Trait-based understanding of plant species distributions along environmental gradients

Ph.D. Thesis

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Cover picture: Typical landscape of the Southern Judean Lowlands in Israel, which harbors more than 200 annual plant species. These communities feature a remarkable diversity in ecological strategies as exemplarily shown by seeds of four annuals: *Crupina crupinastrum* (top-left), *Lomelosia prolifera* (top right), *Erodium ciconium* (botton left), *Geropogon hybridus* (bottom right). *C. crupinastrum* and *G. hybridus* were particularly investigated in chapter III.

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Summary

For more than two centuries, plant ecologists have aimed to understand how environmental gradients and biotic interactions shape the distribution and co-occurrence of plant species. In recent years, functional trait–based approaches have been increasingly used to predict patterns of species co-occurrence and species distributions along environmental gradients (trait–environment relationships). Functional traits are measurable properties at the individual level that correlate well with important processes. Thus, they allow us to identify general patterns by synthesizing studies across specific taxonomic compositions, thereby fostering our understanding of the underlying processes of species assembly. However, the importance of specific processes have been shown to be highly dependent on the spatial scale under consideration. In particular, it remains uncertain which mechanisms drive species assembly and allow for plant species coexistence at smaller, more local spatial scales. Furthermore, there is still no consensus on how particular environmental gradients affect the trait composition of plant communities. For example, increasing drought because of climate change is predicted to be a main threat to plant diversity, although it remains unclear which traits of species respond to increasing aridity. Similarly, there is conflicting evidence of how soil fertilization affects the traits related to establishment ability (e.g., seed mass). In this cumulative dissertation, I present three empirical trait-based studies that investigate specific research questions in order to improve our understanding of species distributions along environmental gradients.

In the first case study, I analyze how annual species assemble at the local scale and how environmental heterogeneity affects different facets of biodiversity—i.e. taxonomic, functional, and phylogenetic diversity—at different spatial scales. The study was conducted in a semi-arid environment at the transition zone between desert and Mediterranean ecosystems that features a sharp precipitation gradient (Israel). Different null model analyses revealed strong support for environmentally driven species assembly at the local scale, since species with similar traits tended to co-occur and shared high abundances within microsites (trait convergence). A phylogenetic approach, which assumes that closely related species are functionally more similar to each other than distantly related ones, partly supported these results. However, I observed that species abundances within microsites were, surprisingly, more evenly distributed across the phylogenetic tree than expected (phylogenetic overdispersion). Furthermore, I showed that environmental heterogeneity has a positive effect on diversity, which was higher on functional than on taxonomic diversity and increased with spatial scale. The results of this case study indicate that environmental heterogeneity may act as a stabilizing factor to maintain species diversity at local scales, since it influenced species distribution according to their traits and positively influenced diversity. All results were constant along the precipitation gradient.

In the second case study (same study system as case study one), I explore the trait responses of two Mediterranean annuals (*Geropogon hybridus* and *Crupina crupinastrum*) along a precipitation gradient that is comparable to the maximum changes in precipitation predicted to occur by the end of this century (i.e., −30%). The heterocarpic *G. hybridus* showed strong trends in seed traits, suggesting that dispersal ability increased with aridity. By contrast, the homocarpic *C. crupinastrum* showed only a decrease in plant height as aridity increased, while leaf traits of both species showed no consistent pattern along the precipitation gradient. Furthermore, variance decomposition of traits revealed that most of the trait variation observed in the study system was actually found within populations. I conclude that trait responses towards aridity are highly species-specific and that the amount of precipitation is not the most striking environmental factor at this particular scale.

In the third case study, I assess how soil fertilization mediates—directly by increased nutrient addition and indirectly by increased competition—the effect of seed mass on establishment ability. For this experiment, I used 22 species differing in seed mass from dry grasslands in northeastern Germany and analyzed the interacting effects of seed mass with nutrient availability and competition on four key components of seedling establishment: seedling emergence, time of seedling emergence, seedling survival, and seedling growth. (Time of) seedling emergence was not affected by seed mass. However, I observed that the positive effect of seed mass on seedling survival is lowered under conditions of high nutrient availability, whereas the positive effect of seed mass on seedling growth was only reduced by competition. Based on these findings, I developed a conceptual model of how seed mass should change along a soil fertility gradient in order to reconcile conflicting findings from the literature. In this model, seed mass shows a U-shaped pattern along the soil fertility gradient as a result of changing nutrient availability and competition.

Overall, the three case studies highlight the role of environmental factors on species distribution and co-occurrence. Moreover, the findings of this thesis indicate that spatial heterogeneity at local scales may act as a stabilizing factor that allows species with different traits to coexist. In the concluding discussion, I critically debate intraspecific trait variability in plant community ecology, the use of phylogenetic relationships and easily measured key functional traits as a proxy for species' niches. Finally, I offer my outlook for the future of functional plant community research.

Zusammenfassung

Seit über 200 Jahren erforschen Ökologinnen und Ökologen den Einfluss von Umweltgradienten, biotischen Interaktionen und zufälligen Prozessen auf die Artenzusammensetzung von Pflanzengemeinschaften. Um generelle Muster und die zugrundeliegenden Mechanismen unabhängig von der gegeben Artenzusammensetzung besser zu verstehen, wurden vermehrt funktionelle Eigenschaften (‚*functional traits*') als methodischer Ansatz genutzt. In den vergangenen Jahren wurde deutlich, dass die Faktoren, die die Artenzusammensetzung bestimmen, abhängig von der betrachteten räumlichen Skala sind. Es bleibt jedoch unklar, inwieweit Umweltheterogenität auf kleiner, lokaler Skala die Artenzusammensetzung beeinflusst. Des Weiteren ist Skalenabhängigkeit wichtig, um den Einfluss von spezifischen Umweltgradienten, wie Trockenheit oder Bodenfertilität, auf die funktionellen Eigenschaften von Pflanzengemeinschaften zu ermitteln. In der vorliegenden Dissertation beschäftige ich mich in drei unabhängigen, empirischen Studien mit dem Einfluss von Umweltgradienten bzw. Umweltheterogenität auf die funktionellen Eigenschaften von Pflanzengemeinschaften unter besonderer Berücksichtigung der Skalenabhängigkeit.

In der ersten Fallstudie untersuche ich, welche Faktoren die Artenzusammensetzung in einem semi-ariden Ökosystem auf lokaler Skala bestimmen. Das Untersuchungsgebiet befindet sich entlang eines starken Niederschlagsgradienten in Israel (*Southern Judean Lowlands*) und wird von einjährigen Pflanzen dominiert. Mit Hilfe von Nullmodellen, analysiere ich die Artenzusammensetzung in Mikrohabitaten (0.06 m² und 1 m²) hinsichtlich ihrer funktionellen Eigenschaften sowie ihrer Phylogenie. Der phylogenetische Ansatz nimmt dabei an, dass nahverwandte Arten ähnliche Nischen besetzen. Ich kann zeigen, dass innerhalb der lokalen Skala (15 m × 15m) die die Artenzusammensetzung nicht zufällig ist, da vor allem Arten mit ähnlichen funktionellen Eigenschaften zusammen in Mikrohabitaten auftreten. Ebenso besitzen Arten mit einer hohen Stetigkeit innerhalb der Mikrohabitate ähnliche funktionelle Eigenschaften. Beide Ergebnisse deuten auf eine Selektion durch Umweltfaktoren hin und verdeutlichen deren Einfluss auch auf kleiner räumlicher Skala. Der phylogenetische Ansatz konnte teilweise diese Ergebnisse unterstützen. Jedoch zeigte die phylogenetische Analyse auch, dass Nischendifferenzierung ein wichtiger Mechanismus für die Artenzusammensetzung innerhalb der Mikrohabitate sein kann. Des Weiteren untersuche ich in dieser Studie den Effekt von lokaler Umweltheterogenität auf die Diversität der Pflanzengemeinschaften auf verschiedenen räumlichen Skalen und Ebenen (funktionelle, phylogenetische und Artendiversität). Ich kann unter anderem zeigen, dass mit Zunahme der räumlichen Skala der positive Effekt von Umweltheterogenität auf die verschiedenen

Ebenen der Diversität ansteigt. Umweltheterogenität wirkt dabei stärkerauf die funktionelle Diversität als auf die Artendiversität. Aus den Ergebnissen dieser Studie folgere ich, dass lokale Umweltheterogenität ein wichtiger Faktor für die Koexistenz in diesen Pflanzengemeinschaften ist. Im selben Untersuchungsgebiet, analysiere ich in der zweiten Studie die Anpassung von mediterranen Pflanzenarten an die Umweltverhältnisse entlang des Niederschlagsgradienten. Dieser Gradient entspricht den vorausgesagten Niederschlagsveränderungen bis zum Ende dieses Jahrhunderts (eine Verringerung von ca. 30%). Dafür wurden funktionelle Eigenschaften von zwei typischen mediterranen Arten in 16 Populationen gemessen. Die untersuchten Arten, *Geropogon hybridus* und *Crupina crupinastrum*, gehören zur Pflanzenfamilie der *Asteraceae* und haben sehr ähnliche Habitatansprüche. Überraschenderweise zeigten die Arten jedoch unterschiedliche Anpassungen entlang des Gradienten. Während *G. hybridus* starke Anpassungen in generativen Merkmalen entlang des Niederschlagsgradienten zeigte, wurde bei *C. crupinastrum* lediglich eine kleinere Pflanzenhöhe mit Zunahme der Trockenheit festgestellt. Des Weiteren wird in der Studie deutlich, dass der Niederschlagsgradient zwar ein wichtiger, aber kein bestimmender Faktor auf der entsprechenden Skala ist, da ein großer Anteil der intraspezifischen Merkmalsvariation innerhalb der Populationen gefunden wird. Die Ergebnisse der Studie deuten darauf hin, dass die vorhergesagte Abnahme des Niederschlags nur einen geringen Einfluss auf das Überleben der untersuchten Pflanzenarten hat.

In der dritten Studie untersuche ich inwieweit Bodenfruchtbarkeit den Etablierungserfolg von Pflanzen mit unterschiedlichen Samengewichten beeinflusst. Da Bodenfruchtbarkeit zum einen direkt durch erhöhte Nährstoffverfügbarkeit und zum anderen indirekt durch erhöhte Konkurrenz die Etablierung beeinflusst, wurde ein Experiment mit vollfaktoriellem Versuchsaufbau durchgeführt. Hierzu wurden Samen von 22 Pflanzenarten aus Trockenrasen Nordost-Brandenburgs ausgewählt, die sich hinsichtlich ihrer Samengewichte unterschieden, und der Etablierungserfolg der Keimlinge anhand von vier Parametern quantifiziert: Keimung (ja/nein), Keimungszeitpunkt, Überleben und Wachstum. Das Samengewicht hatte keinen Effekt auf die Keimung und den Keimungszeitpunkt. Jedoch zeigte sich, dass sich der positive Effekt des Samengewichts auf die Überlebenswahrscheinlichkeit stärker unter nährstoffarmen Bedingungen war. Weiterhin zeigte sich, dass der positive Samengewicht-Effekt auf das Wachstum stärker unter Konkurrenz war, jedoch unabhängig von der Nährstoffverfügbarkeit. Diese Ergebnisse verdeutlichen die Komplexität des Zusammenspiels von funktionellen Merkmalen mit der Umwelt, da verschiedene Prozesse beeinflusst werden. Auf der Basis der Ergebnisse dieser Studie und Literatur, stelle ich ein konzeptionelles Model vor, dass eine U-förmige Beziehung zwischen Bodenfruchtbarkeit und Samengewicht in Pflanzengemeinschaften postuliert und somit widersprüchliche Ergebnisse aus der Literatur synthetisiert.

Zusammengenommen zeigen die Ergebnisse meiner empirischen Untersuchungen, dass funktionelle Eigenschaften wichtige Erkenntnisse über die Prozesse liefern, die das Auftreten von

Pflanzen und deren Anpassung entlang von Umweltgradienten bestimmen. In der abschließenden Diskussion beleuchte ich kritisch die Verwendung von intraspezifischer Variabilität funktioneller Eigenschaften in der Gemeinschaftsökologie, die Phylogenie als Surrogat für die Nische einer Art und die Standardisierung funktioneller Eigenschaften als methodische Aspekte. Abschließend gebe ich einen Ausblick über zukünftige Pflanzenökologie-Forschung mit funktionellen Eigenschaften.

