 2010) than to colonization ability (Thomson *et al.* 2011). As explained above, in the mesic environment, seedling competition may be intense, and the competitive advantage conveyed by larger seeds may result in the exclusion of species with smaller seeds from isolated patches (Moles & Westoby 2004). If immigration rates are low in these isolated patches, the process of exclusion of competitively inferior species might be faster than the immigration of good colonizers (Eriksson 1996; Lindborg 2007; Johansson *et al.* 2011). Moving south, this relationship disappears as seedling competition and thus the competitive advantage of large seedlings become less important with lower productivity and lower plant density (Harel *et al.* 2011).

The association of seed mass to patch area showed the inverse pattern of the seed number response and might therefore be driven by the association of seed number with patch area – as discussed in the following – and the seed size-seed number trade-off. Our prediction of a negative association between seed number and patch area was confirmed, but this association was limited to the mesic sites (Fig. 4.3h). Species with high seed number are expected to be better colonizers due to the higher probability that at least some seeds are dispersed over long distances when the total number of dispersed seeds is high (Dupré & Ehrlén 2002; Higgins *et al.* 2003). Small patches will favour species with high colonization ability if these patches are sufficiently connected to neighbouring patches by propagule input and populations are therefore maintained by the rescue-effect. The association between seed number and patch area was not detected in the more arid land units – Lachish and Dvir. Typically, in arid environments adaptations for long-distance dispersal are rare, while adaptations to climatic variability and/or seed predation, e.g. lignified seed containers or attachment of the seeds to the dead mother plant, restrict dispersal distance (Ellner & Shmida 1981; Venable *et al.* 2008). We presume that this selection against long-distance dispersal adaptations is responsible for the absence of the associations between seed traits and habitat fragmentation in the more arid sites of the S-N gradient studied here.

All associations between community-mean trait values and fragmentation indices discussed here were selected in the models with high statistical confidence. Nevertheless the absolute changes of the community-mean trait values predicted by the models as a response to fragmentation were comparably low. This general finding corresponds closely to previous studies, which found that fragmentation tends to have a lower explanatory power with respect to plant functional traits than environmental variables (Dupré & Ehrlén 2002; Hérault & Honnay 2005; Lindborg *et al.* 2012). In this context it is also important to note one conceptual and statistical key challenge in trait-based ecology. Even if there are significant associations of community-mean trait values with environmental drivers, such as productivity or precipitation, an enormous amount of trait variation is often found among species within the same community (McGill *et al.* 2006). For example Wright *et al.* (2004) found that the impressive proportion of 36% of the global variation of species' SLA occurred within sites. This indicates that there is still a need for better understanding, how local processes and factors as competition and small-scale environmental heterogeneity structure trait distributions at small spatial scales (Götzenberger *et al.* 2012).

In this study, we focused on inter-specific trait variation at the landscape scale within a highly divers system. Functional traits also vary within species, but sampling intra-specific trait variation for the number of species and for the number of plots considered here, is hardly feasible.Cornwell & Ackerly (2009) found that the response of community-level traits to environmental gradients is dominated by species turnover and thus by inter-specific variation, while intra-specific variation plays a minor role. Furthermore, functional traits are expected to shift in the same direction along environmental gradients at the species and at the community level (Ackerly & Cornwell 2007; Harel *et al.* 2011). Therefore, intra-specific variation in trait values is unlikely to affect our main conclusions. According to previous findings of corresponding changes in population and community-mean trait values, we rather expect that considering intra-specific trait variation would increase the statistical power and effect-sizes of the analysis presented here (Cornwell & Ackerly 2009; Jung *et al.* 2010).

4.5 Conclusions

To our knowledge, this study provides the first empirical test of community assembly processes and plant functional trait associations with habitat fragmentation along an abiotic environmental gradient. Our findings clearly indicate the importance of choosing appropriate null-models and species pools for studying community-assembly processes (De Bello 2012). Furthermore our results highlight that community ecology still lacks a predictive theory and empirical evidence on the issue if and under which conditions competition results in trait divergence by excluding species with high trait similarity, or in trait convergence by excluding species with low trait similarity (Mayfield & Levine 2010). With respect to trait-environment relationships, our findings closely match results of previous studies investigating plant traits along environmental gradients and thus strongly suggest that habitat filtering by varying precipitation and productivity is the main driving factor for the trait distribution along the S-N gradient investigated here. Accordingly, we suggest that the varying associations between seed traits and habitat fragmentation are driven by the interactive effects of productivity and fragmentation on species distributions and community composition. Our findings emphasize the need to consider species adaptations to dispersal for projections of environmental change effects and, vice versa, to consider species environmental adaptations for projections of land use and fragmentation effects. In this way our study highlights the importance of addressing the interactive effects of important environmental drivers on plant functional traits in order to improve our understanding and the predictability of plant community responses to global change.

Chapter 5

Discussion and synthesis

This thesis aims at an improved understanding of plant community dynamics in fragmented landscapes, which is a prerequisite for predictions of communities' responses to fragmentation and for the mitigation of further biodiversity loss. To approach this aim, I developed and analysed spatially explicit simulations and statistical models that facilitate a mechanistic and process-based understanding of plant community dynamics at the landscape scale. In this chapter, I reflect and synthesize my findings with respect to the implications of different processes and factors for the diversity and functional trait composition of plant communities. The distributions of species in a fragmented landscape depend on their ability to disperse into suitable habitat patches and on their ability to persist in these patches given the local environmental conditions there. Accordingly, I discuss the implications of dispersal and fragmentation "per se" and the consequences of the local environmental conditions, including patch size as measure of local habitat availability, in separate paragraphs. Finally, I highlight the main conclusions for community ecology and conservation biology and I provide an outlook on further research that builds on the approaches and findings presented here.

5.1 The roles of dispersal and habitat configuration

The dispersal capability of species is an important driver of community dynamics, as it determines the rate of species immigrations into habitat patches (Loreau & Mouquet 1999) as well as the mixing or the spatial segregation among species (Pacala 1997). A high rate of species immigrations into any patch or survey area increase local diversity, as it usually results in a high number of locally rare species (Shmida & Ellner 1984; Pulliam 1988, 2000). In contrast, high species mixing, i.e. reduced species segregation, decreases diversity due to a higher rate of interspecific compared to intraspecific competition and thus a higher rate of competitive exclusion (Stoll & Prati 2001; Levine & Murrell 2003). The relative balance between these two processes – species immigrations vs. exclusions – provides the mechanistic background behind all scale-dependent dispersal-diversity relationships presented in chapter 2. Also the U-shaped relationship I found, emerges from the interplay of immigrations and competitive exclusions. If dispersal capability is low, slight increases in mean dispersal distance will first lead to a reduction of local diversity due to higher mixing and higher interspecific competition until a minimum of diversity is reached at the "minimizing dispersal distance" (MDD). With further increases of dispersal capability local diversity increases again, because with mean dispersal distances that are longer than the MDD, the positive effects of immigrations outweigh the negative effects of higher species mixing (Fig. 2.1).

Previous studies of dispersal-diversity relationships could not detect a U-shaped pattern, as they used spatially implicit models, which by definition exclude species segregation at the local scale (Hubbell 2001; Mouquet & Loreau 2003; Economo & Keitt 2008). Due to the same reason, these studies also never found negative effects of dispersal on local diversity. The spatially explicit approach introduced in chapter 2 overcomes this limitation by considering the possibility of species segregation at all spatial scales, i.e. at the survey area scale as well as at the landscape scale.

For small ratios of survey area to landscape size, my results perfectly match previous findings that increasing dispersal capability fosters local diversity. However, in contrast to previous studies, my approach revealed that increasing dispersal capability can also lead to a decline of local diversity, either if the survey area comprises a large fraction of the entire landscape, or if the metacommunity is too species-poor to provide a diverse pool of immigrants to the local scale.

In a meta-analysis of the consequences of dispersal on species diversity, Cadotte (2006a) found consistent support for positive effects of dispersal on local diversity. However, in studies addressing plant communities, the most common approach to manipulate dispersal was adding seeds to local communities (see Table 1 in Cadotte 2006a). This method directly provides immigrants of new species to experimental local communities and thus corresponds to model scenarios with the presence of a diverse species pool in the metacommunity. Therefore, I conclude that the meta-analysis of Cadotte (2006a) does not necessarily contradict my findings, as previous experimental approaches do not mirror the scenarios, where the survey area comprised a large fraction of the metacommunity or where the metacommunity was species-poor.

Only in these scenarios did the neutral model predict negative effects of dispersal capability on local diversity.

Examples for negative effects of dispersal on diversity at large spatial scales are provided by species invasions, which are currently among the main drivers of biodiversity loss (Sala *et al.* 2000; Brook *et al.* 2008). In this context, entire landscapes or states represent the "local" scale, while one or several continents represent the metacommunity scale. The increased rate of anthropogenic introductions of non-native species essentially corresponds to higher dispersal capability at intercontinental scales. In natural plant communities it is expected that invasions depend on properties of the invading species and of the invaded community (Shea & Chesson 2002). Even if such properties of invading species and resident communities were not included in the neutral model, invasions with negative effects on native species diversity mirror the model prediction that increasing dispersal capability can result in declines of diversity in local communities.

In fragmented landscapes the overall connectivity between local communities is jointly determined by dispersal and by habitat configuration (Fahrig 2003). While habitat configuration defines the distance between habitat patches, dispersal capability defines the probability that species are able to disperse propagules over this distance (Damschen *et al.* 2008). Therefore, fragmentation "per se", which increases the distances between patches, is expected to have analogous consequences for local diversity in patches than decreasing dispersal capability (Fahrig 2003). For this reason, I suggest that my findings from chapter 2, which are based on variations of dispersal capability, can also be applied to landscapes with reductions of habitat connectivity due to fragmentation "per se".

Habitat connectivity and the spatial distribution of suitable habitat were suggested as the main criteria to distinguish different types of regional population and community dynamics in fragmented landscapes (Eriksson 1996; Freckleton & Watkinson 2002; Alexander *et al.* 2012). The prevalence of different types of regional dynamics has been the central issue of an on-going debate among plant ecologists (Freckleton & Watkinson 2002, 2003; Ehrlén & Eriksson 2003; Alexander *et al.* 2012), which underlines the importance of this question for community ecology as well as for conservation biology.

I addressed this crucial question in chapter 3 and found strong evidence for low habitat connectivity in the SJL. Accordingly, I classified the type of regional community dynamics as "island communities", following the classification of regional population dynamics by Freckleton & Watkinson (2002). This result implies that fragmentation “per se” in the SJL has reached a degree that largely prevents seed dispersal between habitat patches. The finding of low connectivity closely agrees to a complementary genetic analysis of the annual species *Catananche lutea* in the SJL. In this study, we found high genetic differentiation among populations in different patches, which is a strong indication of a very low rate of seed and pollen exchange between these populations (Gemeinhölzer *et al.* 2012).

The metapopulation and metacommunity concepts postulate that connectivity between local populations or communities, respectively, is an important driver of population and community dynamics at the landscape scale (Hanski 1999; Leibold *et al.* 2004). This perspective is challenged at the population-level by the study of Gemeinhölzer *et al.* (2012) and at the community-level by the IFM approach (chapter 3). Both studies indicate that plant populations and communities are highly isolated in the SJL and landscape scale dynamics are thus not well reflected by the metapopulation and metacommunity concepts. This finding provokes the question, if island communities are a common type of regional plant community dynamics or if the SJL provides a rather specific example. Furthermore, an open question with high relevance for conservation concerns the threshold of habitat connectivity at which regional community dynamics might switch from a “metacommunity” to an “island communities” type. I suggest that my approach based on the combination of a multi-species IFM with species occupancy data offers a promising generic tool to address these questions for a wide range of fragmented landscapes and potentially even for different taxa than plants (see Risk *et al.* 2011, for an IFM example for two bird species).

The issue of habitat connectivity is closely linked to the questions of equilibrium vs. transient community dynamics and of extinction debts in fragmented landscapes (Jackson & Sax 2009). Previous empirical approaches investigating transient dynamics and extinction debts usually correlated present species richness with past and present fragmentation indices (e. g. Lindborg & Eriksson 2004). In this framework a closer correlation of present species richness to past fragmentation compared to the correlation of present species richness to present fragmentation has been interpreted as evidence for an extinction debt (reviewed in Cousins 2009; Kuussaari *et al.* 2009). However, while this correlative approach is able to test, if the landscape carries an extinction debt or not, it is not able to predict the number of species that is expected to go extinct during transient community dynamics. Kuussaari *et al.* (2009) highlighted spatially explicit, data-based simulation models as a promising tool to study extinction debts, but they also pointed to the fact that this approach has been only implemented for single species so far. This gap can be filled using the multi-species IFM approach of chapter 3, which is able to provide quantitative predictions of the extinction debt for species-rich communities and can thus be considered as a major advance compared to previous approaches. Of course, the IFM presented in chapter 3, describes community dynamics in a simplified way. Nevertheless the approach bears the potential to incorporate additional ecological information and processes in order to improve the predictions of community dynamics (see 5.4).

The neutral model presented in chapter 2, as well as the IFM presented in chapter 3 did not consider differences in species' dispersal capabilities. In chapter 2, I applied the assumption of neutrality, and thus of equal dispersal capabilities, to facilitate a general understanding of dispersal-diversity relationships. In chapter 3, only differences in species' abundances, but not in dispersal capabilities were considered to enable the parameterization of the multi-species IFM from one temporal snap-shot of data. However, the dispersal capability of species in natural communities and thus their response to fragmentation might vary with their functional traits (Lindborg *et al.* 2012). Therefore, in chapter 4 I analysed, if and how plant functional traits are associated with fragmentation indices. For this purpose, I developed and applied an advanced connectivity index that considers patch shapes and orientations in a spatially explicit way (see 4.2.2) and thus provides more reliable representations of patch connectivities than previously used indices (reviewed in Moilanen & Nieminen 2002).

I found a significant negative association of community-mean plant height with patch connectivity (Fig. 4.3), which indicates that taller plants are disproportionately represented in patches with low connectivity. This result might be interpreted as a higher dispersal capability of taller plants (Thomson *et al.* 2011), but due to the high isolation among patches found in chapter 3, I rather hypothesize that this association is confounded by a correlation between habitat fragmentation and local environmental conditions, as explained below (see 5.2).

In chapter 2, I found that local diversity can be either fostered or reduced by higher species' dispersal capabilities and in chapter 3 I found that connectivity between patches is very low in the SJL. Together, these two findings give rise to the question, how variations in dispersal capability or habitat configuration would affect patch-scale species diversity in the SJL. In chapter 3, the IFM simulations based on the metacommunity scenario, which included at least low connectivity and colonization rates, predicted on average higher species richness than simulations based on the island communities scenario, which completely excluded connectivity and colonization (Fig. 3.5). Therefore, I hypothesize that an increase in dispersal capability or lower fragmentation “per se”, e.g. by the establishment of habitat corridors or stepping stones, would foster species diversity in habitat patches. With respect to the scenarios described for the neutral model in chapter 2, I presume that habitat patches in the SJL comprise only a small proportion of the species in the entire metacommunity. Accordingly, patch-scale diversity could be considerably increased by higher dispersal capability and the resulting increases in immigration rates into patches.

5.2 The roles of patch size and local environmental conditions

The diversity and species composition of a focal habitat patch is not only driven by its connectivity to other patches, but also by its size and its local environmental conditions (Leibold *et al.* 2004). A positive association between the size of a patch or survey area and the species richness found there, is one of the most general and ubiquitous patterns in ecology and well-known as the species-area relationship (Rosenzweig 1995; Drakare *et al.* 2006). However, despite the phenomenological simplicity of the species-area relationship, it can potentially be attributed to three different explanations: (i) sampling effects, (ii) island-biogeography effects and (iii) habitat heterogeneity (reviewed in Hoyle 2004; Turner & Tjørve 2005).

In the models presented in chapters 2 and 3, the local conditions were completely characterized by the size of the survey area (chapter 2) or by patch size (chapter 3) and the models did not consider habitat heterogeneity. Accordingly, the simulation results derived from the spatially-explicit neutral model in chapter 2 reflect the first two explanations for species-area relationships, which do not rely on habitat heterogeneity. In a homogeneous landscape of constant size, species richness increased with survey area solely due to the higher chance of finding more species, when sampling more individuals (sampling effect). In contrast, when the landscape size was increased in the model, the resulting increase of local species richness in a constant survey area could exclusively be attributed to increased species immigrations from the metacommunity to the survey area (island-biogeography effects).

The multi-species IFM used in chapter 3 simulates species presences/absences based on patch sizes and on habitat configuration, but does not consider habitat heterogeneity or variations in species' abundances among patches, following the approaches of Hanski & Gyllenberg (1997) and Hovestadt & Poethke (2005). Therefore, only island-biogeography effects can explain species-area relationships emerging from the model.

The ABC approach applied in chapter 3 revealed large differences in the uncertainty of the IFM parameters that were estimated from patch-scale species richness data. The estimates of the model parameters relating patch connectivity with colonization rate included high uncertainty, while the model parameter that relates patch size with extinction rate could be estimated from the data with high confidence (Fig. 3.3). These results imply a low correlation of patch species richness with patch connectivity, but a close correlation of patch size with species richness in the SJL. According to the predictions of island-biogeography theory, the species-area relationship in the IFM thus emerges due to the decrease of extinction rate with increasing patch size.

In an extensive review of the effects of fragmentation on biodiversity, Fahrig (2003) found consistently negative effects of habitat loss on biodiversity, but only ambiguous effects of fragmentation "per se". This general finding is in perfect agreement with the low correlation of species richness with patch connectivity and the high correlation of species richness with patch size found in chapter 3.

In a complementary study in the SJL, we assessed the associations of species richness in hierarchically nested sampling plots with patch size and patch connectivity (Giladi *et al.* 2011). We found a positive association between patch size and species richness measured at the patch scale, but we did not find any correlation between patch size or patch connectivity, respectively, and local species richness measured in equally-sized sampling plots (Giladi *et al.* 2011). According to Holt (1992) the lack of an association between patch size and local species richness in equally-sized sampling plots, called "standardized species-area curve", is typical for vascular plants and indicates high dispersal limitation even within habitat patches. Therefore, these findings of our study based on a static regression approach (Giladi *et al.* 2011) closely resemble the result of low connectivity derived from the dynamic modelling approach in chapter 3.

While Giladi *et al.* (2011) focussed on species richness in the SJL, in chapter 4 I analysed, how plant functional trait distributions are affected by community assembly processes and how community-mean traits are associated with fragmentation and with the position along the S-N precipitation gradient. The clear associations of community-mean traits with the precipitation gradient revealed by statistical models, closely correspond to previous knowledge on plant strategies along precipitation and productivity gradients at different spatial scales (Westoby *et al.* 2002; Wright *et al.* 2004; Cornwell & Ackerly 2009; Metz *et al.* 2010). Furthermore, I detected significant trait convergence, which indicates habitat filtering as predicted by community assembly theory. In contrast, I found only ambiguous results with respect to the effects of interspecific competition on trait distributions. The evidence for trait divergence due to competition fundamentally depended on the way how the null-model of community assembly accounted for habitat filtering.

The inconsistent results among the different null-models point to two important knowledge gaps in community assembly theory. First, there has been an on-going debate, whether and when biotic interactions, such as interspecific competition, result in trait divergence or in trait convergence among co-occurring plant species (MacArthur & Levins 1967; Stubbs & Wilson 2004; Grime 2006; Kraft *et al.* 2008; Mayfield & Levine 2010; Kunstler *et al.* 2012; Spasojevic & Suding 2012). This debate revealed that it is unclear yet, to which degree observed patterns of trait convergence are driven by abiotic habitat filtering, by biotic interactions, or by both processes simultaneously (Mayfield & Levine 2010; Spasojevic & Suding 2012). Recently, De Bello *et al.* (2012) suggested an approach to disentangle trait convergence due to abiotic and biotic processes. However, their approach does not rely on a separation of species' fundamental and realized niches, which can be considered as an essential step to distinguish abiotic and biotic effects on community assembly in a rigorous way.

5.3 Conclusions

In this thesis I aimed at improving the mechanistic understanding and the predictability of plant community dynamics in fragmented landscapes. I conclude that the spatially explicit perspective used in all models was crucial to reach this aim. More specifically, in chapter 2 complex dispersal-diversity relationships could only emerge from the neutral model due to the spatially explicit simulation of the survey area and the metacommunity. The investigation of patch connectivity as a predictor of local species diversity (chapter 3) and of community-mean functional traits (chapter 4) required well-founded estimates of patch connectivity. Therefore, I developed an advanced connectivity index that considers habitat configuration, patch shapes and patch sizes in a spatially explicit way.

In chapter 2, I found that variations of dispersal capability or habitat connectivity, respectively, can have contrasting consequences for local diversity in a certain survey area. These findings are relevant for conservation biology and landscape planning, as management strategies to increase habitat connectivity, e.g. by the creation of habitat corridors, stepping stones or by the (re)introduction of animals as dispersal vectors, have often been often suggested as a promising way to foster species diversity within certain target area, e.g. within a nature reserve. I conclude that it is important to consider the diversity and composition of the potential metacommunity, before implementing such conservation measures. An increase in connectivity can be beneficial, if the metacommunity offers a diverse species pool to the target area. However, increasing connectivity can also be detrimental for local species diversity, if the metacommunity is species poor, or it contains species, such as invasive species, which acquire high local dominance after immigrating into the target area.

The findings of low connectivity between habitat patches and of a significant extinction debt in the SJL (chapter 3) indicate that the conservation of biodiversity in this Mediterranean landscape will require the allocation of additional habitat to natural succession. Additional natural habitat is needed to lower species extinction rates and to increase the connectivity between currently isolated habitat patches. The assessment of specific management scenarios to identify an optimal allocation and configuration of additional natural habitat was beyond the scope of the thesis. However, I propose that the approach presented in chapter 3 is suitable to address this question. In combination with scenarios of potential future habitat distributions, the multi-species IFM is able to project species diversity for these scenarios and to compare their effectiveness with respect to specific conservation objectives. Furthermore, I suggest that the inverse modelling approach presented in chapter 3 offers a promising generic tool to investigate regional community dynamics and extinction debts in different fragmented landscapes and for different taxa. The analysis of plant functional traits (chapter 4) revealed that we still lack a thorough understanding of the effects of interspecific competition on plant functional trait distributions. Accordingly, I conclude that future research on community assembly processes needs to address the following questions: How does competition affect functional trait distributions of different functional traits, in different plant communities and along environmental gradients? How can the effects of abiotic environmental factors and biotic interactions on community assembly be separated?