Chapter I

General Introduction

1.1 What determines the distribution and co-occurrence of plant species?

For more than two centuries, ecologists have sought to identify the mechanisms that drive the distributions of plant species and patterns of species co-occurrence. The early naturalist Alexander von Humboldt (1807) made detailed observations of how climate affects the distribution of species and specific growth types. During his extensive journey through South America, he noticed, for example, that plants from tropical alpine regions and polar regions have the same morphological characteristics (von Humboldt 1807). Based on this, Griesebach (1872) developed the first global vegetation map with respect to climatic factors. Additionally, Schimper (1898) described plant distributions based on ecophysiology; in particular, he summarized how specific environmental factors, such as water availability, temperature and soil conditions, affect the morphology of plants. While these early works were mainly descriptive, Clements (1916) and Gleason (1926) developed individual theories of how plant species assemble at a given site and form plant communities. These theories resulted in contrasting perspectives. Clements (1906) emphasized the importance of positive interactions among plants and referred to plant communities as ‘superorganisms,’ whereas Gleason (1926) predicted in his ‘individualistic concept’ model that species distributions are driven by the species’ tolerance to specific environmental factors, as well as chance. However, both Clements and Gleason underlined the great importance of environmental conditions for plant communities. To illustrate the selective effects of environmental conditions on species distributions, Mueller-Dombois and Ellenberg (1974) introduced the concept of ‘environmental filters’, in which species from a given species pool must pass a series of environmental filters to successfully establish in a local community. Van der Valk (1981) argued that the process of environmental filtering should lead to a restriction of ecological strategies in the community compared with the pool of possible species, as the environment selects for species with similar characteristics. The concept of environmental filtering was adapted and further developed by various researchers and remains at the heart of modern coexistence and community assembly theory (Keddy 1992, Cornwell and Ackerly 2009, Jung *et al. 2*010, Laughlin *et al. 2*012, HilleRisLambers *et al. 2*012, Kraft *et al. 2*015, Cadotte and Tucker 2017, Thakur and Wright *et al. 2*017). However, our knowledge of how specific environmental conditions select plant species is still limited (e.g., Weiher *et al. 2*011, Laughlin *et al. 2*018, Moles 2018).

Environmental conditions and interactions with other species may work in concert to determine the co-occurrence of species. In his seminal work, On the Origin of Species, Darwin (1859) predicted that the ‘struggle for existence’ (or competition) between closely related species is more intense than that between distantly related species (see also Violle *et al. 2*011). He based his hypothesis on the fact that closely related species have the same ancestor and thus the descendants should have very similar requirements. Later, Gause (1932) formulated the principle of competitive exclusion, which predicts that if two species compete for the same resource, one will be outcompeted by the other (under constant environmental conditions). Therefore, co-occurring species should have different requirements or, in other terms, exploit different ecological niches to avoid interspecific competition. As a result, MacArthur and Levine (1967) predicted that there is a limit to similarity ('limiting similarity') between co-existing species in a community. Although some plant studies have found evidence for limiting similarity and niche differentiation in plant communities (e.g., Stubbs and Wilson 2004, Silvertown 2005, Kraft *et al. 2*008, Götzenberger *et al.* 2012 de Bello *et al. 2*015) it is often doubted that limiting similarity plays an important role in plant communities. For example, Adler *et al.* (2013) showed that the detection of limiting similarity may actually be the result of small-scale environmental filtering. Finally, Levine and Mayfield (2010) argued in a theoretical paper that competition may also lead to a restriction of niches in plant communities, which contrasts with the classical view of limiting similarity. Hence, it remains surprisingly unclear how competition affects species composition in communities, despite a long history of research.

In 2001, Hubbell proposed his unified neutral theory, which assumes that community assembly is purely driven by stochastic events (see also Bell 2001). This theory contrasts with the classical view that niche-based processes—i.e., environmental conditions and biotic interactions—structure the species composition of plant communities by selecting for species with specific characteristics. The theory postulates that all species have equivalent per capita growth, birth, and mortality rates, while speciation and dispersal are random. It should also be noted that earlier theories assumed species equivalence (e.g., the equilibrium theory of island biogeography: MacArthur and Wilson 1967) and the importance of stochastic dispersal events (e.g., Gleason 1926, MacArthur and Wilson 1967). However, the simplicity of the unified neutral theory challenged the classical view of ecologists and initiated a debate on whether neutral processes, such as random dispersal or niche-based processes, control species assembly and diversity (McGill 2003, Chase and Leibold 2003, Hubbel 2005, Kraft *et al. 2*007, Chase 2014, Garzon-Lopez *et al. 2*014, May *et al. 2*016, Wiegand *et al. 2*017).

In summary, the underlying mechanisms of species distribution, co-occurrence, and coexistence, as well as their importance are not understood at all. A central question is whether there are 'general laws' and 'assembly rules' that allow precise prediction of species compositions in plant communities (Keddy 1992, Lawton 1998, McGill *et al. 2*006). In this thesis, I aim to extend our knowledge of how different processes shape plant communities by using functional traits with a particular focus on how scale-dependency influences the observed pattern.

1.2 Functional trait approach

Functional traits have been highlighted as suitable tools to identify patterns of community assembly and mechanisms that shape biodiversity (McGill *et al.* 2006, Kraft *et al.* 2008, Violle *et al.* 2012, Perronne *et al.* 2017). Functional traits are measurable properties at the individual level that correlate well with an organism's performance; i.e., establishment, reproduction, dispersal ability, and persistence (Weiher *et al.* 2011). The usage of functional traits has two main advantages: (1) patterns of functional traits may help elucidate underlying mechanisms because specific traits correlate with important processes such as seedling establishment or competitive ability for light (e.g., Westoby 1998, Westoby *et al.* 2002, Weiher *et al.* 1999); and (2) the results of different studies can be compared irrespective of their specific taxonomic composition and synthesized to identify general patterns (McGill *et al.* 2006, Moles *et al.* 2007, Sandel *et al.* 2010, Diaz *et al.* 2016, La Bagousse-Pinguet *et al.* 2017).

Key functional traits

Several studies have suggested 'key functional traits' of plants that are relatively easy to measure and correlate well with the most important processes in the lifecycles of plants (Grime *et al.* 1997, Weiher *et al.* 1999, Westoby 1998, Westoby *et al.* 2002, Perez- Harguindeguy *et al.* 2012). Probably the most puristic plant functional concept is the Leaf–Height–Seed scheme by Westoby (1998). Based on Grime's CSR triangle (Grime 1974, 1977), which postulates trade-offs between competitive ability, stress tolerance and ruderality, Westoby (1998) uses three functional traits (plant height, specific leaf area and seed mass) to characterize the ecological strategies of plants. Plant height correlates with the competitive ability for light because large plants receive disproportionally more light than small plants. Furthermore, it was recently shown that plant height negatively correlates with the ability to cope with disturbance (Moles 2018). Specific leaf area (leaf area/dry leaf weight) is a reliable predictor of relative growth rate and photosynthetic capacity in plants (Westoby *et al.* 2002, Moles 2018). Therefore, it should correlate with stress tolerance (small specific leaf area) and competitive ability (high specific leaf area) (Westoby 1998). Seed mass is related to the regeneration strategies of plants. Although it is one of the best researched plant traits, its relationship to environmental factors remains unclear. Salisbury (1942) observed that, on average, mean seed mass for a species is higher in shady habitats than in open habitats. Since then, many empirical studies have shown that seed mass is beneficial during the establishment phase due to the additional resources (e.g., Westoby *et al.* 2002). However, seed mass comes at the expense of seed number, as the resources of the mother plant are finite (seed mass–seed number trade-off; e.g., Jacobsson and Eriksson 2000). Therefore, seed mass is the trade-off between stress tolerance (high seed mass) and dispersal ability (low seed mass). Because such key functional traits characterize a species' niche in a simple, appropriate way, they may identify general rules for how environmental conditions and biotic interactions affect species compositions in plant communities.

Trait–environment relationships

Trait–environment relationships (i.e., how traits change along environmental gradients) are frequently analyzed to reveal the effects of environmental conditions on species distributions. In addition, trait–environment relationships may be helpful for predicting species compositions under environmental change (Diaz and Cabido 1997, Sandel *et al.* 2010). For example, in semi-arid environments, decreasing precipitation is expected to lead to dramatic shifts in plant species composition (Harrison *et al.* 2015, Knapp *et al.* 2015). In temperate ecosystems, anthropogenic fertilization of soils is a main driver of species loss and species composition, although the mechanisms are still poorly understood (Bobbink *et al.* 2010, Borer *et al.* 2014, Moles 2018).

The history of trait–environment relationships dates to Bergmann's rule. Bergmann (1847) observed that body size in endotherm species increases towards the poles, presumably because the lower surface area:volume ratio of larger bodies has lower energy costs in cold environments. In plant ecology, trait–environment relationships were mainly investigated at the community level using species mean trait values and calculating the average trait value of a community; i.e. community (weighted) mean traits (e.g., Diaz and Cabido 2001, Pakeman *et al.* 2008, Azcarate *et al.* 2010, May *et al.* 2013a). Some general trait–environment relationships have emerged in the past few years (reviewed in Moles 2018). For instance, increasing productivity due to water availability or soil fertility favors species with high specific leaf area and plant height (e.g., May *et al.* 2013a, Wright *et al.* 2004). However, the relationship between productivity and seed mass is less clear (Moles 2018). Since seed mass is particularly beneficial under harsh conditions, it is assumed that species with high seed mass dominate habitats with high-stress conditions, such as nutrient deficiency or drought (Muller-Landau 2010, Dainese *et al.* 2013, Nunes *et al.* 2017). However, productive environmental conditions are also associated with shade due to established plants, increased litter production, and increased competition among seedlings (Manning *et al.* 2009). Therefore, high seed mass may also be beneficial under productive conditions. Published findings have been inconsistent, including reports of positive (Grubb and Coomes 1997, Manning *et al.* 2009) and negative (Parolin 2000, Dainese and Sitzia 2013) relationships between seed mass and soil fertility, or none at all (Pakeman *et al.* 2008, Azcárate *et al.* 2010). One main problem is that nutrient availability in soils indirectly affects competition for light. Therefore, disentangling direct and indirect effects of soil fertility may help clarify how seedling establishment is mediated by seed mass.

Trait–environment relationships within species have been studied far less. Although it can be assumed that the same trait–environment relationship can be found within and among species, i.e., at the community level (Westoby 1998), several studies have shown that intraspecific responses along environmental gradients are much more complex (Albert *et al.* 2010, Cochrane *et al.* 2015). How species respond to decreasing precipitation in semi-arid environments remains particularly unclear. Unfortunately, most studies have included a very limited number of populations along precipitation gradients ($n < 5$, Kurze *et al.* 2017). However, mean values of trait among populations were recently shown to vary considerably with, but independent of, precipitation gradients (Kurze *et al.* 2017). Therefore, it is difficult to assess whether trait shifts observed in four or fewer populations can be attributed to the precipitation gradient. Because precipitation is predicted to decrease in semi-arid environments (IPCC 2013) and the plant communities found there are expected to be particularly vulnerable to increasing aridity (Harrison *et al.* 2015, Knapp *et al.* 2015), a comprehensive understanding of how plants respond to aridity in these regions is essential.

Trait- and phylogeny-based species assembly

Trait-based analyses can be used to disentangle the processes of species assembly; i.e., environmental filtering, biotic interactions, and neutral processes. While trait–environment relationships may serve as indications of environmental filtering, another body of literature is investigating how species assemble from a given species pool in local communities with respect to their traits (e.g. Weiher and Keddy 1992, Cornwell and Ackerly 2009, Peronne *et al.* 2017). These studies use null models to identify particular trait patterns of co-occurring species. Environmental filtering should restrict ecological strategies (see above), and therefore should result in more trait similarity compared with a randomly assembled species composition (trait convergence, Van der Valk 1981, Keddy 1992, Cornwell *et al.* 2006). Competition is assumed to cause trait divergence; i.e., co-occurring species have more trait dissimilarity compared with a randomly assembled species composition (MacArthur and Levine 1967, Stubbs and Wilson 2004). On the other hand, competition may also cause trait convergence if species with divergent traits are outcompeted (Mayfield and Levine 2010). The detection of particular trait patterns may therefore distinguish between neutral processes (random species assembly) and niche-based processes (trait convergence or divergence).