In the analysis of the association of community-mean traits with fragmentation and precipitation, I found that especially generative traits, such as seed mass and seed number, can be interactively influenced by climate, fragmentation and potentially land use. These results emphasize the importance of considering the synergistic effects of these drivers in order to improve projections of plant communities' responses to land-use or climatic changes in fragmented landscapes.

5.4 Prospects for further research

In this thesis, I chose several methodological approaches to address different specific objectives. The simulations and statistical models I developed and analysed were suitable to address the respective objectives, but of course each model included certain simplifying assumptions. However, I propose that combining the approaches used in this thesis bears high potential for further investigations of plant community dynamics. Specifically, I suggest integrating plant functional traits into simulation models of plant communities in fragmented landscapes. Furthermore, I argue that incorporating species interactions into trait-based, spatial and dynamic models is pivotal to resolve current controversies in community assembly theory.

5.4.1 Integrating plant functional traits into spatial simulation models

The neutral model and the IFM include the simplifying assumption that species share equal *per-capita* rates of birth, death and dispersal (chapter 2) or only differ in their species-specific abundances (chapter 3). In contrast, I found that community-mean traits significantly responded to the precipitation gradient in the SJL and at least weakly to fragmentation (chapter 4). The availability of plant functional trait data from large data bases (Kleyer *et al.* 2008; Kattge *et al.* 2011) as well as our knowledge of trait-environment relationships (e. g. McGill *et al.* 2006; Westoby & Wright 2006; Lindborg *et al.* 2012) has been substantially increased during the last years. Despite the increase in data availability, we still lack predictive, dynamic models for species-rich plant communities, which utilize the available functional trait information. Arguably, this gap reflects the difficulty of parameterising and testing complex simulation models with different and potentially incomplete data sources, such as species abundances, presences/absences and spatial environmental data. However, recent advances in hierarchical Bayesian analysis and approximate Bayesian computation (ABC) now provide tools to tackle these methodological challenges (Clark &

Gelfand 2006; Hartig *et al.* 2011).

I propose the IFM introduced in chapter 3 as a useful starting point for integrating plant functional traits into landscape-scale simulation models. Instead of estimating one set of parameter values for the entire community as in chapter 3, functional traits could be used to derive plant functional groups, by clustering species in multivariate trait space (Hérault & Honnay 2005). Then, a specific IFM parameter set for each plant functional group could be estimated using ABC. In the last step, the analysis of the relationship between functional trait values and the respective IFM parameter estimates will provide insights into the relationship between plant functional traits and species' responses to fragmentation (see Dupré & Ehrlén 2002 for a similar approach using simple static species distribution models).

The IFM in chapter 3 included differences in patch size and patch connectivity, but not in patch quality. Nevertheless, similar to previous single species examples (Moilanen & Hanski 1998; Vos *et al.* 2000), it is possible to integrate relationships between presences/absences of plant functional groups and environmental variables into an IFM, if sufficient environmental data, e.g. on soil and topography, are available.

Furthermore, similar to previous IFM implementations, I assumed that every colonization event is related to dispersal among habitat patches, although especially in semi-arid landscapes (re)colonizations from seed banks might be even more relevant than dispersal (Venable 2007; Siewert & Tielbörger 2010). Of course, integrating seed bank dynamics into an IFM would ideally require sampling the soil seed bank in addition to species presences/absences in the vegetation. Overall, an IFM approach that considers several plant functional groups, environmental heterogeneity and seed dormancy would require high efforts in data collection. Nevertheless, I suggest that this approach would be a big step forward towards an improved understanding and more reliable predictions of plant community dynamics in fragmented landscapes.

5.4.2 Integrating species interactions into spatial simulation models

In chapter 2, I found species segregation due to dispersal limitation to be an important determinant of scale-dependent dispersal-diversity relationships. As species segregation influences the relative importance of interspecific and intraspecific competition (Levine & Murrell 2003), this finding implies that interspecific competition can be an important driver of community dynamics in fragmented landscapes. Nevertheless, the multi-species IFM used in chapter 3 did not consider species interactions, following the approaches of Hanski & Gyllenberg (1997) and Hovestadt & Poethke (2005). Despite the long interest in the consequences of interspecific competition for community assembly (reviewed in Götzenberger *et al.* 2012), it is still intensively debated how species interactions influence the trait distributions in plant communities (Stubbs & Wilson 2004; Kraft *et al.* 2008; Mayfield & Levine 2010) and how abiotic and biotic drivers of community assembly can be separated (De Bello *et al.* 2012). These knowledge gaps were also apparent in the analysis of plant functional traits in the SJL (chapter 4), where the evidence for trait divergence due to interspecific competition was highly sensitive to the choice of null-models.

For these reasons, I conclude that integrating species interactions into trait-based dynamic simulation models is necessary, first, to address current knowledge gaps in community assembly theory and second, to incorporate species interactions into predictions of community responses to fragmentation and environmental changes. I suggest developing a model that includes species niches, modelled as trait-environment relationships (e. g. Laughlin *et al.* 2012), as well as stochastic dispersal and colonization events (e. g. Gravel *et al.* 2006). Species interactions should be implemented considering the two contrasting scenarios that competition either results in trait convergence or in trait divergence among co-occurring species (Chesson 2000; Mayfield & Levine 2010; Kunstler *et al.* 2012).

In a first step, such a model could be analysed based on theoretical scenarios in order to refine expectations of community assembly theory. In this context it would be of high interest to evaluate scenarios with varying strength of trait-environment relationships and for the complex, but realistic case that competition simultaneously drives trait convergence in certain traits, but trait divergence in other traits (Grime 2006). In a second step, the model could be parameterised using (approximate) Bayesian computation based on environmental data, vegetation surveys and functional trait data. This approach will allow assessing the relative importance of abiotic and biotic drivers of community assembly in natural landscapes and comparing the credibility of models that consider different scenarios of interspecific competition. Accordingly, this model will be of high relevance for fundamental ecological questions and for predictions of how communities of interacting species respond to environmental changes or specific management scenarios.

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Appendix A

Supplementary material:
Metacommunity, mainland-island system or island communities? – Assessing the regional dynamics of plant communities in a fragmented landscape

A.1 Implementation of the approximate Bayesian computation approach (ABC)

This section provides details on the implementation of our ABC approach and describes the generation of approximate posterior distributions. Prior distributions for the parameters were uniform (at log-scale) with the following minimum and maximum parameter values: K_0 in [1, 1000] (unit: individuals), Y in [1, 1000] (unit: number of immigrants), X in [0.1, 2] (dimensionless), α in [5, 500] (unit: meter). These uniform prior distributions are restricted to biologically plausible intervals, but reflect our lack of prior knowledge within these intervals.

In order to derive posterior distributions we used a two-step procedure for all three scenarios. First, we randomly sampled 100,000 parameter sets from the prior distributions. For each parameter set we simulated three replicate runs and averaged their distances $[d(S_{obs}, S_{sim})]$ between the simulated and observed summary statistics (species richness or Sørensen-similarity indices) to obtain a characteristic distance metric for this parameter set. The five parameter sets with the lowest average $d(S_{obs}, S_{sim})$, which indicates the closest match to the data, were then chosen as starting values for Markov chain Monte Carlo sampling (MCMC) that was implemented according to Hartig *et al.* (2011). All parameters were sampled at the log-scale to avoid sampling of negative parameter values. We used a multivariate normal distribution centred at the current parameter values to propose new parameter values (ter Braak & Etienne 2003). The new parameter set was only accepted, if $d(S_{obs}, S_{sim}) < epsilon$, with $epsilon = 75,000$ for species richness and $epsilon = 12$ for Sørensen-similarity (based on three replicate simulations) (Hartig et al. 2011). These acceptance thresholds were chosen to produce appropriate acceptance rates of 0.3-0.4 and convergence times in the MCMC sampling (Gelman *et al.* 2004). We run 5 replicate chains with 25,000 iterations each. Convergence was assessed using the Gelman-Rubin convergence diagnostic (Gelman *et al.* 2004). The first 5 000 iterations were discarded as burn-in and from the remaining 20,000 iterations every tenth was used as a posterior sample. Therefore, each approximate posterior distribution is based on $5 \times 2,000 = 10,000$ samples.

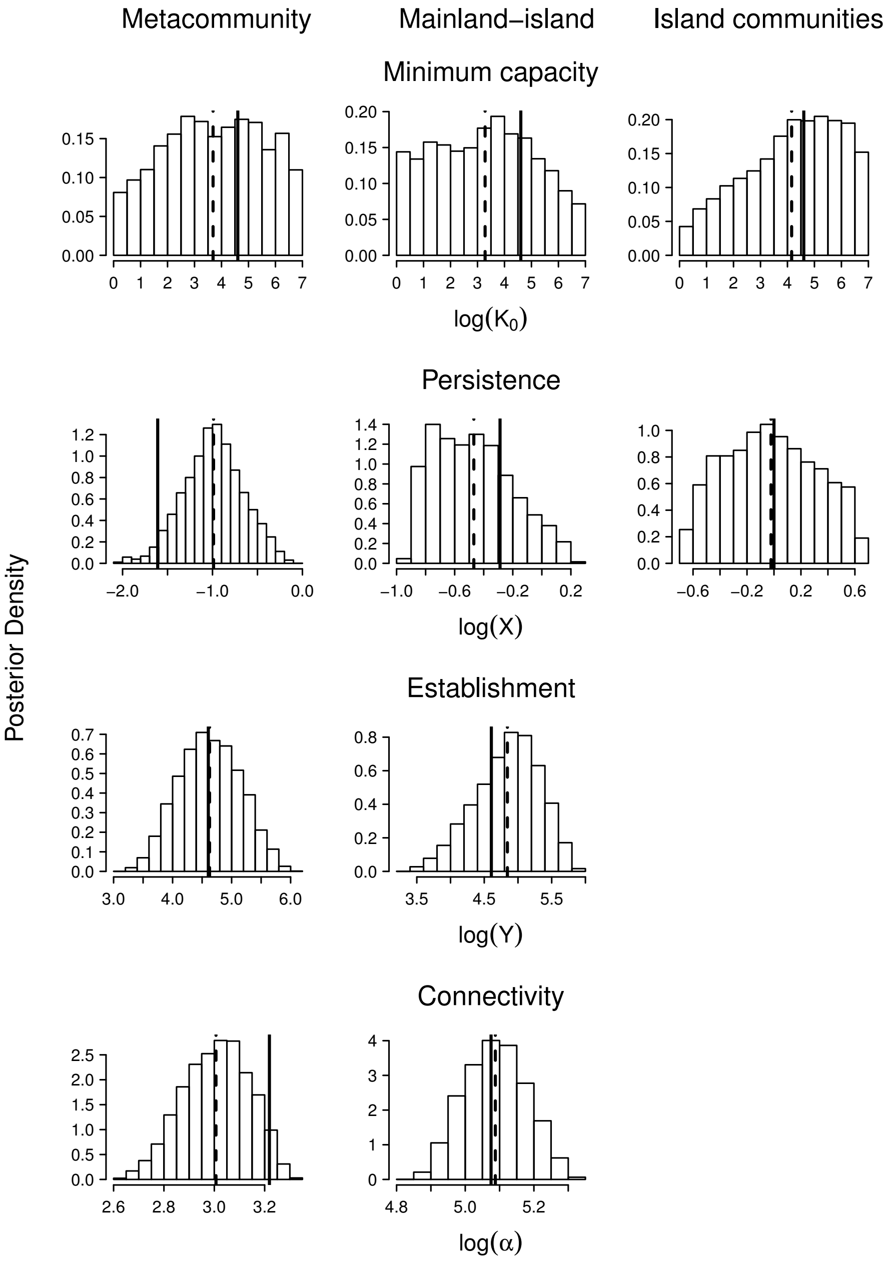

Figure A.1. Approximated posterior distributions for model parameters K_0, X, Y and α (at the log-scale) based on simulated "data". The solid vertical lines indicate the parameter values used for simulating the "data" and the dashed lines indicate estimated parameter values (posterior means). The histograms were constructed based on 10,000 samples (2000 samples from 5 replicate chains). Parameter values used for simulating the "data" were: Metacommunity scenario: $K_0 = 100$, $Y = 100$, $X = 0.2$, $\alpha = 25$; Mainland-island scenario: $K_0 = 100$, $Y = 100$, $X = 0.75$, $\alpha = 160$; Island communities scenario: $K_0 = 100$, $X = 1.0$.

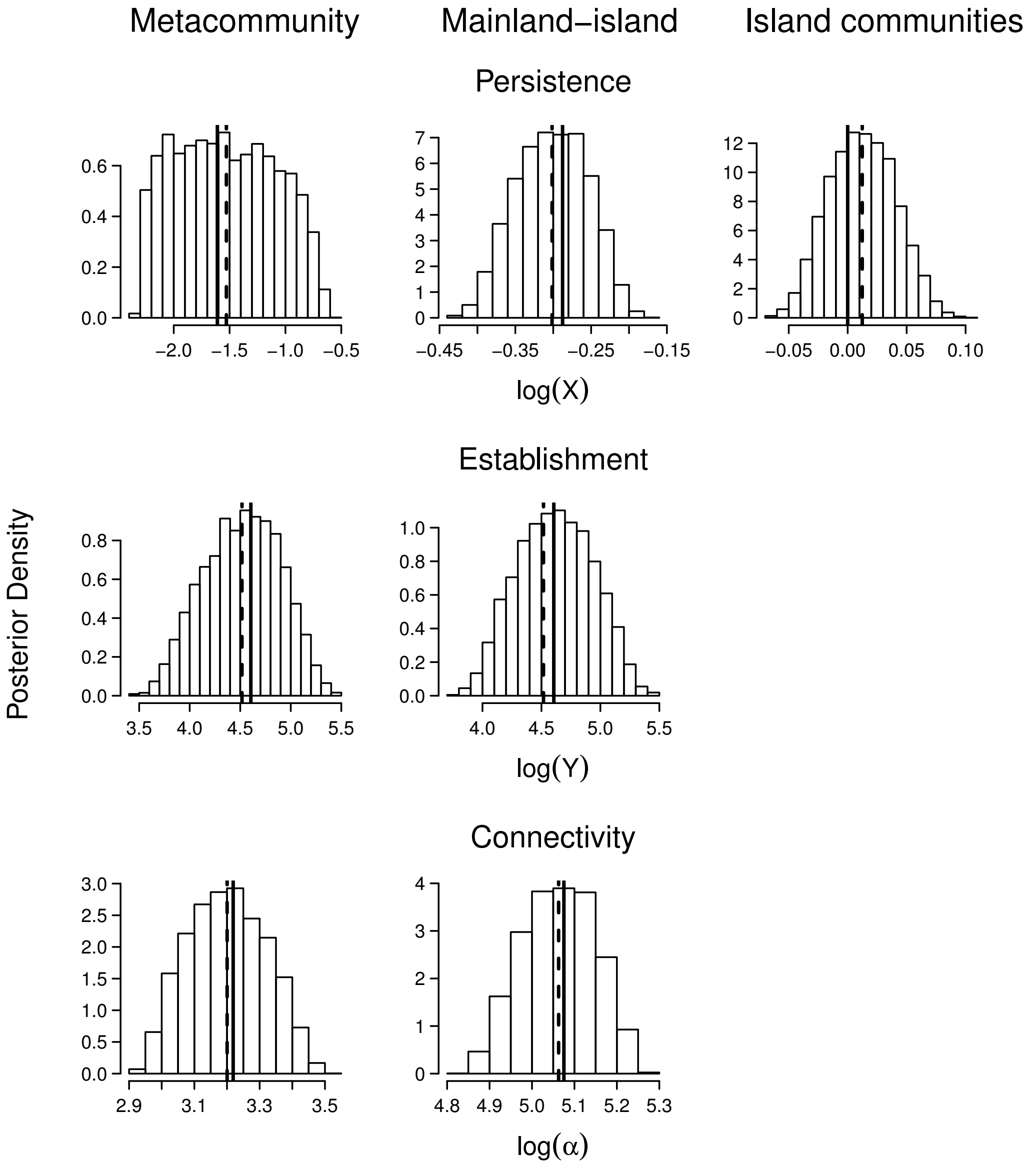

Figure A.2. Approximated posterior distributions for model parameters X, Y and α (at the log-scale) based on simulated "data". The parameter K_0 was kept constant at a value of 100. The solid vertical lines indicate the parameter values used for simulating the "data" and the dashed lines indicate estimated parameter values (posterior means). The histograms were constructed based on 10,000 samples (2000 samples from 5 replicate chains). Parameter values used for simulating the "data" were: Metacommunity scenario: $K_0 = 100$, $Y = 100$, $X = 0.2$, $\alpha = 25$; Mainland-island scenario: $K_0 = 100$, $Y = 100$, $X = 0.75$, $\alpha = 160$; Island communities scenario: $K_0 = 100$, $X = 1.0$.

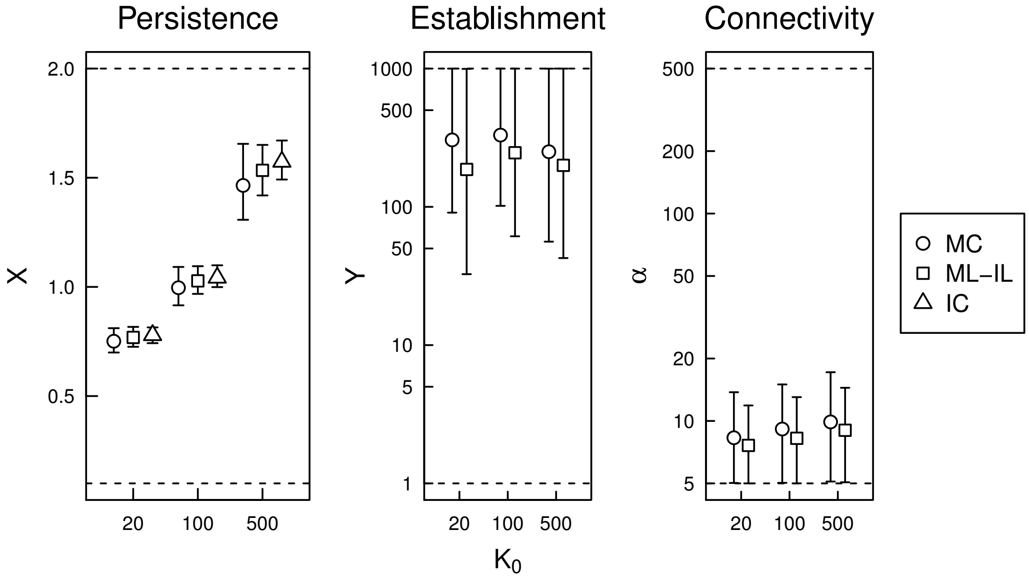

Figure A.3. Posterior mean values and 90% credible intervals for model parameters X, Y and α for different constant value of K_0. As summary statistic the species richness of the 40 patches sampled was used. Plotting characters indicate the scenarios of landscape-scale dynamics: metacommunity (MC), mainland-island (ML-IL), island communities (IC). The dashed horizontal lines indicate the range of uniform prior distributions for each parameter.

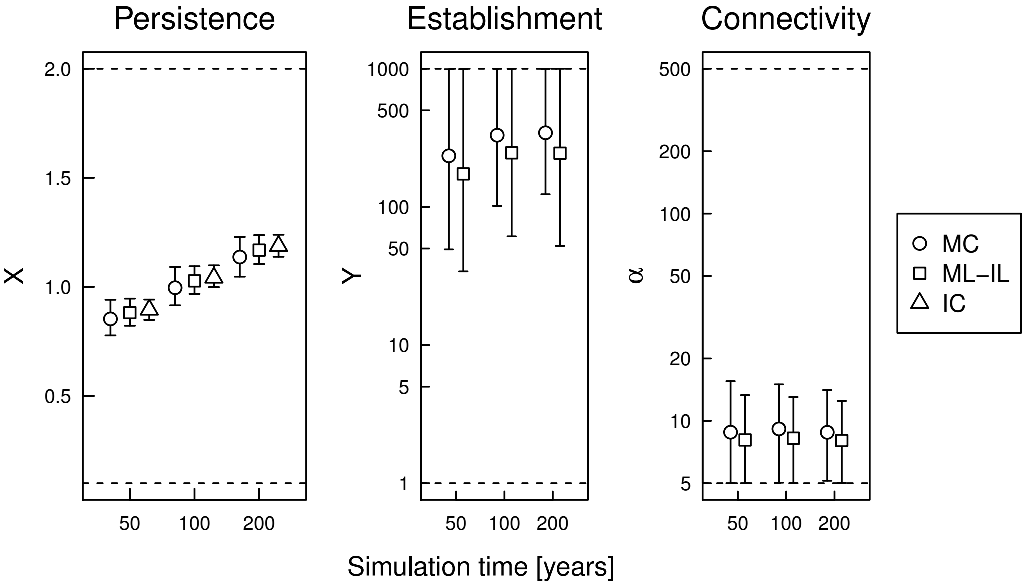

Figure A.4. Posterior mean values and 90% credible intervals for model parameters X, Y and α for different simulation times (50, 100 and 200 time steps). As summary statistic the species richness of the 40 patches sampled was used. Plotting characters indicate the scenarios of landscape-scale dynamics: metacommunity (MC), mainland-island (ML-IL), island communities (IC). The dashed horizontal lines indicate the range of uniform prior distributions for each parameter.

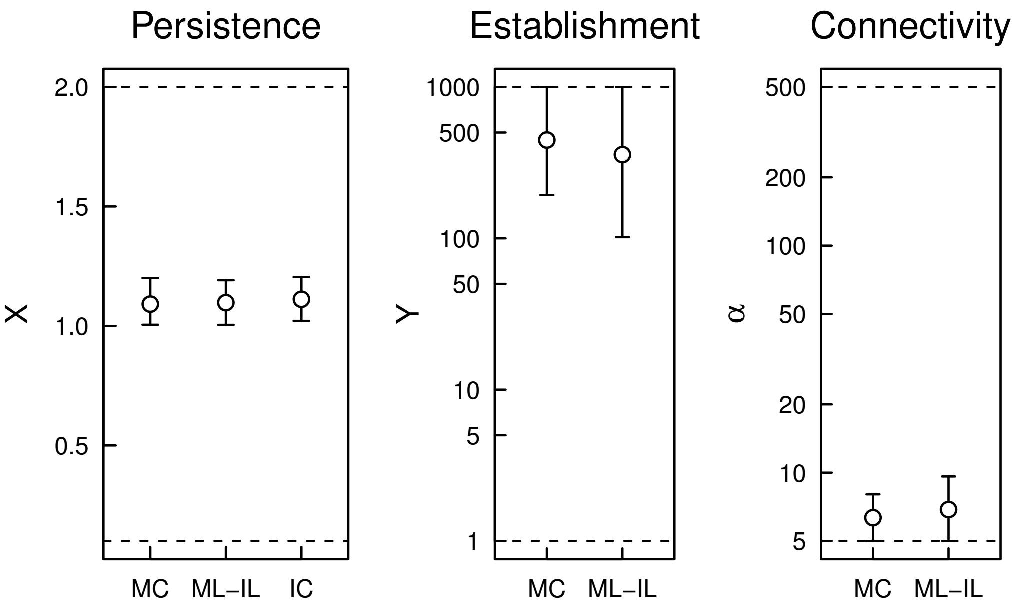

Figure A.5. Posterior mean values and 90% credible intervals for model parameters X, Y and α for the metacommunity scenario (MC), the mainland-island scenario (ML-IL) and the island communities scenario (IC). As summary statistic the pair wise Sørensen-similarity indices for all 40 sampled patches were used. The dashed horizontal lines indicate the range of uniform prior distributions for each parameter.