At the beginning of this century, Webb *et al.* (2002) introduced the idea of community phylogenetics (see also Webb 2000). The authors stated that the phylogenetic distance between species may serve as a proxy for the species' niche, based on Darwin's assumption that closely related species share similar requirements. Under this consideration, the phylogenetic relationships between co-occurring species may be used to infer processes of species assembly. Environmental filtering should then lead to phylogenetic clustering (i.e., closely related species tend to co-occur), whereas competition should lead to phylogenetic overdispersion (i.e., co-occurring species should be distantly related; but see Levine and Mayfield 2010). The application of phylogenetic relationships to infer processes of community assembly has received frequent criticism (Losos 2008, Cavender-Bares *et al.* 2009, Gerhold *et al.* 2015). Phylogenetic relationships may be a poor predictor for species niches because traits can either be phylogenetically conserved or divergent; i.e., closely related species have different traits (Cavender-Bares *et al.* 2004, Cavender-Bares *et al.* 2009). Additionally, different processes can result in the same phylogenetic patterns, which impedes the interpretation of observed patterns (Cavender-Bares *et al.* 2009, Gerhold *et al.* 2015). However, in combination with functional traits, phylogenetic analyses may assure that different niche dimensions are represented (Kraft and Ackerly 2010, de Bello *et al.* 2015).

1.3 Environmental heterogeneity and species diversity

Spatially patchy resource distribution (henceforth ‘environmental heterogeneity’) is considered to influence two properties of species composition. As outlined above, the distinct environmental conditions of a habitat may select for species with traits adapted to those conditions. Therefore, the qualitative species composition—i.e., which species are found in the community—should be the result of the particular habitat conditions. Additionally, environmental heterogeneity may also control quantitative species composition; i.e., how many species are found. Although both the qualitative and quantitative species compositions are entirely linked to each other, they are generally analyzed separately in the literature. With respect to quantitative species composition, MacArthur and MacArthur (1961) showed that heterogeneous habitats contain more (bird) species than homogeneous ones presumably because increasing environmental heterogeneity also increases the number of available niches. Although there is compelling evidence that environmental heterogeneity does positively affects species diversity (see Stein *et al.* 2014 for a review), the underlying mechanisms are still poorly understood (Lundholm 2009, Tamme *et al.* 2010, Stein *et al.* 2014). For instance, theoretical studies suggest that environmental heterogeneity should have a unimodal rather than positive effect on species diversity because high heterogeneity also entails habitat loss and fragmentation effects (Kadmon and Allouche 2007). Indeed, some empirical studies have confirmed that a unimodal relationship describes the observed species diversity–heterogeneity relationship better than a linear one (Allouche *et al.* 2012). However, empirical studies have focused mostly on the relationship between environmental heterogeneity and species diversity, and have thus far neglected functional traits (but see Price *et al.* 2017, Stark *et al.* 2017). Since environmental heterogeneity is assumed to increase the available niches, analyses of the relationship between environmental heterogeneity and functional trait diversity would provide valuable insights into the mechanisms that drive species diversity.

1.4 Scale-dependency in trait-based research

A central challenge in ecology is that observed patterns highly depend on the spatial scale under consideration. For instance, one of the main lessons from the intense debate over whether neutral or niche-based processes control species co-occurrence and diversity is that the importance of environmental filtering, biotic interaction, and neutral processes changes with spatial scale (Chase 2014). Modern theory of community assembly assumes that speciation, dispersal limitation, and chance play an important role at large spatial scales, while environmental filtering and competition act at finer scales (Götzenberger *et al.* 2012, HilleRisLambers *et al.* 2012). However, at very fine scales, the importance of stochastic dispersal events may increase further (Weiher *et al.* 2011, Chase 2014). As a result, community assembly studies have found that trait patterns change with the scale at which the species pool/community is defined (Kraft *et al.* 2010, de Bello *et al.* 2013). The same holds true for phylogenetic analyses (e.g., Swenson *et al.* 2007, Kraft and Ackerly 2010). Although Weiher *et al.* (2011) stated that "scaling of assembly is clearly an area that deserves increased attention," trait-based approaches often use a regional perspective and analyze how species assembled from a regional species pool (Cornwell and Ackerly 2009, Kraft and Ackerly 2010, Götzenberger *et al.* 2012, May *et al.* 2013a, but see Bernard-Verdier *et al.* 2012, de Bello *et al.* 2013). Hence, little is known about how species assemble at local scales. This is of particular interest in study systems that consist of isolated habitat islands with negligible regional processes like central European grasslands (Weiss *et al.* 2014) and Mediterranean grasslands (May *et al.* 2013b).

Similarly, there is mounting evidence that the relationship between environmental heterogeneity and species diversity depends on the spatial scale (Lundholm 2009, Tamme *et al.* 2010, Stein *et al.* 2014). Some studies have shown that the positive effect of heterogeneity increases with spatial scale (e.g., Lundholm 2009, Giladi *et al.* 2011). By contrast, at fine spatial scales, environmental heterogeneity may even have a negative effect due to micro-fragmentation and subsequent species loss (Tamme *et al.* 2013). Still, it remains unclear how the postulated unimodal relationship between heterogeneity and species diversity (and functional diversity) changes with spatial scale (Allouche *et al.* 2012).

Scale-dependency has received far less attention in studies of trait–environment relationships. For instance, surveying the literature on trait responses to aridity reveals that no study has explicitly justified its selection of a specific gradient amplitude (e.g. Aronson *et al. 1*992, Petrů *et al. 2*006, Dyer *et al. 2*016, Kurze *et al. 2*017). Most likely, the authors searched for the maximum amplitude in a specific region to increase the chance of detecting trait shifts along the gradient. High gradients are also claimed to reveal generality, while findings along lower gradients may be specific to a study system or the result may be even confounded by other factors. However, trait–environment relationships may be a good tool for predicting trait responses under environmental change (Sandel *et al. 2*010). For such cases, the amplitude of trait–environment relationships should match predicted changes to reveal whether environmental changes actually lead to trait shifts. On the other hand, even high gradients often only represent a subset of the whole global environmental gradient. Since the importance of biotic interactions and environmental filters changes along environmental gradients (Spasojevic and Suding 2012), trait–environment relationships may also differ depending on where the study is situated along the environmental gradient. Therefore, the inclusion of scale-dependency may resolve contradictory results among study sites.

1.5 Outline of this thesis

The overall aim of the thesis is to improve our understanding of how environmental gradients affect plant species distributions and patterns of co-occurrence based on functional traits. The following three chapters present empirical case studies investigating specific research questions that are currently in the research spotlight. Hence, these chapters are thematically stand-alone articles that can be read independently. All three studies are published in international, peer-reviewed journals and are written in first-person plural, since co-authors contributed to them. However, as I am the lead author of all chapters, the views expressed are mine.

Chapter II bridges two research approaches that investigate different questions: which and how many species are in a community; i.e., the qualitative and quantitative species compositions. I conducted this observational study in a semi-arid region with a high proportion of annual plant species within the transition zone of Mediterranean and desert ecosystems (Israel). Along a sharp precipitation gradient, I analyzed (a) how species assemble at both the local scale (within 15 m × 15 m plots) and the microhabitat scale (0.06 m^2 and $1m^2$) with respect to their traits (qualitative species composition). The long-standing debate on whether phylogeny elucidates species assembly motivated a comparison between a functional approach based on three key functional traits, and a phylogenetic approach. With respect to the quantitative species composition, I analyzed (b) the effect of local environmental heterogeneity on diversity at different spatial scales. Further, I investigated whether the effects differed between taxonomic, functional, and phylogenetic diversity. Finally, I assessed whether the observed species assembly pattern and effects of environmental heterogeneity on diversity changed along the precipitation gradient.

In chapter III, I ask how functional traits of Mediterranean annuals respond to a precipitation gradient that encompasses the range of precipitation changes predicted to occur within this century. This study was conducted in the same study region as chapter II. The study region lies at the southern limit of many Mediterranean species distributions due to decreases in precipitation towards the south. Hence, Mediterranean species should be particularly threatened by decreasing amounts of precipitation in this region. As study organisms, I chose two widespread Mediterranean annuals, *Crupina crupinastrum* (Moris) Vis. and *Geropogon hybridus* (L.) Sch. Bip., which share similar habitat preferences but differ in their regeneration strategy. *Crupina crupinastrum* produces one single seed type (homocarpic), whereas *G. hybridus* produces two different seed types (heterocarpic). My goal was to demonstrate a shift from competitive ability in the northern mesic sites to stress tolerance in the southern arid sites. Thus, I sampled different functional traits in 16 populations along the precipitation gradient and analyzed whether both species showed trait adaptations along the precipitation gradient. I also explored how intraspecific trait variability is distributed across scales; i.e. within and between populations.

In chapter IV, I investigate how nutrient addition affects the establishment ability of plants with differing seed masses. Most previous studies have focused only on the indirect effects of soil fertilization, so I chose instead to disentangle the direct effect of nutrient addition and the indirect effect of competition resulting from soil fertilization. To do this, I devised an experiment with 22 perennial plant species from dry grasslands in Germany with differing seed masses. Since seedling establishment may be hampered by different processes, I analyzed interacting effects of nutrient addition, competition and seed mass on four different processes: seedling emergence, timing of seedling emergence, seedling survival, and seedling growth. Based on my experimental results and the literature, I developed a conceptual model that unifies contrasting findings and provides a sound framework that can be empirically tested.

In the general discussion (chapter V), I first synthesize the findings of the three empirical studies and discuss the possibilities and merits of functional traits to distinguish between environmental filtering, competitive exclusion and neutral processes. Afterwards, I discuss the importance of the scale-dependency, intraspecific trait variability, and phylogenetic relationships in community ecology. Finally, I describe how I envision trait-based plant ecology in the future.

Chapter II

Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment[1]

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[1] An article with equivalent content was published as: **K. Bergholz**, F. May, M. Ristow, I. Giladi, Y. Ziv, F. Jeltsch (2017) Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment. *Perspectives in Plant Ecology and Evolution, 24,* 138–146.
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Summary

Spatial environmental heterogeneity is considered a fundamental factor for the maintenance of plant species richness. However, it still remains unclear whether heterogeneity may also facilitate coexistence at fine grain sizes or whether other processes, like mass effects and source sink dynamics due to dispersal, control species composition and diversity at these scales. In this study, we used two complimentary analyses to identify the role of heterogeneity within 15 m × 15 m plots for the coexistence of species-rich annual communities in a semi-arid environment along a steep precipitation gradient. Specifically, we: (a) analyzed the effect of environmental heterogeneity on species, functional and phylogenetic diversity within microsites (alpha diversity, 0.06 m^2 and 1 m^2), across microsites (beta diversity), and diversity at the entire plot (gamma diversity); (b) further we used two null models to detect non-random trait and phylogenetic patterns in order to infer assembly processes, i.e. whether co-occurring species tend to share similar traits (trait convergence) or dissimilar traits (trait divergence). In general, our results showed that heterogeneity had a positive effect on community diversity. Specifically, for alpha diversity, the effect was significant for functional diversity, and not significant for either species or phylogenetic diversities. For beta diversity, all three measures of community diversity (species, functional, and phylogenetic) increased significantly, as they also did for gamma diversity, where functional measures were again stronger than for species or phylogenetic measures. In addition, the null model approach consistently detected trait convergence, indicating that species with similar traits tended to co-occur and had high abundances in a given microsite. While null model analysis across the phylogeny partly supported these trait findings, showing phylogenetic underdispersion at the 1m^2 grain size, surprisingly when species abundances in microsites were analyzed they were more evenly distributed across the phylogenetic tress than expected (phylogenetic overdispersion). In conclusion, our results provide compelling support that environmental heterogeneity at a relatively fine scale is an important factor for species co-existence as it positively affects diversity as well as influences species assembly. Our study underlines the need for trait-based approaches conducted at fine grain sizes in order to better understand species coexistence and community assembly.