Appendix B

Supplementary material: Plant functional traits and community assembly along interacting gradients of productivity and fragmentation

B.1 Correlation among connectivity indices

We tested the correlation of our new connectivity index to connectivity or isolation indices, which are commonly used in studies of fragmentation effects and have been also applied for the analysis of species richness in the SJL before (Giladi *et al.* 2011). The Euclidian nearest neighbour distance (ENN), as a simple measure of patch isolation, does not correlate with our improved connectivity index, since it does not take into account patch areas and only considers the nearest neighbour of each patch.

The proximity index considers patch areas and patch-to-patch distances in certain search radius and is defined as

$$PI_i = \sum_{j=1}^{N} \frac{A_j}{d_{ij}^2}, \tag{B.1}$$

where A_j is the area of patch patch j and d_{ij} is the distance between target patch i and neighbour patch j (Giladi *et al.* 2011). The proximity index was significantly correlated to our connectivity index (Fig. B.1). However, the relatively low correlation coefficient ($\rho = 0.43$) indicated that the incorporation of patch shapes and orientations clearly influences the values of our improved connectivity index.

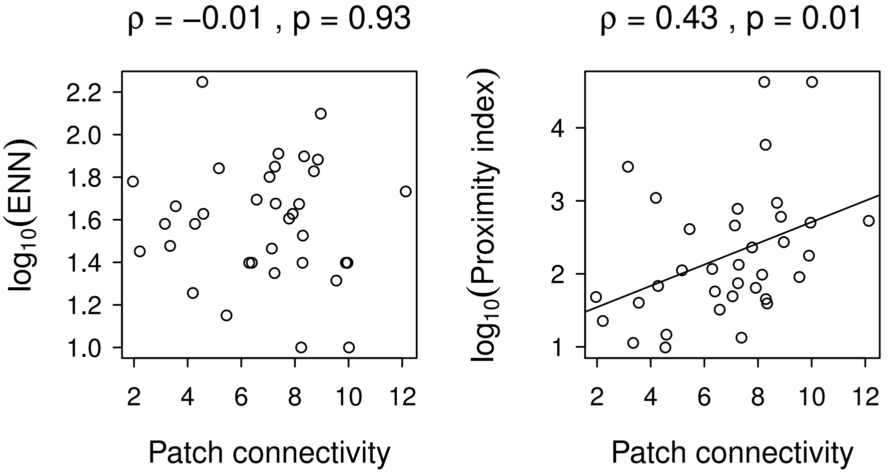

Figure B.1. Correlations between isolation and connectivity indices. Patch connectivity refers to the index explained in the manuscript in detail and considers patch distance, areas and shapes. ENN is the Euclidian distance (edge to edge) from the target patch to the nearest neighbour patch. The proximity index considers the areas and distances of all neighbouring patches within in within a search radius of 1000 m. The definition of the proximity index is provided in Eq. B.1. Correlation tests were based on Spearman's rank correlation coefficient (ρ).

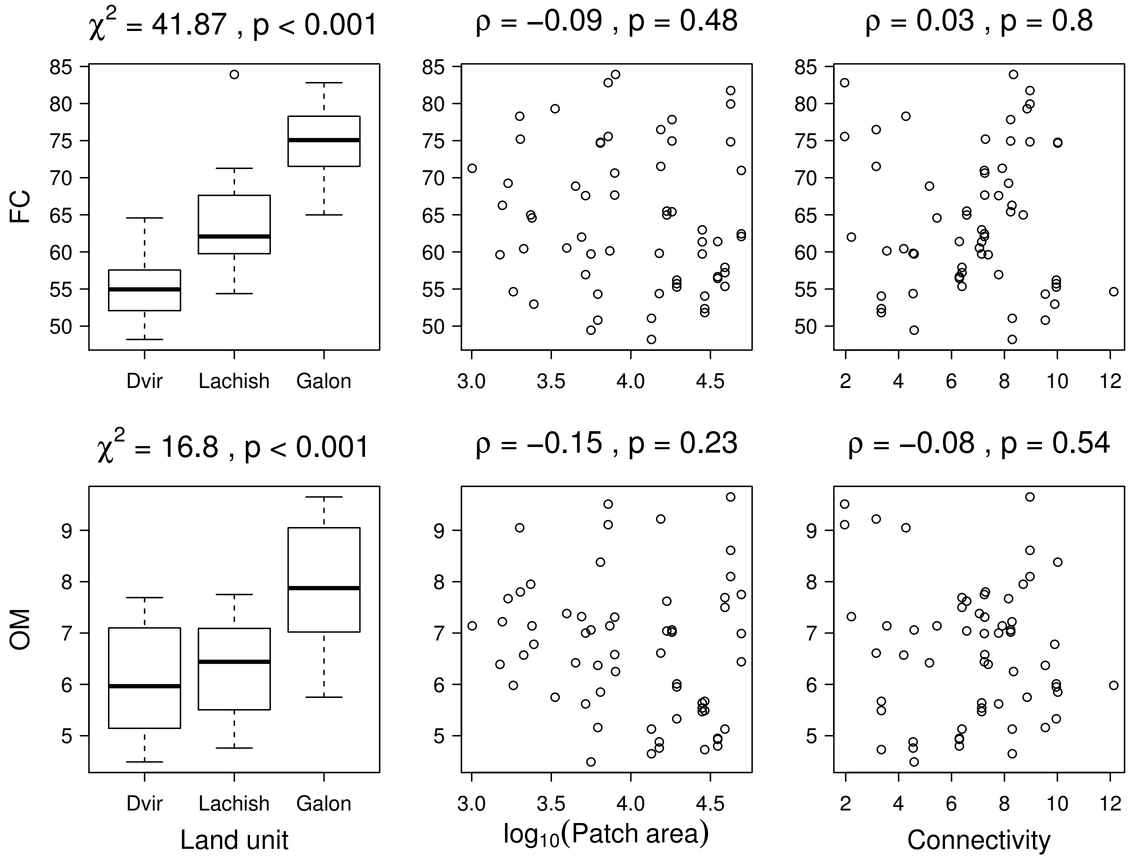

Figure B.2. Correlations between soil properties and the explanatory variables that were used in models of community-mean traits. Kruskal-Wallis tests were applied for the categorical variable "land unit" and correlation tests based on Spearman's rank correlation coefficient (ρ) for continuous variables. The soil variables are field capacity (FC) measured in percent volumetric water content and soil organic matter (OM) in mol C per kg dry soil.

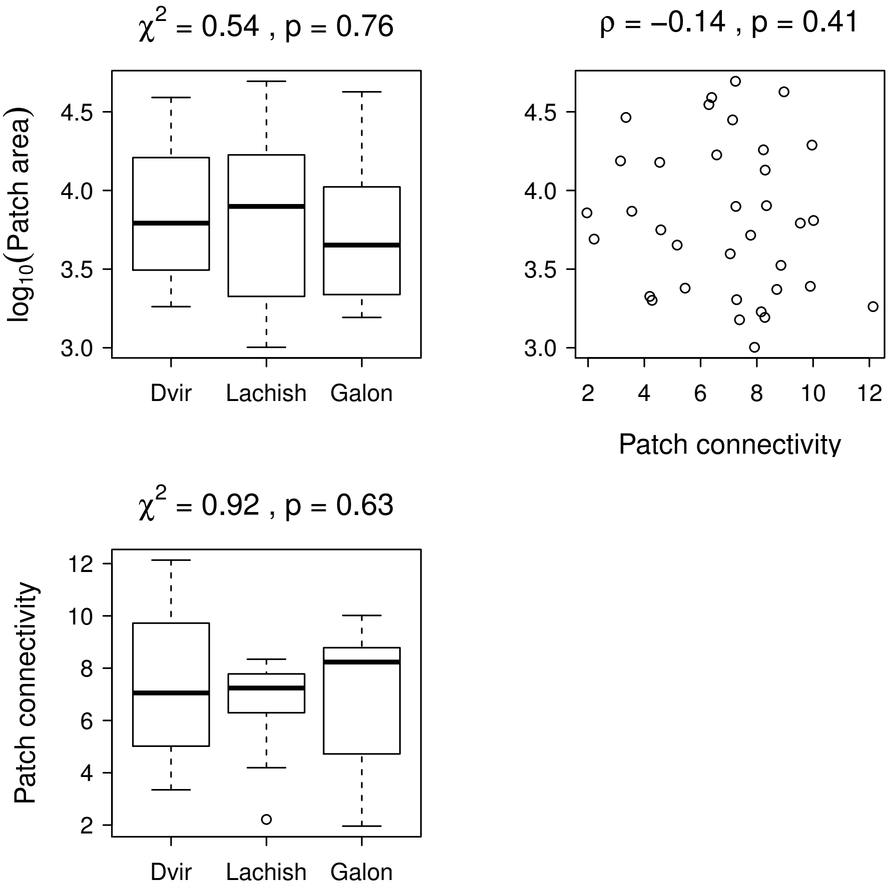

Figure B.3. Pair-wise correlations between the explanatory variables land unit, $\log_{10}$(patch area) and patch connectivity. For the tests of the correlation between land unit and patch area or connectivity, respectively, non-parametric Kruskal-Wallis tests were used. For the test of correlation between patch connectivity and patch area Spearman's rank correlation coefficient (ρ) was used.

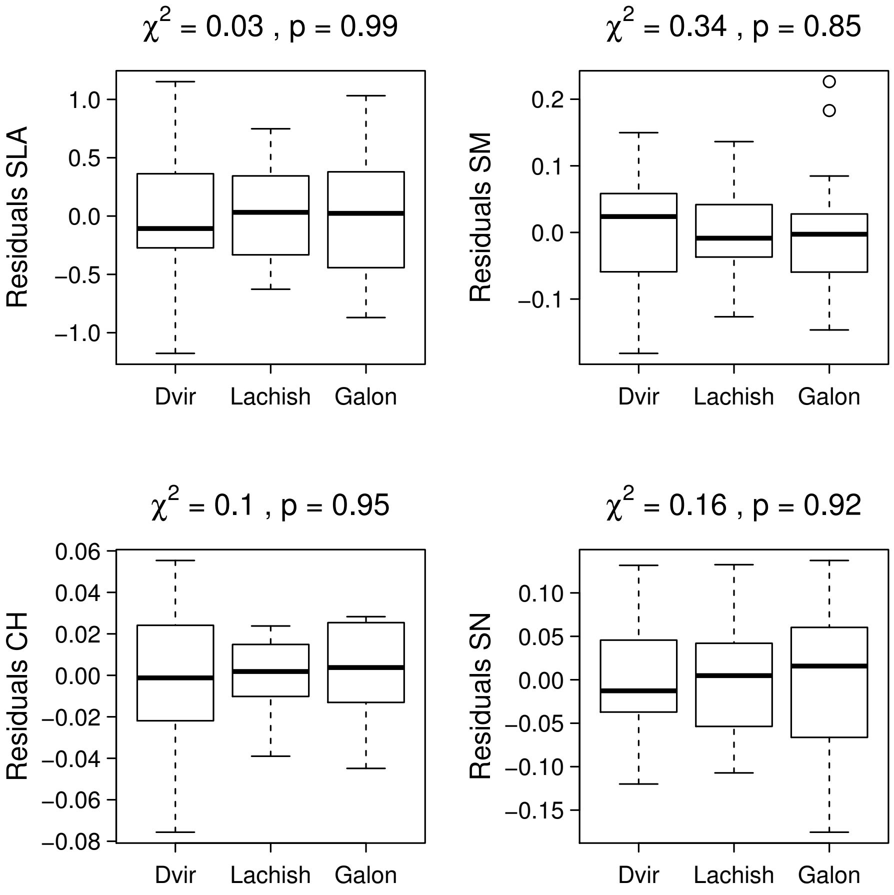

Figure B.4. Comparison of model residuals among land units for each community-mean trait. The residuals were derived from the models with the lowest AIC$_c$ for each trait (Table 4.5). Non-parametric Kruskal-Wallis tests were used to test for differences among land units

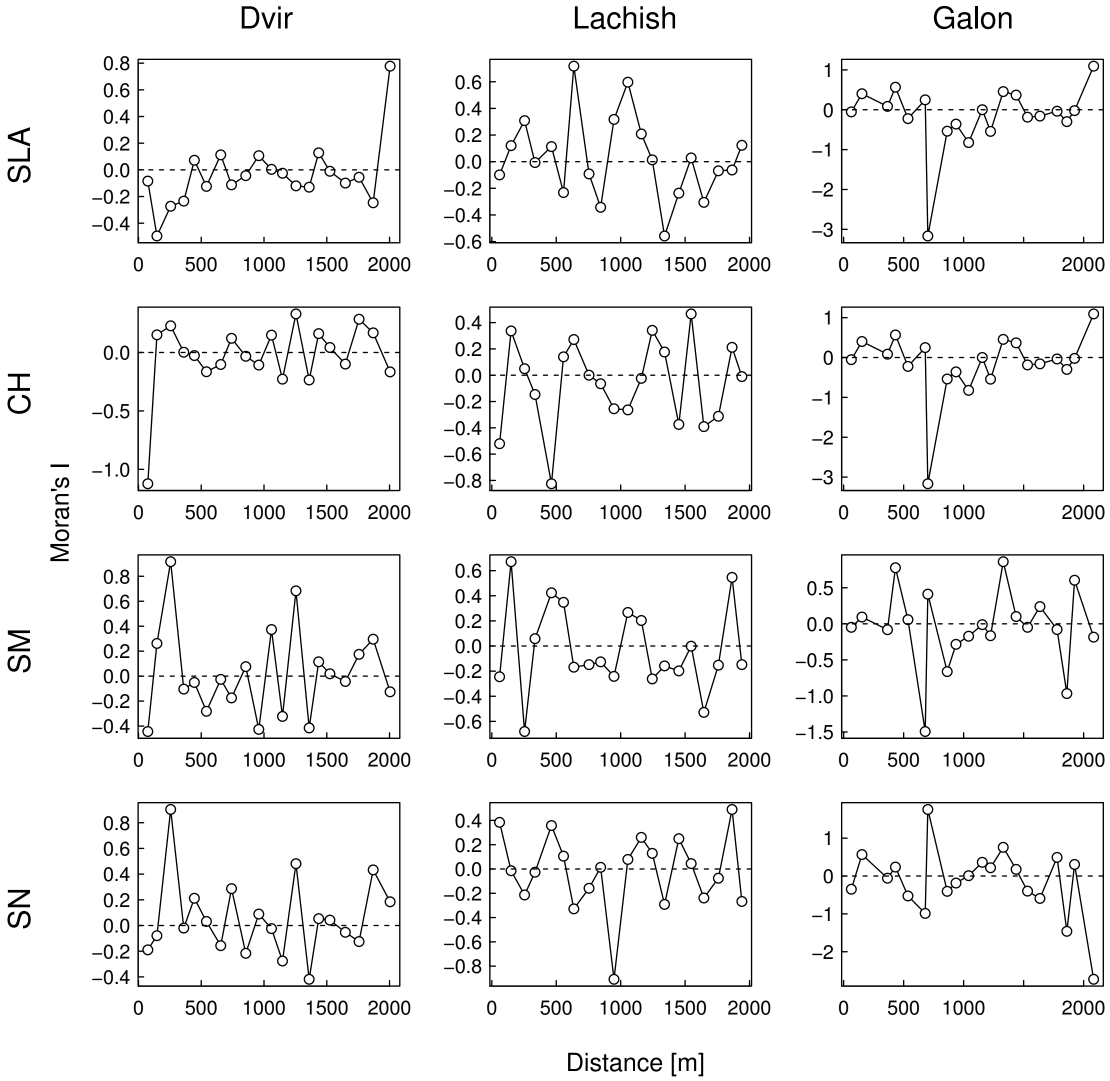

Figure B.5. Correlograms of model residuals for each land unit and each community-mean trait. The residuals were derived from the models with the lowest AIC_c for each trait (Table 4.5). Moran's I was calculated up to a distance of 2000 m using distance classes of 100 m. Spatial autocorrelation of model residuals would be indicated by high values of Moran's I at low distances and a decreasing trend with increasing distances.

Table B.1. Wilcoxon signed rank tests and standardized effect sizes (SES) of trait convergence, measured as reduction in trait ranges and variances. Two different null-models were used: (a) Null-model 1 did not control for trait convergence due to habitat filtering. (b) Null-model 2 controlled for trait convergence within land units. P-values are reported for the one-tailed and paired test of the hypothesis that the observed trait index is lower than under the null-model. Significant deviations from the null-model ($p < 0.05$) are shown in bold. Standard effect sizes were calculated as SES = (observed – expected) / (sd expected). Mean SES values ± one standard error (averaged over of all sampling plots) are provided here. Trait abbreviations: SLA – specific leaf area, CH – canopy height, SM – seed mass, SN – seed number. See text for further explanations of trait indices and the implementation of the null-models

Trait & Scale	**Range**		**Variance**	
	p	**SES**	**p**	**SES**
(a) Null-model 1 – regional species pool				
SLA				
15 m	**0.008**	**−0.25 ± 0.11**	0.529	−0.03 ± 0.12
5 m	**0.024**	**−0.11 ± 0.06**	0.429	0.00 ± 0.06
1 m	0.164	−0.07 ± 0.04	**0.032**	**−0.04 ± 0.04**
CH				
15 m	**0.011**	**−0.65 ± 0.18**	**0.001**	**−0.48 ± 0.14**
5 m	**<0.001**	**−0.50 ± 0.07**	**<0.001**	**−0.40 ± 0.07**
1 m	**<0.001**	**−0.28 ± 0.04**	**<0.001**	**−0.24 ± 0.05**
SM				
15 m	**0.003**	**−0.39 ± 0.11**	**0.004**	**−0.31 ± 0.11**
5 m	**<0.001**	**−0.24 ± 0.06**	**<0.001**	**−0.20 ± 0.06**
1 m	**<0.001**	**−0.14 ± 0.04**	**<0.001**	**−0.13 ± 0.04**
SN				
15 m	0.109	−0.16 ± 0.13	0.077	−0.19 ± 0.10
5 m	0.096	−0.12 ± 0.07	0.179	−0.09 ± 0.06
1 m	**0.033**	**−0.09 ± 0.05**	0.164	−0.05 ± 0.05

Table B.1. Continued.

Trait & Scale	**Range**		**Variance**	
	p	**SES**	**p**	**SES**
(b) Null-model 2 – land-unit specific species pool				
SLA				
15 m	0.054	-0.27 ± 0.14	0.461	-0.05 ± 0.13
5 m	**0.028**	$\mathbf{-0.13 \pm 0.07}$	0.229	-0.03 ± 0.07
1 m	0.104	-0.09 ± 0.05	**0.020**	$\mathbf{-0.06 \pm 0.04}$
CH				
15 m	**0.009**	$\mathbf{-0.43 \pm 0.14}$	**0.001**	$\mathbf{-0.36 \pm 0.13}$
5 m	**<0.001**	$\mathbf{-0.38 \pm 0.07}$	**<0.001**	$\mathbf{-0.33 \pm 0.06}$
1 m	**<0.001**	$\mathbf{-0.27 \pm 0.04}$	**<0.001**	$\mathbf{-0.22 \pm 0.04}$
SM				
15 m	**0.007**	$\mathbf{-0.33 \pm 0.12}$	**0.009**	$\mathbf{-0.27 \pm 0.11}$
5 m	**<0.001**	$\mathbf{-0.26 \pm 0.06}$	**<0.001**	$\mathbf{-0.19 \pm 0.06}$
1 m	**<0.001**	$\mathbf{-0.20 \pm 0.04}$	**<0.001**	$\mathbf{-0.16 \pm 0.04}$
SN				
15 m	**0.036**	$\mathbf{-0.11 \pm 0.11}$	0.157	-0.12 ± 0.09
5 m	0.284	-0.02 ± 0.06	0.608	-0.02 ± 0.06
1 m	0.075	-0.08 ± 0.04	0.166	-0.04 ± 0.05

Table B.2. Wilcoxon signed rank tests and standardized effect sizes (SES) of trait divergence, measured as limiting similarity and/or even spacing of trait values. Three different null-models were used to account for trait convergence at different scales. (a) Null-model 1 did not consider trait convergence. (b) Null-model 2 controlled for trait convergence within land units and (c) null-model 3 for trait convergence at the sampling plot scale. In null-model 3 trait ranges observed at the 15 m × 15 m scale were used to restrict simulated trait ranges at the 5 m × 5 m and 1 m × 1 m sampling scales. P-values are reported for the one-tailed and paired test of the hypothesis that the observed trait index is lower than under the null-model. Significant deviations from the null-model ($p < 0.05$) are shown in bold. Standard effect sizes were calculated as SES = (observed – expected) / (sd expected). Mean SES values ± one standard error (averaged over all plots) are provided here. Abbreviations of trait divergence indices: sdNN – standard deviation of nearest-neighbour distance; sdNNr – sdNN divided by trait range; sdNDr – standard deviation of ordered neighbour distances divided by trait range. Trait abbreviations: SLA – specific leaf area, CH – canopy height, SM – seed mass, SN – seed number. See the main text for further explanations of trait indices and the implementation of the null-models.

Trait & Scale	**Kurtosis**		**sdNN**		**sdNNr**		**sdNDr**	
	p	**SES**	**p**	**SES**	**p**	**SES**	**p**	**SES**
(a) Null-model 1 – regional species pool								
SLA								
15m	**0.050**	**−0.12 ± 0.09**	**<0.001**	**−0.42 ± 0.08**	**<0.001**	**−0.43 ± 0.08**	**<0.001**	**−0.33 ± 0.09**
5m	0.188	0.00 ± 0.06	**<0.001**	**−0.19 ± 0.05**	**<0.001**	**−0.17 ± 0.05**	**0.038**	**−0.11 ± 0.06**
1m	0.106	0.05 ± 0.05	**0.005**	**−0.05 ± 0.04**	**0.039**	**−0.02 ± 0.05**	0.106	−0.01 ± 0.05
CH								
15m	**0.035**	**−0.22 ± 0.14**	**0.001**	**−0.29 ± 0.12**	**0.004**	**−0.18 ± 0.12**	**<0.001**	**−0.33 ± 0.13**
5m	**<0.001**	**−0.24 ± 0.07**	**<0.001**	**−0.34 ± 0.06**	**<0.001**	**−0.25 ± 0.06**	**<0.001**	**−0.28 ± 0.06**
1m	**<0.001**	**−0.21 ± 0.04**	**<0.001**	**−0.25 ± 0.04**	**<0.001**	**−0.21 ± 0.04**	**<0.001**	**−0.22 ± 0.04**

Table B.2. Continued.