2.1 Introduction

Spatial environmental heterogeneity is a fundamental factor affecting the coexistence of plant species (Chesson 2000). The unequal distribution of water, nutrients and light provides niches for species with different environmental preferences and ecological strategies. Although the positive effect of environmental heterogeneity on species richness as well as the influence on species assembly is well documented in the literature (Götzenberger *et al.* 2012, Adler *et al.* 2013, Stein *et al.* 2014), the underlying mechanisms of how heterogeneity facilitates plant coexistence are still poorly understood. For instance, it was commonly accepted that species richness increases with heterogeneity, since heterogeneous habitats provide more niches than homogenous ones (MacArthur and MacArthur, 1961). However, this view has been recently challenged, suggesting that the effect of heterogeneity on species richness is highly scale-dependent with an increasing positive effect with grain size, i.e. the spatial scale the vegetation is recorded (Lundholm 2009, Tamme *et al.* 2010, Giladi *et al.* 2011, Stein *et al.* 2014). At small spatial grains, high environmental heterogeneity leads to the loss of effective habitat area for species and micro-fragmentation with subsequent species loss (Kadmon and Allouche 2007, Laanisto *et al.* 2012). Therefore, heterogeneity may have a unimodal or even negative effect on species richness (Kadmon and Allouche 2007, Laanisto *et al.* 2012, Gazol *et al.* 2013). In contrast, theory of community assembly assumes that the fingerprint of environmental heterogeneity on species sorting, i.e. the co-occurrence of species, becomes less important with decreasing grain size (Götzenberger *et al.* 2012, HilleRisLambers *et al.* 2012). As a result, species sorting appears increasingly random with decreasing grain size (Weiher *et al.* 2011, Chase 2014). Hence, whether heterogeneity is considered as important factor for species co-existence depends on the investigated spatial grain size and response variable, i.e. species diversity or species sorting. Therefore, the joint analysis of these two response variables may provide a better understanding of the effect of heterogeneity on the coexistence of plant species.

Trait-based approaches are increasingly used to infer mechanisms of species coexistence and improve understanding of species distributions (Cornwell and Ackerly 2009, Götzenberger *et al.* 2012, Dainese and Sitzia 2013, May *et al.* 2013a). Environmental heterogeneity should lead to predictable species assembly from a larger species pool (Keddy 1992). Since all species in a given location experience the same environmental conditions, co-occurring species are assumed to exhibit similar ecological strategies and share similar traits (Keddy 1992, Cornwell *et al.* 2006,). The exclusion of species with dissimilar or non-adapted traits from the site may arise either because these species may not survive under those conditions (environmental filtering *sensu strictu*; e.g. Mayfield and Levine 2010, Kraft *et al.* 2015) or due to the species weak competitive ability under the particular environmental conditions (‘weaker competitor exclusion’ sensu de Bello *et al.* 2012). While disentangling these processes may be challenging (Mayfield and Levine 2010, Kraft *et al.* 2015, but see de Bello *et al.* 2012), they both lead to trait convergence in species assemblages (Mayfield and Levine 2010). In contrast, the concept of ‘limiting similarity’ (MacArthur and Levins 1967) entails that competitive interactions lead to trait divergence, because species with similar ecological strategies experience strong niche overlap and may thus not coexist in the long run (MacArthur and Levins 1967, Cornwell and Ackerly 2009). In order to reveal species assembly processes, an extension to trait-based approaches is the detection of distinct phylogenetic patterns of co-occurring species (Webb *et al.* 2002). The phylogenetic relationships between species may serve as a predictor for their ecological strategy, since closely-related species are expected to share similar traits (Blomberg *et al.* 2003). If this assumption is met, the same processes entailing trait convergence should lead to phylogenetic underdispersion, i.e. closely-related species tend to co-occur, whereas limiting similarity should lead to phylogenetic overdispersion, i.e. distantly-related species tend to co-occur (Webb *et al.* 2002). The application of phylogenetic relationships to infer community assembly processes receives frequent criticism, since the same phylogenetic pattern can be generated by different processes (Cavender-Bares *et al.* 2009, Gerhold *et al.* 2015). However, assembly processes may affect traits differently (e.g. Spasojevic and Suding 2012) and trait-based approaches frequently use the same easy-measurable ‘key functional traits’. Complex traits are often not feasible to measure for species-rich communities, but these can be well phylogenetically conserved (de Bello *et al.* 2015). Therefore, “a combination of key measured traits and phylogeny may better assure that different axes of differentiation between species are being considered” (de Bello *et al.* 2015, p. 355).

The detection of both trait patterns and phylogenetic patterns varies with the scale under consideration (Swenson *et al.* 2007, Kraft and Ackerly 2010). Environmental filters presumably act at larger scales, which should lead to the detection of trait convergence (Cavender-Bares *et al.* 2009). At finer grains, species assembly is assumed to be driven by limiting similarity or by stochastic dispersal events (Weiher *et al.* 2011, Götzenberger *et al.* 2012). Some small-scale studies confirmed limiting similarity by detecting trait divergence (Bernard-Verdier *et al.* 2012, de Bello *et al.* 2013), while others found random trait pattern (Thompson *et al.* 2010). However, Adler *et al.* (2013) argued that trait divergence may be the result of environmental filtering at even finer grain sizes. Consequently, trait pattern should be analyzed at different spatial scales, in order to identify the effect of environmental heterogeneity on species assembly.

The framework of alpha, beta and gamma diversity (Whittaker 1972) enables analysis of the effect of heterogeneity on species diversity at different spatial grain sizes simultaneously. Since the study presented in the current article focuses on describing patterns at fine scales, we define gamma diversity as the species pool at a plot-scale (i.e. 15 m × 15 m), alpha diversity as the diversity within microsites (two grain sizes, 0.06 m^2 and 1 m^2) and beta diversity as turnover among microsites. Environmental heterogeneity, measured at the plot-scale, may positively affect alpha, beta and gamma diversity through different mechanisms. Gamma diversity may increase with heterogeneity, as heterogeneous environments offer more opportunities for niche differentiation and species sorting across environmental variation. In line with that, species turnover between microsites should increase with environmental heterogeneity, if environmental differences between microsites favor distinct species, as the concept of ‘environmental filtering’ would suggest (see above). In contrast, diversity within microsites may increase either due to a higher environmental heterogeneity within the microsite (if there is a correlation between microsite and plot-scale environmental heterogeneity) or simply due to the inflow of species from the surrounding area through spatial mass effects (Shmida and Wilson 1985). Hence, the positive effects of environmental heterogeneity include niche-based as well as dispersal-based mechanisms. Negative effects of heterogeneity on species richness may emerge due to high extinction risk, e.g. demographic stochasticity, of small populations (Kadmon and Allouche 2007). Depending on which mechanisms act, heterogeneity may affect functional and species diversity differently (as observed by Meynard *et al.* 2011), since species may be functional redundant. Therefore, comprehensive analyses of the effect of environmental heterogeneity on species, functional and phylogenetic diversity at different spatial grain sizes may help to reveal the underlying mechanisms of environmental heterogeneity effects on the maintenance of species richness and to link results of species assembly studies.

Finally, the effect of heterogeneity on diversity and species assembly may depend on the position along environmental gradients. Yang *et al.* (2015) proposed a model in which heterogeneity has a positive effect on species richness at the extreme ends of a stress-productivity gradient and a hump-shaped effect at the intermediate position. With respect to species assembly, Price *et al.* (2014) showed in an elegant experiment that with increasing small-scale heterogeneity and productivity niche overlap (i.e. trait convergence) increased, due to the suppression of slow-growing species. However, we are not aware of any studies that analyze the heterogeneity’s effect on both species diversity and species assembly along stress-productivity gradients.

In this study, we use two complimentary analyses with different research approaches in order to reveal how environmental heterogeneity affects species coexistence. Specifically, we: i) identify trait- and phylogeny-based assembly processes that structure co-occurrence and species abundances in microsites; ii) analyze whether increasing plot-scale environmental heterogeneity feature a higher species diversity within and across microsites (alpha and beta diversity, respectively) as well as a higher plot-scale species diversity (gamma diversity). Our study system is located at the transition zone between Mediterranean and desert ecosystems along a steep precipitation gradient in Israel. The fragmented semi-steppe batha and grassland vegetation in this area features a high proportion (79%) and diversity of annual plants (14.8 ± 6.7 species/m²). We use vegetation surveys at two different grain sizes (0.06 m² and 1 m²) nested within 15 m × 15 m plots. A previous study has found evidence for both trait convergence and divergence when these communities are compared to regional species pools of ca. 6 km × 4 km land units (May *et al.* 2013a). At the same time, regional processes, i.e. propagule exchange between habitat patches, are negligible in this area (Gemeinholzer *et al.* 2012, May *et al.* 2013b). Therefore, it is especially relevant to investigate coexistence mechanisms at the plot-scale.

We address the following questions:

i) Does environmental heterogeneity affect species assembly within plots, indicated by trait convergence in microsites?

ii) Does the phylogenetic approach point to the same species assembly pattern as the functional approach does?

iii) How does environmental heterogeneity, measured at the plot-scale, affect the diversity within microsites (alpha), turnover between microsites (beta) and the diversity of the plot (gamma diversity)?

iv) Is the heterogeneity's effect on diversity consistent between species, functional and phylogenetic diversity and along a steep precipitation gradient?

2.2 Methods

Study area

The study area is situated in the Southern Judean Lowlands, Israel (31°24'00''–31°40'50''N, 34°48'30''–34°50'30''E), at the transition zone between Mediterranean and desert ecosystems. Rainfall in this area is restricted to winter (October-April) with decreasing annual amounts from north (430 mm) to south (291 mm) along a distance of 30 km (May *et al.* 2013a). The fragmented landscape contains patches of semi-natural vegetation, set within a matrix of intensive agricultural land. The semi-natural vegetation has resulted from heavy grazing since the Bronze Age and can be referred to as semi-steppe batha and grassland (see Giladi *et al.* 2011 for further details). These vegetation types feature a high diversity of annual plant species. Woody vegetation is dominated by small shrubs (mostly *Sarcopoterium spinosum*) and some larger bushes. The common tussock grass *Hyparrhenia hirta* is frequently found in grasslands, where it builds dense populations. Previous studies showed that the species composition changes drastically along the precipitation gradient, including a decrease of species richness and density towards aridity (Giladi *et al.* 2011) accompanied by a decrease of community weighted mean traits of specific leaf area, plant height and seed mass (May *et al.* 2013a). These shifts indicate a stress-productivity gradient from north (productive) to south (stressful).

Vegetation sampling & environmental heterogeneity measurements

The vegetation sampling was conducted in three land units (6 km × 4 km each), which were placed from north to south along the precipitation gradient (see Giladi *et al.* 2011 for details of the vegetation sampling). In each land unit, we established 15 m × 15 m plots (south n=25, mid n=28, north n=28) in different patches of semi-natural vegetation. Each of these plots contained 12 small quadrats 0.0625m² in size (0.25 m × 0.25 m, henceforth 0.06 m²), nested in six larger quadrats of 1 m² (1 m × 1 m) (Fig. 2.1). These quadrats define our 'microsites' at two different grain sizes. In spring 2009, all plant species were recorded for each quadrat and the number of individuals was counted in the finer quadrats (0.06 m²).

In order to estimate environmental heterogeneity, we determined the diversity of microhabitats within the plots. Along two transects that form the diagonals of the plots, we placed at each half meter a 0.06 m² quadrat left and right of the transect (Fig. 1). We visually assessed the most common microhabitat within each of the resulting 84 quadrats per plot and assigned each to one of six microhabitat types: 'large bush', '*Sarcopoterium spinosum*', 'small shrub' (other than *S. spinosum*), '*Hyparrhenia hirta*', 'exposed rock' and 'herbaceous patch'. Shrubs and perennial grasses are key structures that modulate the light and water availability for annual plants, which has a strong impact on the annual species composition (Luzuriaga *et al.* 2012, Segoli *et al.* 2012). Similarly, differences in soil depth and micro-topography, indicated by exposed rocks, influences the species composition in Mediterranean ecosystems (Bernard-Verdier *et al.* 2012). The proportions of the different microhabitat types within the plots were used to calculate the Shannon index, which defines our environmental heterogeneity (Giladi *et al.* 2011). We are aware that our index quantifies the environmental heterogeneity of the whole 15 m × 15 m plot and that the scale at which environmental heterogeneity is measured may influence the effect on species richness (Tamme *et al.* 2010). However, previous analyses have shown that this index is also highly correlated (r=0.87) with small-scale heterogeneity at 1 m² (Giladi *et al.* 2011).

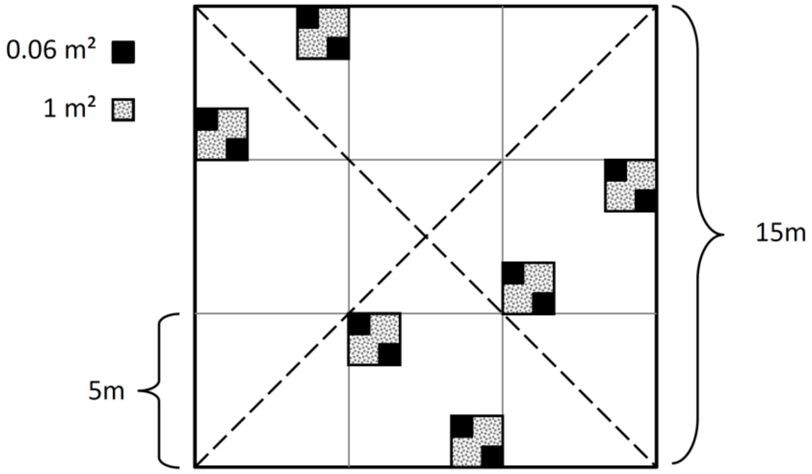

Figure 2.1. Sampling design of the study. Vegetation surveys were done at two different scales: 0.25 m × 0.25 m and 1 m × 1 m within a plot of 15 m × 15 m. The environmental heterogeneity was assessed along two transects that represent the diagonals of the plot (dashed lines). Along these transects the diversity of microhabitats was quantified within the 15 m × 15 m plot.

Trait sampling & construction of the phylogenetic tree

Following standard protocols (Cornelissen *et al.* 2003), we measured species mean traits of specific leaf area [mm²/mg], seed mass after removing appendages [mg] and canopy height [cm] for 129 of the 237 observed annual species in the study area. For specific leaf area and seed mass, we measured ten individuals; for canopy height 25 individuals of one healthy population within the whole study area (see May *et al.* 2013a for details of trait measurements). Since mostly abundant species were measured, we covered 89% and 85% of the annual species occurrences at the 0.06 m² and 1 m² grain size, respectively. The three measured traits constitute the principle axes of the Leaf-Height-Seed (LHS) plant ecological strategy scheme by Westoby (1998), which is a simple, generic way to characterize the ecological strategy of plants.

We constructed a phylogenetic tree of all annuals present in the study area. At first, we built a tree of the respective plant families based on the proposed phylogeny of The Angiosperm Phylogeny Group (2009). Notes and branch lengths of this tree were adjusted to divergence times estimated by molecular data, which were calibrated to known fossil ages (Bell *et al.* 2010). The relationships between species within the families were resolved with 39 further publications (see Appendix A1 for details).

Analyses

Phylogenetic trait conservatism

First, we revealed whether the investigated traits are phylogenetically conserved by using K-statistics (Blomberg *et al.* 2003), implemented in the R-package 'picante'. K quantifies the degree of trait conservatism in comparison to a Brownian motion model of trait evolution. $K<1$ signifies that traits are more divergent than predicted by the model, whereas $K>1$ indicates a high degree of trait conservatism. The observed K values were compared to expected K values, under the consideration of no relationship between traits and phylogeny, derived from 999 random trait-tree associations.

Calculation of diversity indices

We used the mathematical framework of Rao's quadratic entropy (RaoQ) to estimate the mean diversity of microsites (alpha), turnover between microsites (beta) and plot-scale diversity (gamma). RaoQ is known to reflect community assembly processes well (Mouchet *et al.* 2010) and allows a comparison of species (often referred as taxonomic), functional and phylogenetic diversities using the same index. Here, we followed the approach of de Bello *et al.* (2010). Alpha diversities were calculated for each microsite (i.e. 0.06 m² and 1 m²) as follows:

$$\alpha_{Rao} = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij}p_i p_j$$

with d_{ij} the dissimilarity between species i and j where p is their relative abundance in the microsite. For species diversity, d_{ij} between species is always 1. Functional dissimilarities between species were gathered from the Euclidean distance of the three log-transformed and standardized traits (seed mass, canopy height, specific leaf area). Phylogenetic dissimilarities were derived from the phylogenetic tree with the cophenetic function of the R-package '*picante*'. The relative abundance of the species was gathered from the number of individuals, which was counted within the 0.06 m² microsites. For 1 m² microsites, no relative abundances were available and presence-absence data were used. The alpha diversities of all microsites for a given grain size (either 0.06 m² or 1 m²) within a 15 m × 15 m plot were averaged to estimate the mean alpha diversity. Gamma diversity was calculated in the same way as alpha diversity, but with the addition of pooling all microsites (either 0.06 m^2 or 1 m^2) of the plot into one sample. Beta diversity can finally be calculated as the proportional [$\beta_{prop} = (\gamma - \bar{\alpha})/\gamma$] or additive difference [$\beta_{add} = \gamma - \bar{\alpha}$] between gamma and mean alpha diversity (de Bello *et al.* 2010). We report in the manuscript only findings of the proportional beta diversity, since both indices showed very similar results. Pearson's correlation coefficient was used to assess the correlation between species, functional and phylogenetic diversity indices.

Null model analyses

We used two different null models in order to reveal species assembly processes. The first null model assessed how species assembled from the plot-scale species pool (15 m × 15 m) and was conducted for both grain sizes considered (0.06 m^2 and 1 m^2). For this approach, observed mean alpha functional and phylogenetic diversities were compared to expected mean alpha diversities under the consideration of random species assembly within the plots. The null model shuffled species occurrences (presence-absence) among microsites of the same plot by keeping the frequency of species within the plot and the number of species in the microsites constant. We used the *trialswap* algorithm implemented in the R-package *picante* with 999 repetitions and 10 000 permutations. The second null model assessed how species abundances at the very fine scale (0.06 m^2) are related to traits and phylogenetic relationships, respectively. If the particular environmental conditions of a microsite favor a specific ecological strategy, species with high abundances should have similar traits, leading to trait convergence. Otherwise, if niche differentiation prevails, species with high abundances should have dissimilar traits, which would cause trait divergence (Bernard-Verdier *et al.* 2012). We used the abundance-weighted RaoQ to quantify the (alpha) functional and phylogenetic diversity within the 0.06 m^2 microsites. The observed values were compared with expected values derived from a null model that shuffled abundances among the species within the plots (999 repetitions). This analysis was only conducted for microsites (n=712) that contained more than two annual species whose traits were available. Since assembly processes may act contrastingly on different traits (Spasojevic and Suding 2012), we performed both null model analyses for each trait separately as well as jointly in a multidimensional analysis. In both null model approaches, we calculated the standardized effect size, in order to assess the deviation of the observed diversities (D) from the expected diversities, $SES = \left(D_{obs} - \overline{D}_{exp}\right)/\ sd(D_{exp})$. For each plot, we calculated a mean SES for both null models. Significance across 15 m × 15 m plots was evaluated with a two-tailed Wilcoxon test.

Heterogeneity & precipitation effect on diversity

In order to reveal whether heterogeneity and precipitation gradient affect the diversity indices as well as the assembly pattern of species, we fitted a series of linear models. As response variables, we used observed mean alpha, beta (log-transformed) and gamma diversity indices (species, phylogenetic and functional) and the standardized effect size (SES) of both null models. As predictors we used the linear and quadratic term of the environmental heterogeneity index, land unit as categorical effect and the interaction between both heterogeneity terms and land unit. Since beta diversity indices often are dependent on the size of the species pool (Kraft *et al.* 2011), the number of species of each plot was incorporated as covariate in these models. Models that had SES as response variable included additionally the number of species and the observed functional diversity included in the null model, since both variables have a strong impact on the magnitude of SES (de Bello 2012). Following Crawley (2007), we did a stepwise backwards selection and removed non-significant terms ($p<0.05$) with a single-term deletion F-test to obtain the minimal adequate model. If the quadratic term of heterogeneity was significant (three out of 27 models), we additionally fitted models that did not include the quadratic term, in order to test the significance of the linear term of heterogeneity. The analyses were conducted with presence-absence data for both grain sizes and including abundances on the finer grain size (0.06 m^2).

Spatial autocorrelation of CWM traits

Finally, we investigated whether the environment selects upon traits at a specific scale, i.e. whether closely-situated microsites share more species with similar traits than do distantly-situated microsites. For this purpose, we analyzed the spatial autocorrelation of community weighted mean (CWM) traits. For each plot, we calculated Moran's I correlograms for the CWM traits of the 0.06 m^2 microsites for seven distance classes with *correlog* (R-package *ncf*). All statistics were carried out in R version 3.1.1 (R Core Team 2012).

2.3 Results

Our three investigated traits were moderately conserved, although they were less conserved than a Brownian motion model of trait evolution would predict (seed mass $K=0.35$, $p<0.001$; specific leaf area $K=0.29$, $p<0.001$; canopy height $K=0.24$, $p<0.001$), indicating that closely-related species tended to share similar traits. Community weighted mean traits showed no apparent spatial autocorrelation within our plots (15 m × 15 m) (Appendix A2).

Species assembly was assessed with a null model that assumes random species assembly within the plots. The comparison between observed and expected functional diversities revealed strong support for non-random assembly processes (Table 2.1). Functional diversity of the multidimensional leaf-height-seed approach was lower than expected, indicating trait convergence at both grain sizes considered (0.06 m^2 and 1 m^2). Similar results were obtained when functional diversity was calculated solely for seed mass as well as for canopy height (Table 2.1). Specific leaf area showed no deviation from the null model. The phylogenetic approach revealed that at the 1 m^2 grain size closely-related species tended to co-occur (phylogenetic underdispersion). At the finer grain size (0.06 m^2), species appeared to assemble randomly with respect to their phylogeny (Table 2.1).

The second null model analyzed how species abundances within fine microsites (0.06 m^2) are related to the species' traits and phylogeny. This null model detected trait convergence for all traits considered, indicating that species with high frequencies share similar traits (Table 2.1). In contrast, species abundances were more evenly distributed across the phylogeny than expected by chance (phylogenetic overdispersion). We found no indication that the results of both null models changed along the precipitation gradient or with plot-scale heterogeneity (one exception: null model 2, specific leaf area, interaction between heterogeneity and land unit $p=0.049$; Appendix A3).

Table 2.1. Results of both null model approaches that analyzed species assembly within 15 m × 15 m plots (NM 1) and the trait abundances within 0.06 m^2 quadrats (NM 2). Observed functional and phylogenetic diversities were compared with the expected diversities generated by the null models. The deviation between observed and expected diversities was quantified with the Standard Effect Size (SES). + and – indicate whether the mean SES is positive (obs > exp) or negative (obs < exp). The table shows significant ($p<0.05$) deviations of the SES from zero across all 81 plots, with the respective p-values revealed by a two-tailed Wilcoxon test. LHS stands for the Leaf-Height-Seed strategy by Westoby (1998), which is a multidimensional analysis of the three log-transformed traits; seed mass (SM), canopy height (CH) and specific leaf area (SLA).