Trait & Scale	**Kurtosis**		**sdNN**		**sdNNr**		**sdNDr**	
	p	**SES**	**p**	**SES**	**p**	**SES**	**p**	**SES**
(a) Null-model 1 – regional species pool								
SM								
15m	**0.035**	**−0.21 ± 0.10**	**<0.001**	**−0.35 ± 0.10**	**0.001**	**−0.29 ± 0.10**	**<0.001**	**−0.32 ± 0.09**
5m	**<0.001**	**−0.20 ± 0.06**	**<0.001**	**−0.28 ± 0.05**	**<0.001**	**−0.27 ± 0.05**	**<0.001**	**−0.25 ± 0.05**
1m	**<0.001**	**−0.19 ± 0.04**	**<0.001**	**−0.22 ± 0.04**	**<0.001**	**−0.24 ± 0.04**	**<0.001**	**−0.19 ± 0.04**
SN								
15m	0.074	−0.10 ± 0.12	**0.007**	**−0.10 ± 0.09**	**0.041**	**−0.05 ± 0.10**	**0.017**	**−0.15 ± 0.11**
5m	**<0.001**	**−0.13 ± 0.06**	**<0.001**	**−0.11 ± 0.05**	**0.001**	**−0.07 ± 0.06**	0.148	0.03 ± 0.06
1m	**<0.001**	**−0.12 ± 0.04**	**<0.001**	**−0.09 ± 0.04**	**<0.001**	**−0.07 ± 0.04**	0.103	0.03 ± 0.04

Table B.2. Continued.

Trait & Scale	**Kurtosis**		**sdNN**		**sdNNr**		**sdNDr**	
	p	**SES**	**p**	**SES**	**p**	**SES**	**p**	**SES**
(b) Null-model 2 – land-unit specific species pool								
SLA								
15m	0.286	−0.02 ± 0.09	**<0.001**	**−0.35 ± 0.09**	**<0.001**	**−0.32 ± 0.09**	**0.024**	**−0.13 ± 0.09**
5m	0.480	0.06 ± 0.06	**0.001**	**−0.13 ± 0.06**	**0.003**	**−0.11 ± 0.06**	0.362	−0.03 ± 0.06
1m	0.173	0.07 ± 0.05	**0.006**	**−0.05 ± 0.05**	0.057	−0.01 ± 0.05	0.336	0.03 ± 0.05
CH								
15m	0.190	0.00 ± 0.13	**<0.001**	**−0.30 ± 0.11**	**0.002**	**−0.25 ± 0.11**	**0.013**	**−0.19 ± 0.12**
5m	**0.001**	**-0.08 ± 0.07**	**<0.001**	**−0.20 ± 0.07**	**<0.001**	**−0.14 ± 0.07**	**0.001**	**−0.11 ± 0.07**
1m	**<0.001**	**−0.19 ± 0.04**	**<0.001**	**−0.22 ± 0.04**	**<0.001**	**−0.17 ± 0.04**	**<0.001**	**−0.18 ± 0.04**
SM								
15m	**0.024**	**−0.22 ± 0.10**	**0.002**	**−0.27 ± 0.10**	**0.009**	**−0.21 ± 0.10**	**<0.001**	**−0.27 ± 0.10**
5m	**<0.001**	**−0.26 ± 0.06**	**<0.001**	**−0.28 ± 0.06**	**<0.001**	**−0.26 ± 0.06**	**<0.001**	**-0.27 ± 0.05**
1m	**<0.001**	**−0.22 ± 0.04**	**<0.001**	**−0.25 ± 0.04**	**<0.001**	**−0.24 ± 0.04**	**<0.001**	**−0.2 ± 0.04**
SN								
15m	0.123	−0.06 ± 0.11	**0.003**	**−0.14 ± 0.09**	**0.015**	**−0.13 ± 0.09**	**0.009**	**−0.21 ± 0.10**
5m	**0.003**	**−0.08 ± 0.05**	**0.001**	**−0.10 ± 0.05**	**0.004**	**−0.08 ± 0.05**	0.178	−0.03 ± 0.05
1m	**<0.001**	**−0.13 ± 0.04**	**<0.001**	**−0.10 ± 0.04**	**<0.001**	**−0.08 ± 0.04**	0.087	−0.01 ± 0.04

Table B.2. Continued.

Trait & Scale	**Kurtosis**		**sdNN**		**sdNNr**		**sdNDr**	
	p	**SES**	**p**	**SES**	**p**	**SES**	**p**	**SES**
(c) Null-model 3 – plot specific species pool								
SLA								
15m	0.870	0.16 ± 0.10	0.887	0.25 ± 0.10	0.244	0.04 ± 0.10	0.076	-0.09 ± 0.09
5m	0.913	0.13 ± 0.06	0.982	0.22 ± 0.06	0.339	0.06 ± 0.06	0.247	-0.04 ± 0.06
1m	0.399	0.10 ± 0.05	0.761	0.14 ± 0.05	0.331	0.06 ± 0.05	0.076	-0.01 ± 0.05
CH								
15m	1.000	0.67 ± 0.12	0.817	0.26 ± 0.13	0.198	0.04 ± 0.13	0.45	0.08 ± 0.13
5m	1.000	0.45 ± 0.08	0.825	0.22 ± 0.08	0.214	0.04 ± 0.07	0.726	0.16 ± 0.07
1m	0.529	0.19 ± 0.05	0.406	0.19 ± 0.05	0.303	0.07 ± 0.05	0.168	0.08 ± 0.05
SM								
15m	1.000	0.62 ± 0.09	1.000	0.62 ± 0.10	1.000	0.40 ± 0.10	1.000	0.44 ± 0.10
5m	1.000	0.40 ± 0.08	1.000	0.73 ± 0.10	0.996	0.38 ± 0.08	0.939	0.32 ± 0.07
1m	0.093	0.08 ± 0.05	0.88	0.29 ± 0.06	0.074	0.07 ± 0.05	**0.019**	$\mathbf{0.02 \pm 0.05}$
SN								
15m	0.996	0.40 ± 0.12	1.000	0.52 ± 0.11	0.934	0.29 ± 0.11	0.669	0.15 ± 0.13
5m	0.917	0.20 ± 0.07	1.000	0.34 ± 0.06	0.577	0.14 ± 0.06	0.93	0.21 ± 0.07
1m	**0.014**	$\mathbf{0.02 \pm 0.04}$	0.907	0.16 ± 0.05	0.066	0.05 ± 0.04	0.336	0.08 ± 0.05

Table B.3. Trait values and occurrence in 15 m × 15 m plots and land units of all annual species. Seed mass measurements adopted from Osem *et al.* (2006) are marked with an asterisk (*). The species are sorted after occurrence in one, two or three land units. For the species occurrence in land units the following abbreviations are used: D – Dvir, L – Lachish, G – Galon. Nomenclature follows Euro+Med (2012). Trait abbreviations: SLA – specific leaf area, CH – canopy height, SRH – seed release height, SM – seed mass, SN – seed number.

Species	**Trait values and units**					**Species occurrence**			
						# Plots 15m × 15m			**Land units**
	SLA $\left[\frac{\mathbf{mm^2}}{\mathbf{mg}}\right]$	**CH** [cm]	**SRH** [cm]	**SM** [mg]	**SN**	**D**	**L**	**G**	
Carrichtera annua	18.8	7.2	9.9	0.92	667	4	0	0	D
Plantago weldenii	14.6	3.7	0.8	0.26	98	3	0	0	D
Schismus arabicus	23.6	7.8	11.3	NA	NA	6	0	0	D
Asphodelus fistulosus s.l.	16.7	7.8	22.2	1.4	83	0	1	0	L
Scandix iberica	25.8	7.4	12.6	5.76	25	0	6	0	L
Asteriscus aquaticus	26.0	20.1	20.1	1.42	308	0	0	3	G
Avena barbata subsp. barbata	22.8	34.6	53.6	5.01	5	0	0	2	G
Centaurea verutum	23.6	54.1	57.9	NA	570	0	0	5	G
Centaurium tenuiflorum	39.6	15.2	16.3	NA	NA	0	0	9	G
Convolvulus pentapetaloides	26.9	15.0	13.5	4.79	22	0	0	17	G
Galium divaricatum	NA	8.2	8.5	0.095	281	0	0	3	G
Lathyrus ochrus	22.8	46.8	41.8	113.2	13	0	0	4	G
Linum corymbulosum	23.1	18.2	19.4	0.21	151	0	0	14	G
Linum nodiflorum	22.4	21.8	21.6	NA	183	0	0	1	G
Ononis alopecuroides	27.8	24.3	30.9	7.57	399	0	0	12	G
Ononis hirta	33.9	21.9	21.8	2.98	234	0	0	8	G
Ononis mitissima	18.5	29.2	29.2	3.31	553	0	0	9	G
Phalaris paradoxa	38.1	33.1	38.1	NA	NA	0	0	8	G
Polygala monspeliaca	21.5	6.2	16.7	0.76	55	0	0	9	G
Stachys neurocalycina	20.6	11.7	11.5	0.93	366	0	0	3	G
Trifolium alexandrinum	22.2	21.8	24.7	1.21	NA	0	0	22	G

Table B.3. Continued.