NM	Grain size [m^2]	LHS	SM	CH	SLA	Phylo
1	0.06	– **0.0007**	– **0.0005**	– **0.0025**	0.31	0.94
	1	– **0.003**	– **0.006**	– **0.0002**	0.58	– **0.006**
2	0.06	– **<0.0001**	– **0.0017**	– **0.038**	– **<0.0001**	+ **0.009**

The effect of environmental heterogeneity and precipitation gradient (represented by three land units) on diversity within microsites (alpha diversity, 0.06 m^2 and 1 m^2), turnover between microsites (beta) and plot-scale diversity (gamma) was analyzed for species (SD), functional (FD) and phylogenetic (PD) diversity. Observed SD, FD and PD indices were highly correlated with each other, though the relationships were less strong with increasing grain size (Appendix A4). Both heterogeneity and land unit affected the diversity indices, but we found no evidence for significant heterogeneity by land unit interaction (Table 2.2, analyses of presence-absence data; Figure 2.2, analyses including species abundances). Beta diversity (SD, FD and PD) consistently increased with heterogeneity, particularly at the finer grain size (0.06 m^2), indicating that environmental heterogeneity increases the turnover among microsites (Figure 2.2). Along the precipitation gradient, beta diversity showed no differences among the three land units if the analyses included species abundances (Figure 2.2) and decreased with precipitation, if presence-absence data were used (Table 2.2, Appendix A5). The analyses and comparisons of alpha and gamma diversities revealed some remarkable differences between SD, FD and PD in relation to heterogeneity and precipitation gradient. Heterogeneity had no significant effect on alpha SD and positively influenced gamma SD (Table 2.2). In contrast, heterogeneity had a stronger effect on FD compared to SD and positively affected both alpha and gamma FD. Furthermore, FD showed in some models an unexpected U-shape pattern, if quadratic terms were included in the maximal models (Table 2.2, Appendix A5). Alpha and gamma PD appeared to be independent of heterogeneity (one exception gamma PD, 0.06 m^2 including species abundances). With respect to the precipitation gradient, species diversity increased with annual precipitation amount at all grain sizes. In contrast, alpha and gamma FD was highest in the intermediate land unit (particularly at the 1 m^2 grain size, Appendix A5). Alpha and gamma PD increased with precipitation at the fine spatial grain sizes (0.06 m^2) and showed a similar pattern like FD diversity at the 1 m^2 grain size.

Table 2.2. Effect of environmental heterogeneity (Het) and land unit on mean alpha, beta, gamma species (SD), functional (FD) and phylogenetic (PD) diversity for both grain sizes (0.06 m^2, 1 m^2) and presence-absence data (see Appendix A5 for graphical illustration). The maximal models included heterogeneity as linear and quadratic term, land unit und the interaction between heterogeneity and land unit. The table reports the minimal adequate models with marginally significant ($p<0.1$) terms, which were revealed with single-term deletion F-test. The interaction between land unit and heterogeneity was not significant in any model. F-values marked with ‘$^{\#}$’ base on models that did not include the quadratic term of the heterogeneity index (see methods, chapter 2.2 for details). Statistical models of beta diversities also included the species richness of the 15 m × 15 m plot, since beta diversity indices are often influenced by the number of species. **** $p<0.0001$, *** $p<0.001$, ** $p<0.01$, * $p<0.05$, . $p<0.1$.

Scale	Facet	Grain size [m^2]	Het	Het^2	Land unit
			F	F	F
Alpha	SD	0.06			84.17 ****
		1	2.80 .		40.03 ****
	FD	0.06	4.94 *		54.40 ****
		1	$^{\#}$14.45 ***	5.11 *	13.55 ****
	PD	0.06	0.015		63.31 ****
		1	0.029		8.26 ****
log Beta	SD	0.06	12.38 ***		14.86 ****
		1	4.95 *		5.61 **
	FD	0.06	8.80 **		14.47 ****
		1	2.41		10.75 ****
	PD	0.06	15.55 ***		13.62 ****
		1	7.41 **		5.18 **
Gamma	SD	0.06	3.59 .		43.44 ****
		1	7.35 **		35.05 ****
	FD	0.06	$^{\#}$10.92 **	6.80 *	24.03 ****
		1	$^{\#}$18.34 ****	6.89 *	11.34 ****
	PD	0.06	2.06		22.31 ****
		1	0.04		4.65 *

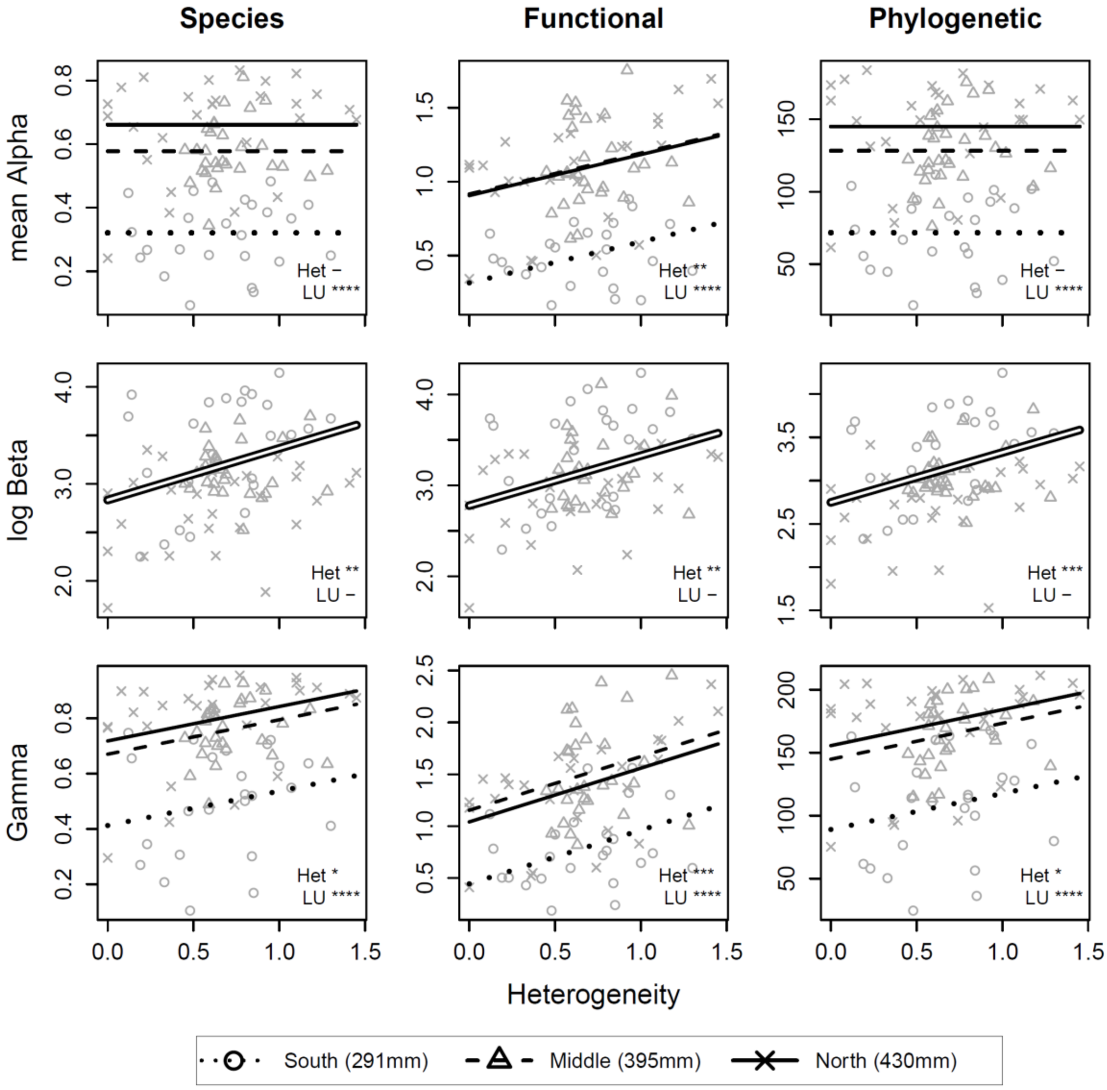

Figure 2.2. Effect of environmental heterogeneity (Het) and land unit (LU) on mean alpha, beta and gamma species, functional and phylogenetic diversity. The figure shows data of the finer grain size (0.06 m²) and considered species abundances (Table 2.2 shows results of presence-absence data). Lines indicate predictions of the minimal adequate models. Significance of both predictors is shown at the right bottom of the figure. Please note that the maximal models also included the interaction between land unit and heterogeneity, which was not significant in any model. Beta diversity models included additionally the number of species as covariate. For the graphical illustration, number of species was set to the median. The legend includes mean annual precipitation amounts at the three land units. ****<0.0001, *** p<0.001, ** p<0.01, * p<0.05, '–' indicates not significant (p>0.05).

2.4 Discussion

Environmental heterogeneity is a key factor in promoting species coexistence and diversity, although the underlying mechanisms are still poorly understood (Chesson 2000, HilleRisLambers *et al.* 2012, Stein *et al.* 2014). In particular, it remains unclear, whether environmental heterogeneity has the potential to facilitate coexistence at fine grain sizes (Tamme *et al.* 2010, Gazol *et al.* 2013, Chase 2014). In this study, we found evidence that within 15 m × 15 m plots species assembly of annual plants is strictly non-random and further environmental heterogeneity positively affected functional and species diversity at different spatial scales.

Null model 1 revealed that annual species are non-randomly distributed within our 15 m × 15 m plots. Species with similar ecological strategies, as quantified by the LHS concept (Westoby 1998), or solely by seed mass and canopy height, tended to co-occur at both grain sizes considered (0.06 m^2 and 1 m^2). This trait convergence pattern can be attributed to environmental differences among microsites, as other processes that may cause trait convergence, e.g. herbivory and pollination (Cavender-Bares *et al.* 2009), are unlikely to affect the investigated traits at the considered scale. The detection of trait convergence shows that environmental heterogeneity has an impact on the assembly and co-occurrence of species. In order to reveal whether the environment selects upon traits at a particular scale, we additionally assessed the spatial autocorrelation of community weighted mean traits. Since community weighted mean traits showed no apparent autocorrelation, it becomes evident that the trait (and species) composition changes considerably even between nearby microsites (1.1 m distance), which is likely to be a result of small-scale heterogeneity; potentially associated with shrubs, perennial grasses and variation of soil depth that modulate the light and water availability for annual plants (Bernard-Verdier *et al.* 2012, Luzuriaga *et al.* 2012, Segoli *et al.* 2012). In congruence with the null model approach, environmental heterogeneity positively influenced beta diversity, particularly at the finer grain size (0.06 m^2). Hence, both analyses – the null model approach and the effect of environmental heterogeneity on beta diversity – provide compelling evidence that local environmental heterogeneity may act as stabilizing factor for coexistence among species by the provision of different microhabitats.

The second null model analyzed whether species abundances are related to traits within microsites (0.06 m^2). Irrespective of which trait was considered, species with high abundances shared similar traits, as indicated by trait convergence. Hence, at the grain size where individuals interact and compete for resources, the environmental conditions favor species with similar strategies.

The consistent detection of trait convergence at fine scales contrasts the expectation and findings of other studies arguing that at very fine spatial grain sizes species assembly appears randomly or that competition creates trait divergence (Weiher *et al.* 2011). For instance, de Bello *et al.* (2013) found trait divergence for temperate grasslands at 1 m²; the same was detected by Bernard-Verdier *et al.* (2012) in Mediterranean grasslands at 54 m². The contradiction between our and other studies may have multiple reasons. While we analyzed annual communities, the other studies focused on perennial-dominated systems. Annual plants are on average smaller compared to perennials and thus the influence of small-scale heterogeneity should have a larger effect on the assembly of annuals compared to perennials. Moreover, competitive intensity is assumed to be lower between annuals compared to perennials (see Emery *et al.* 2009 for a summary of differences between annuals and perennials), especially in less productive system like ours (e.g. Schiffers and Tielbörger 2006). At the same time, a large body of literature highlight differences in regeneration strategies, like dormancy and germination timing, as important co-existence mechanism in annual communities (Pake and Venable 1996; Siewert and Tielbörger 2010; Venable and Brown 1988), while differences in regenerative strategies between perennials seem to be less important (Emery *et al.* 2009). Hence, annual communities may show trait divergence particularly in complex regenerative traits (see below phylogenetic analyses), since low competitive intensities do not drive trait divergence in 'key functional traits'. However, Adler *et al.* (2013) showed that patterns of trait divergence observed at a larger scale can actually result from small-scale environmental filtering within microhabitats. Under this consideration, the trait divergence observed by other studies may need to be re-evaluated. For instance, the trait divergence findings by May *et al.* (2013a), who analyzed the same annual communities as in the current study but from a regional perspective, may be the result of small-scale 'environmental filtering'. Our approach, therefore, underlines the need for a better understanding of how small-scale heterogeneity affects the trait-based assembly of species (Adler *et al.* 2013).