Species	SLA	CH	SRH	SM	SN	D	L	G	Land units
Trifolium cherleri	17.2	8.2	8.4	2.94	13	0	0	7	G
Ziziphora capitata	14.7	5.0	4.7	0.26	41	0	0	5	G
Adonis dentata	18.4	7.5	8.7	2.0	109	16	16	0	D, L
Astragalus callichrous	23.3	6.0	7.8	1.08	411	2	5	0	D, L
Erodium ciconium	14.1	7.3	15.9	17.28	64	3	5	0	D, L
Medicago hypogea	16.1	1.2	-1.5	7.48	5	3	24	0	D, L
Plantago ovata	10.6	5.3	5.1	1.38	120	2	1	0	D, L
Sedum microcarpum	18.4	4.2	4.2	0.145	85	3	3	0	D, L
Velezia rigida	23.1	8.6	9.3	0.27	101	1	0	2	D, G
Asterolinon linum-stellatum	36.7	4.2	3.5	0.28	52	0	3	1	L, G
Centaurea crocodylium	12.2	24.5	34.5	NA	149	0	4	7	L, G
Cichorium pumilum	25.8	35.9	39.8	0.89	NA	0	1	2	L, G
Euphorbia arguta	25.4	27.1	27.1	2.22	157	0	5	3	L, G
Linaria micrantha	26.5	13.4	22.4	0.102	477	0	1	4	L, G
Linum pubescens	34.8	21.4	21.8	NA	154	0	3	7	L, G
Lomelosia prolifera	22.3	21.0	18.8	7.24	34	0	5	15	L, G
Medicago scutellata	21.0	21.4	16.8	13.43	26	0	7	11	L, G
Nigella nigellastrum	17.5	17.8	24.7	3.190	40	0	12	6	L, G
Phalaris brachystachys	26.7	40.2	49.0	NA	NA	0	1	9	L, G
Picris galilaea	20.5	16.4	22.1	0.650	240	0	1	12	L, G
Pisum fulvum	NA	50.9	48.5	NA	NA	0	6	2	L, G
Rapistrum rugosum	17.3	28.4	76.8	1.420	373	0	2	25	L, G
Reichardia intermedia	35.4	8.6	26.5	0.610	281	0	11	2	L, G
Tordylium aegyptiacum	19.5	19.5	22.7	4.210	65	0	1	5	L, G
Tordylium trachycarpum	20.1	32.3	44.8	0.29	379	0	5	15	L, G
Trifolium eriosphaerum	21.5	13.2	13.1	2.400	12	0	1	3	L, G
Tripodion tetraphyllum	14.3	6.5	5.8	13.39	26	0	9	5	L, G
Aegilops peregrina	22.3	15.8	20.3	8.780	21	3	2	10	D, L, G
Ammi majus	17.8	65.9	72.2	NA	9145	3	4	1	D, L, G
Anagallis arvensis	32.6	11.2	9.7	0.310	507	25	29	23	D, L, G
Anisantha fasciculata	24.6	11.3	18.1	1.02*	NA	17	16	15	D, L, G
Anisantha madritensis	33.3	25.7	32.2	NA	NA	10	18	13	D, L, G
Artedia squamata	11.7	38.1	46.6	NA	390	4	3	13	D, L, G
Astragalus asterias	17.3	5.4	4.3	1.400	NA	5	6	1	D, L, G
Atracylis cancellata	10.7	8.0	8.0	NA	NA	8	1	5	D, L, G

Table B.3. Continued.

Species	SLA	CH	SRH	SM	SN	D	L	G	Land units
Avena sterilis subsp. sterilis	21.4	33.4	50.4	9.050	25	26	29	25	D, L, G
Biscutella didyma	13.6	12.2	18.0	0.68*	27	21	28	20	D, L, G
Bromus alopecuros caroli-henrici	30.9	25.0	39.3	NA	NA	2	4	9	D, L, G
Bromus japonicus	25.3	15.9	19.3	NA	NA	1	1	3	D, L, G
Bromus lanceolatus	28.5	27.3	39.0	1.750	15	12	13	20	D, L, G
Bromus scoparius	21.9	16.4	22.7	NA	NA	1	12	17	D, L, G
Calendula arvensis	23.7	19.0	20.6	1.15*	1339	24	15	6	D, L, G
Campanula erinus	32.0	7.9	9.5	0.013	1792	5	7	5	D, L, G
Catananche lutea	27.7	16.4	27.8	2.14*	NA	5	8	15	D, L, G
Centaurea hyalolepis	19.1	30.2	33.5	NA	639	6	10	4	D, L, G
Crassula alata	27.1	2.0	2.0	0.008	121	10	20	1	D, L, G
Crepis sancta	28.7	3.0	11.8	0.09*	NA	10	22	10	D, L, G
Crupina crupinastrum	10.4	11.3	30.8	19.010	39	16	24	10	D, L, G
Diplotaxis erucoides	23.2	12.9	28.9	0.165	2256	18	5	6	D, L, G
Erodium gruinum	22.0	14.0	27.6	29.84	43	26	26	16	D, L, G
Erodium malacoides	21.1	7.8	11.0	1.12	437	14	21	23	D, L, G
Erodium moschatum	28.3	7.8	10.2	0.52	575	3	1	2	D, L, G
Erucaria hispanica	16.8	20.4	44.3	0.37	1439	22	26	6	D, L, G
Euphorbia chamaepeplus	23.8	4.0	4.0	0.28	59	22	28	9	D, L, G
Euphorbia exigua	24.4	6.0	6.0	NA	NA	5	7	12	D, L, G
Euphorbia oxyodonta	26.1	10.0	10.0	2.390	78	15	27	11	D, L, G
Filago contracta	17.1	2.8	1.2	0.153	437	11	8	1	D, L, G
Filago palaestina	26.8	1.1	0.7	0.1*	351	16	10	6	D, L, G
Filago pyramidata	28.3	9.8	9.8	NA	725	22	28	16	D, L, G
Galium judaicum	30.3	8.5	8.9	0.111	NA	2	14	13	D, L, G
Galium setaceum subsp. decaisnei	15.4	8.6	8.6	0.094	83	1	2	3	D, L, G
Geropogon hybridus	21.3	30.0	34.2	8.370	182	2	21	24	D, L, G
Hedypnois rhagadioloides	33.9	8.1	12.8	0.590	223	22	27	9	D, L, G
Helianthemum aegyptiacum	11.6	8.3	10.7	1.450	190	4	15	5	D, L, G
Helianthemum lasiocarpum	13.1	16.9	17.3	0.350	838	18	26	9	D, L, G

Table B.3. Continued.

Species	**SLA**	**CH**	**SRH**	**SM**	**SN**	**D**	**L**	**G**	**Land units**
Helianthemum ledifolium	13.1	20.9	21.1	0.440	1369	6	18	5	D, L, G
Helianthemum salicifolium	16.9	14.1	22.3	NA	3027	18	29	12	D, L, G
Hippocrepis unisiliquosa	13.8	7.7	6.3	1.8*	NA	22	29	10	D, L, G
Hirschfeldia incana	22.0	30.4	54.8	0.280	604	1	9	7	D, L, G
Hordeum vulgare subsp. spontaneum	24.4	46.5	57.6	14.6*	NA	12	26	15	D, L, G
Isatis lusitanica	18.6	23.8	33.9	2.690	70	4	10	4	D, L, G
Lagoecia cuminoides	29.9	21.0	22.0	0.320	300	22	18	20	D, L, G
Lathyrus hierosolymitanus	19.2	53.4	49.2	32.900	96	8	20	21	D, L, G
Linaria albifrons	16.7	8.2	10.4	0.135	923	7	2	6	D, L, G
Linum strictum	15.3	24.1	24.2	0.21*	203	25	29	23	D, L, G
Lolium rigidum	26.2	20.6	41.1	1.050	37	5	4	14	D, L, G
Lophochloa cristata	NA	6.4	11.3	NA	NA	15	26	12	D, L, G
Lotus peregrinus	16.3	8.5	7.5	1.910	156	23	28	23	D, L, G
Medicago coronata	20.7	13.0	13.1	0.570	NA	21	29	18	D, L, G
Medicago monspeliaca	18.7	16.4	14.0	0.710	273	19	29	15	D, L, G
Medicago orbicularis	24.5	15.8	13.1	6.040	66	5	16	12	D, L, G
Medicago polymorpha	31.9	15.7	14.2	2.550	70	6	11	19	D, L, G
Medicago rotata	18.9	22.1	21.5	7.390	164	3	13	13	D, L, G
Medicago truncatula	19.8	13.1	11.3	4.420	32	5	1	4	D, L, G
Mercurialis annua	29.2	15.0	14.6	1.980	70	3	5	9	D, L, G
Nigella ciliaris	21.9	32.8	35.8	3.960	89	3	12	20	D, L, G
Onobrychis caput-galli	13.1	17.6	20.6	24.660	14	1	2	15	D, L, G
Onobrychis crista-galli	12.4	10.4	12.0	12.080	11	25	25	7	D, L, G
Onobrychis squarrosa	17.5	14.5	14.7	11.650	7	5	28	21	D, L, G
Ononis ornithopodioides	17.3	13.7	12.3	1.760	108	11	7	10	D, L, G
Ononis viscosa subsp. breviflora	22.5	27.0	25.2	2.540	505	9	17	17	D, L, G
Ononis viscosa subsp. sicula	18.8	10.0	10.7	1.240	514	16	20	3	D, L, G
Plantago afra	15.5	8.4	9.6	0.700	328	23	29	21	D, L, G
Plantago cretica	21.7	6.3	2.0	1.080	27	13	13	13	D, L, G
Plantago lagopus	21.3	7.2	19.2	0.192	289	1	6	10	D, L, G

Table B.3. Continued.

Species	**SLA**	**CH**	**SRH**	**SM**	**SN**	**D**	**L**	**G**	**Land units**
Pterocephalus brevis	18.5	13.4	23.0	0.510	259	26	29	15	D, L, G
Rhagadiolus stellatus	28.6	7.1	11.7	1.150	111	13	20	12	D, L, G
Scorpiurus muricatus	13.1	4.8	3.5	NA	NA	8	11	12	D, L, G
Sedum pallidum	19.5	1.7	2.1	0.032	233	12	25	9	D, L, G
Silybum marianum	13.7	50.9	60.8	26.79	NA	2	2	14	D, L, G
Sinapis alba	23.0	28.7	63.4	4.48	290	4	20	6	D, L, G
Sinapis arvensis	20.8	34.5	54.3	1.630	453	1	16	14	D, L, G
Sonchus oleraceus	NA	NA	NA	NA	NA	5	23	24	D, L, G
Stipa capensis	19.7	21.5	32.1	2.04	33	26	29	12	D, L, G
Theligonum cynocrambe	20.5	5.0	4.5	2.310	NA	7	22	14	D, L, G
Thesium humile	8.8	18.0	18.0	4.27	510	14	15	13	D, L, G
Torilis tenella	16.4	13.9	16.9	0.67	138	26	28	23	D, L, G
Torilis trichosperma	22.2	9.5	12.1	0.700	313	8	10	15	D, L, G
Trachynia distachyia	21.7	15.2	23.2	3.5*	NA	11	17	23	D, L, G
Trifolium campestre	28.0	16.0	16.4	0.25	596	13	29	25	D, L, G
Trifolium dasyurum	20.1	17.4	19.9	3.76	121	20	28	13	D, L, G
Trifolium purpureum	21.6	24.0	25.7	1.03	231	2	16	24	D, L, G
Trifolium scabrum	16.2	7.1	7.2	0.850	50	1	4	9	D, L, G
Trifolium tomentosum	21.0	10.0	10.2	0.67*	NA	3	9	8	D, L, G
Urospermum picroides	34.9	31.8	41.7	1.32	531	23	29	23	D, L, G
Valerianella vesicaria	35.2	5.7	6.4	1.63	8	1	2	3	D, L, G
Vicia narbonensis	20.6	19.6	14.6	90.34	16	1	2	8	D, L, G

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Declaration

This cumulative dissertation comprises three scientific studies (chapters 2 – 4), which were prepared as independent manuscripts and are published (chapters 2 and 3) or are in review (chapter 4) in international peer-reviewed journals. As I prepared the manuscripts in cooperation with my co-authors, they are written in first person plural. Due to the independent preparation of the manuscripts, especially the studies based on field data overlap in the description of the study area and the data collection (chapters 3 and 4). All three articles include suggestions of referees and journal editors as outcomes of the peer-review process.

As the leading author of all manuscripts, I developed the concept of the studies, implemented the models, conducted the analysis and wrote the text for all chapters. When I used published or unpublished data or methods, or when I cited statements and results provided by others, it is indicated by appropriate references in the text. I took part in the sampling of plant functional traits that provides the basis for chapter 4. All co-authors provided feedback on the concept of the studies and for the revision of the manuscripts. My co-authors Itamar Giladi and Michael Ristow guided and conducted the field work that provided the data for chapters 3 and 4.

Felix May (PhD candidate)

Prof. Florian Jeltsch (supervisor)