Environmental heterogeneity may affect species richness positively by widening the available niche space and negatively by reducing suitable area and increasing micro-fragmentation for species (Kadmon and Allouche 2007, Laanisto *et al.* 2012). We found no indication for the unimodal species richness-heterogeneity pattern predicted by Kadmon and Allouche (2007). In our study, heterogeneity positively influenced species diversity at the plot-scale. As the null model analyses suggest, microhabitats favor species with different traits and thus plots with a higher diversity in microhabitats may contain a higher overall species diversity. Additionally, we observed that heterogeneity had an even larger positive effect on functional diversity compared to species diversity. This pattern indicates that heterogeneity indeed affects the available niche space, since it increases the diversity of ecological strategies of the species. Species may have very similar ecological strategies and traits (functional redundancy) as indicated by the weak correlation between taxonomic and functional diversity at larger spatial extents. As a result, heterogeneity should primarily affect the functional diversity rather than the species diversity *per se*, as our analyses indicate. Moreover, heterogeneity, which was measured at the plot-scale (15 m × 15 m), positively influenced the functional diversity within microsites (0.06 m² and 1 m²). The higher functional diversity in microsites may be the result of small-scale heterogeneity within the microsite, since plots with a high heterogeneity at the plot-scale also feature a higher heterogeneity within microhabitats (see Methods). Spatial mass effects, i.e. the inflow of species from neighboring sites, may also increase the functional diversity of microhabitats. However, such mechanisms seem to be ineffective to increase the species diversity in microsites, which may be due to very limited dispersal distances of annuals in our study system (Siewert and Tielbörger 2010) and small-scale ‘environmental filtering’ even between closely-situated microsites (see above). The strong relationship between heterogeneity and functional diversity across different grain sizes highlights the role of heterogeneity on niche-based processes and shows that analyses that solely rely on species diversity may miss important insights. Moreover, we found an unexpected, although weak, non-linear increase of functional diversity with heterogeneity in some models indicating that not only the strength, but also the shape of heterogeneity may affect species and functional diversity differently.

Along the precipitation gradient, we observed contrasting trends of species and functional diversity. Alpha and gamma species diversity increased with precipitation amount, which is consistent with numerous studies along similar precipitation gradients (e.g. Giladi *et al.* 2011). Noteworthy, the corresponding alpha and gamma functional diversity showed an idiosyncratic pattern towards precipitation amount, with a peak in the intermediate land unit. Our study region is located at the transition zone between desert and Mediterranean ecosystems with a substantial species turnover between the three land units (only half of the species occur in all three land units, Giladi *et al.* 2011). Hence, the intermediate land unit contains possibly the largest overlap of species from these two ecosystems and features therefore the highest diversity in functional traits. While beta diversity did not differ between land units if species abundances were included in the analyses, beta diversity decreases with precipitation, if the analyses based on presence-absence data. The latter pattern is quite surprising, since beta diversity indices generally increase with the size of the species pool (Kraft *et al.* 2011). However, the observed differences in beta diversity between land units are no indication for changing assembly processes along the precipitation gradient. If the size of the species pool varies much between land units, as in our study, observed differences in beta diversity may be a mathematical artefact (Kraft *et al.* 2011). In this context, the effect of heterogeneity on diversity and on species assembly (i.e. SES of null models) appeared to be consistent along the precipitation gradient. Further, we found no indication that species assembly was affected by the heterogeneity of the plot. It should be noted that also ‘environmental homogenous’ plots in terms of microhabitat diversity, may contain some degree of environmental variation across microsites, as for instance differences in soil properties were not assessed with our heterogeneity index. Therefore, it seems likely that the heterogeneity gradient in our study was not sufficiently large to reveal differences in species assembly.

We used phylogenetic relationships in order to extend our functional approach, which relies on three key functional traits (de Bello *et al.* 2015). Corresponding to the observed trait convergence pattern, we expected to detect phylogenetic underdispersion, since closely related species tended to share similar traits. As predicted, phylogenetic underdispersion was found within larger microsites (1 m²), but at the finer grain size (0.06 m²) species appeared randomly assembled with respect to the phylogeny (null model 1). The combination of a lower chance of detecting assembly processes with decreasing species numbers at finer scales (Weiher *et al.* 2011) and a lower sensitivity of phylogenetic approaches (Kraft and Ackerly 2010) may explain the deviation between the trait and phylogenetic approaches at 0.06 m². However, more striking is the phylogenetic overdispersion of the second null model. This pattern indicates that species' abundances are more evenly distributed across the phylogenetic tree than expected by chance, and thus species with high abundances tend to be distantly related. This finding has two alternative explanations. One is that environmental conditions favor species with similar traits, but closely-related species actually have different ecological strategies. This scenario would lead to the detection of phylogenetic overdispersion, but it is unlikely because trait conservatism is in general high, if the investigated community comprises different phylogenetic clades (Cavender-Bares *et al.* 2009). More likely, competition might create divergence in traits that are phylogenetically conserved, but which were not measured in this study. As mentioned above, niche differentiation in generative traits is important in annual plant communities and generative traits show phylogenetic conservatism (e.g. Hoyle *et al.* 2015). The contrasting pattern between trait-based and phylogenetic approaches indicate that species assembly is affected contrastingly by traits (Spasojevic and Suding 2012). Therefore, rather than considering the disadvantages of phylogenetic studies, we think that observed phylogenetic patterns build an excellent starting point for further research to reveal the underlying mechanisms and traits.

In conclusion, our analyses provide compelling evidence that environmental heterogeneity facilitates coexistence among annual plants through the provision of microhabitats and species sorting among these microhabitats. The combination of null models and analyses of heterogeneity-diversity relationships at different grain sizes and diversity facets allowed us to highlight the importance of heterogeneity on niche-based processes. This study, therefore, highlights the need for trait-based approaches that are conducted at small spatial extents in order to analyze coexistence mechanisms at local scales, which remain overlooked or even misinterpreted when a more regional perspective is followed.

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Link to chapter III

In the previous chapter, I analyzed how species assembled at the local scale and how local environmental heterogeneity affects different measures of plant diversity along a sharp precipitation gradient. I found that processes of species assembly were constant along the precipitation gradient. However, species diversity decreased under arid conditions. In a basic study, May *et al.* (2013a) analyzed in the same study system, how the species composition changes along the precipitation gradient with respect to functional traits. The authors found clear trait-responses along the precipitation gradient including a decrease in community weighted mean value of specific leaf area, plant height, and seed mass towards aridity, while seed number increased. As in the previous chapter, the study of May *et al.* (2013a) based on average species values and analyzed solely the species turn-over. However, species may also show intraspecific trait responses along the precipitation gradient, as a result of local adaptation towards the specific conditions. In general, it can be assumed that intraspecific responses mirror interspecific responses (Westoby 1998). However, recent studies showed that intraspecific trait responses are much more complex (Albert *et al.* 2010, Cochrane *et al.* 2015).

Several empirical studies showed that Mediterranean annuals showed adaptations towards competitive ability under mesic conditions and stress tolerance under arid conditions (e.g., Schiffers and Tielbörger 2006, Liancourt and Tielbörger 2009). However, competitive ability and stress tolerance may be expressed in different niche dimensions and include various traits. Moreover, studies that investigated local adaptation of plants along precipitation gradients regularly sampled a small amount of populations (n<5) and used large scale precipitation gradients (Kunze *et al.* 2017). How important are differences in precipitation amounts at a finer, regional scale for local adaptations and trait responses? This is in particular from interest for predictions of trait responses under future climate change. In the Mediterranean basin, it is predicted that precipitation decreases of about 30% until 2100. Several studies predict that semi-arid regions, like the Mediterranean basin, are particularly vulnerable towards future aridification (Harrison *et al.* 2015, Golodets *et al.* 2015), though recent empirical evidence suggest that plants are well adapted to changing precipitation amounts (Tielbörger *et al.* 2014, Bilton *et al.* 2016). Therefore, it is essential to get a better understanding of how plants in this regions respond to decreasing precipitation amounts.

In the next chapter, I explore how two Mediterranean annuals respond along a precipitation gradient that corresponds to predicted precipitation changes until the end of this century.

Chapter III

Two Mediterranean annuals feature high within-population trait variability and respond differently to a precipitation gradient[2]

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[2] An article with equivalent content was published as **K. Bergholz**, F. May, M. Ristow, I. Giladi, Y. Ziv, F. Jeltsch (2017). Two Mediterranean annuals feature high within-population trait variability and respond differently to a precipitation gradient. *Basic and Applied Ecology*, 25, 48–58. doi.org/10.1016/j.baae.2017.11.001.

Summary

Intraspecific trait variability plays an important role in species adaptation to climate change. However, it still remains unclear how plants in semi-arid environments respond to increasing aridity. We investigated the intraspecific trait variability of two common Mediterranean annuals (*Geropogon hybridus* and *Crupina crupinastrum*) with similar habitat preferences. They were studied along a steep precipitation gradient in Israel similar to the maximum predicted precipitation changes in the eastern Mediterranean basin (i.e. -30% until 2100). We expected a shift from competitive ability to stress tolerance with decreasing precipitation and tested this expectation by measuring key functional traits (canopy and seed release height, specific leaf area, N- and P-leaf content, seed mass). Further, we evaluated generative bet-hedging strategies by different seed traits. Both species showed different responses along the precipitation gradient. *C. crupinastrum* exhibited only decreased plant height towards aridity, while *G. hybridus* showed strong trends of generative adaptation to aridity. Different seed trait indices suggest increased bet-hedging of *G. hybridus* in arid environments. However, no clear trends along the precipitation gradient were observed in leaf traits (specific leaf area and leaf N- / P- content) in both species. Moreover, variance decomposition revealed that most of the observed trait variation (>>50%) is found within populations. The findings of our study suggest that responses to increased aridity are highly species-specific and local environmental factors may have a stronger effect on intraspecific trait variation than shifts in annual precipitation. We therefore argue that trait-based analyses should focus on precipitation gradients that are comparable to predicted precipitation changes and compare precipitation effects to effects of local environmental factors.

3.1 Introduction

Climate change has been identified as one of the major threats to biodiversity (Sala *et al.* 2000). Still, our understanding of how plants respond to climate change is scarce (Franks *et al.* 2014, Matesanz and Valladares 2014). Plant communities in semi-arid regions, like the Mediterranean, are predicted to be particularly vulnerable to climate change (Wu *et al.* 2011, Golodets *et al.* 2015, Harrison *et al.* 2015, Knapp *et al.* 2015), since decreasing precipitation and increasing temperature has led to an ongoing aridity in these regions (IPCC 2013, Sheffield and Wood 2008). In contrast, a recent long-term precipitation manipulation experiment revealed that a decrease of precipitation (-30%) has only a marginal effect on the species composition and biomass production, presumably because species are adapted to a high variability in precipitation (Tielbörger *et al.* 2014, Bilton *et al.* 2016). These contrasting findings call for a better understanding of how plants respond to decreasing precipitation.

Theory predicts a fundamental trade-off between competitive ability and stress tolerance in plants (Grime 1974, Grime 1977, Westoby 1998). In the Mediterranean region, plants should show adaptations towards competitive ability under mesic conditions and stress tolerance with increasing aridity (Schiffers and Tielbörger 2006, Liancourt and Tielbörger 2009). However, these adaptations may be expressed in different niche dimensions and include various vegetative and generative functional traits. The competitive environment under mesic conditions should select for large plant height and rapid growth rates, indicated by high specific leaf area and leaf nitrogen content (Westoby 1998, Chapin *et al.* 1993, Cornwell and Ackerly 2009). In contrast, stress tolerance is mediated by low growth rates, i.e. decreasing specific leaf area with aridity (Reich *et al.* 1999, Baruch *et al.* 2017, May *et al.* 2013). With respect to generative strategies, a higher dispersal ability is assumed to be beneficial under arid conditions for two reasons. On the one hand, plants under environmental stress may invest in dispersal ability in order to escape from the adverse conditions of the mother-plant site (e.g. Levin *et al.* 1984, Imbert and Ronce 2001). On the other hand, bet-hedging theory predicts that plants increase risk-spreading strategies, like dispersal, under arid conditions, because precipitation becomes increasingly unpredictable (Siewert and Tielbörger 2010). An increased dispersal ability may be beneficial if the spatial arrangement of suitable habitats changes in time, e.g. through increasing variation of annual precipitation in arid areas (Noy-Meir 1973, Siewert and Tielbörger 2010). Plants may increase their dispersal ability by a higher amount of seeds that have a lower seed mass (Weiher *et al.* 1999). Further, species that produce different seed types (seed heterocarpy) may alter the ratio between specific seed types, for instance they may produce a higher proportion of seeds with a well-developed pappus (Imbert and Ronce 2001). In general, seed heterocarpy is regarded as an alternative bet-hedging strategy to cope with spatio-temporal variability (Venable 1985, Imbert 2002). Therefore, it can be expected that species increase seed heteromorphism under unpredictable, arid conditions. Several studies revealed that heterocarpic species show adaptations towards aridity (Ellner and Shmida 1984, Imbert and Ronce 2001, Gemeinholzer *et al.* 2012) and there is some evidence that seed heterocarpy is associated with dry, unpredictable environments (Ellner and Shmida 1984, Imbert 2002). However, studies are missing that compare responses of generative traits between heterocarpic and homocarpic species.

Trait shifts along natural precipitation gradients can be used as a space-for-time approach, in order to predict long-term trait responses to decreasing precipitation (Sandel *et al.* 2010). On the one hand, trait shifts may indicate ecotypic differentiation along environmental gradients. On the other hand, trait shifts allows to get a mechanistic understanding in which niche dimensions species respond to climate change (Petrů *et al.* 2006). While several empirical studies observed intraspecific trait shifts of plants along precipitation gradients, the majority of these studies investigated only a limited number of populations (n<5) (e.g. Aronson *et al.* 1992, , Petrů *et al.* 2006, Liancourt and Tielbörger 2009, Ariza and Tielbörger 2011, Harel *et al.* 2011) and /or used precipitation gradients that were orders of magnitude more than the predicted precipitation changes (e.g. Volis *et al.* 2002, Lázaro-Nogal *et al.* 2015, Dyer *et al.* 2016,). Hence, it remains unclear whether trait responses along large-scale precipitation gradients are actually of importance along precipitation gradients corresponding to predicted precipitation changes. Additionally, evidence is growing that a substantial proportion of intraspecific trait variability is actually found within populations (Albert *et al.* 2010, Messier *et al.* 2010, Siefert *et al.* 2015). This high intraspecific trait variability may be even more important than interspecific trait variation to buffer negative effects of climate change, such as drought (Jung *et al.* 2014). Therefore, a critical assessment of how intraspecific trait variability is distributed across scales, i.e. within-populations and between populations along precipitation gradients may help to reveal the importance of predicted precipitation changes for trait adaptation under climate change.

The aims of the current study are a) to test whether Mediterranean annuals show adaptations ranging from competitive ability to stress tolerance along a precipitation gradient and b) to quantify how much of the observed intraspecific trait variation can actually be attributed to differences in amounts of precipitation. As in other semi-arid regions, Israel is experiencing a decline in annual precipitation with a shortened growing season for the last centuries (IPCC 2013, Ziv *et al.* 2014), which is predicted to continue (IPCC 2013). Our study region in Israel is set at the transition zone between Mediterranean and desert ecosystems along a steep precipitation gradient (300 mm – 420 mm). Furthermore, the study region is located within the most Southern distribution edge of many Mediterranean plants. Thus, Mediterranean species should be particularly vulnerable to reduced precipitation in this region. Our study species are two widespread Mediterranean annuals *Geropogon hybridus* and *Crupina crupinastrum*, having similar environmental preferences but differing in their regeneration strategy (heterocarpic and homocarpic, respectively). We measured key functional traits that are expected to respond to decreasing precipitation and estimated their bet-hedging strategies with different trait indices.

3.2 Methods

Study region

Our study region is situated in the Southern Judean Lowlands in Israel (31°24' – 31°41'N; 34°46'-24°52'E) (Figure 3.1). The region consists of a mosaic of semi-natural vegetation, with grazing by cattle and goats since the Bronze Age, and intense agricultural farming. As a result, the semi-natural vegetation features semi-steppe batha types and grasslands with a high proportion of annual species (>65%) (see Giladi *et al.* 2011 for a detailed description of the study region). The precipitation decreases drastically along a short stretch of 30 km from approximately 420 mm in the north to about 300 mm in the south, resulting in a 30% decrease that corresponds roughly to maximum predicted precipitation change until 2100 in the Mediterranean basin (IPCC 2013, see Evans 2008, Lelieveld *et al.* 2012, Saaroni *et al.* 2015 for predicted precipitation changes in Israel). Soil fertility increases with precipitation (May *et al.* 2013a), while diversity of microhabitats, due to shrubs, bare rocks and varying soil depths remains constant along the precipitation gradient (Bergholz *et al.* 2017). Previous vegetation studies in the region revealed a decrease of species richness and individual plant density towards the arid end of the precipitation gradient (Giladi *et al.* 2011) accompanied by a decrease of community-weighted mean traits of specific leaf area and plant height (May *et al.* 2013a). These findings indicate a shift from a more competitive environment in the north to more stressful conditions in the south. During the sampling season in 2010-2011, the annual precipitation was approximately 66% of the mean annual precipitation (see Appendix B1).

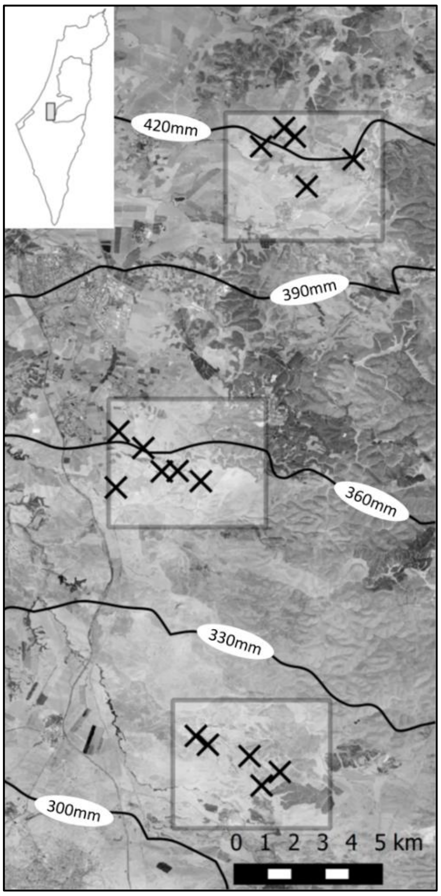

Figure 3.1. Study region Southern Judean Lowlands with the three land units in Israel. Precipitation isoclines were derived from worldclim.org. Crosses mark the sampling sites.

Study species

We selected two annual species that are common in the entire Mediterranean region: *Geropogon hybridus* (L.) Sch.Bip. and *Crupina crupinastrum* (Moris) Vis. Both species belong to the family Asteraceae and are primarily found in batha on various soil types. Furthermore, both species occur under very similar environmental conditions in Israel (Table 3.1). The study region is situated at the Southern margin of their distribution range (Appendix B2). *Crupina crupinastrum* is homocarpic and produces one to six similar seeds in each of the one to 16 capitulas produced by an individual. *Geropogon hybridus* is heterocarpic and produces two different seed types. At the central whorls of the capitula seeds with a fully developed pappus are produced (henceforth pappus seeds). Seeds at the outer whorls contain a reduced pappus with three elongated and two rudimentary aristate scales (henceforth trident seeds), which are much heavier (mean±SE: 17.65±0.25 mg) than the pappus seeds (9.75±0.13 mg). About 2% of the seeds are of an intermediate type, which were excluded from further analyses. Individuals in our study region produce mainly one flower (up to four) with five to 60 seeds (see Feinbrun-Dothan 1978, for further description of the species).

Table 3.1. Comparison of environmental preferences of both species in Israel. The table shows mean and standard errors of key environmental factors, where both species occurred. Number of sampling points: *Geropogon hybridus* n=350, *Crupina crupinastrum* n=321. Asterisk (*) indicates that environmental factor significantly differ between species. Data were taken from BioGIS, 2012. Israel Biodiversity Information System (http://www.biogis.huji.ac.il/).

	Geropogon hybridus	***Crupina crupinastrum***
Mean annual rainfall [mm]	520.32 (±9.02)	534.93 (±10.23)
Mean January temp. [°C]	10.20 (±0.09)	10.13 (±0.11)
Altitude [m]*	306.51 (±15.33)	348.32 (±17.86)
Aspect [°]	194.11 (±3.62)	191.72 (±3.43)
Slope [°]	5.57 (±0.28)	5.56 (±0.31)
Seasonal temp. range [°C]	15.58 (±0.83)	15.22 (±0.85)

Trait measurements

The trait sampling was conducted in three land units (6 km × 4 km), which were placed along the precipitation gradient from North to South (Figure 3.1). In each area, we selected five study sites where both species co-occurred (central land unit six study sites). Each study site represented an isolated patch (size mean±SE: 40.1±26 ha, distance between study sites, mean±SE: 1298±135 m) of semi-natural vegetation in the agricultural landscape, except for the Southern land unit. Here, we had to sample three populations on one large patch, as the frequency of both species decreased towards South (distances between the study sites within the large patch: 927m, 1296m and 1395m). Since the dispersal ability of Mediterranean annuals is low (Siewert and Tielbörger 2010) and neighboring populations of *G. hybridus* in the study region show a strong genetic differentiation (Müller *et al.* 2017), these sampling sites were regarded as separate populations.

At each study site we randomly chose ten individuals within an area of approximately one hectare and measured plant height (canopy and seed release height), specific leaf area, nitrogen and phosphorous content of leaves following standard sampling protocols (Perez-Harguindeguy *et al.* 2013). For *C. crupinastrum*, we counted all open flowers and collected all ripe seeds of the first flower and weighted them afterwards. For *G. hybridus*, trait sampling was done in two steps, since leaves were already withered when seeds of the first flower were fully ripe. First, we sampled all traits as described above except of seed mass. Second, we collected all seeds of the first flower and recorded the maximum plant height of ten additional individuals per study site. Seeds were counted and seed types (pappus vs. trident seeds) distinguished. From each individual four seeds of each seed type (if available) were weighed. Sampling was conducted from 01/04/ 2011 to 30/04/2011 at the end of the raining season.

Mean seed mass of *G. hybridus* was calculated by the sum of both seed type masses (mean seed mass × number of seeds of the specific seed type) divided by the total number of seeds in order to reflect seed mass and proportion differences between both seed types. For analyses of bet-hedging strategies, we calculated the coefficient of variance of seed masses of each individual, which estimates the degree of seed heteromorphism of each individual. For *G. hybridus*, we further calculated the seed mass ratio between both seed types (mean seed mass of pappus seeds / mean seed mass of trident seeds) as a second index for seed heterocarpy (Ellner and Shmida 1984) and the proportion of pappus seeds as a surrogate for dispersal ability (Imbert and Ronce 2001).

Statistical analyses

We used linear mixed-effects models in order to reveal effects of the precipitation gradient on functional traits and bet-hedging indices. As response variable we used the traits canopy and seed release height, specific leaf area, nitrogen and phosphorous leaf content, mean seed mass, seed number as well as total seed mass (mean seed mass × seed number). We included the land unit as categorical fixed effect and the population as random effect to account for the nested study design. Since generative traits (e.g. seed mass, seed number) commonly depend on plant size (Westoby *et al.* 2002), these models included also seed release height (henceforth plant height) as predictor. In this way, we ensure that possible trends of generative traits are not just a result of varying plant height along the precipitation gradient. All traits were log-transformed prior to analysis (except ‘prop pappus seeds’, which was arcsine-square root transformed) in order to meet statistical assumptions. Significance of the fixed effects was assessed with a F-test via Kenward-Roger approximation (Halekoh and Hojsgaard 2014) as recommended by Bates *et al.* (2015).

We used variance decomposition to estimate the proportion of observed trait variation along the precipitation gradient between populations of the same land unit and within populations. For this purpose, we used linear mixed-effects models with hierarchically nested random effects (Messier *et al.* 2010), which are population nested in the land unit. Models of generative traits included seed release height as a predictor (see above). Variance components of the random effects were extracted with the R-function *varcomp*.

All analyses were conducted for both species separately and were carried out with R Version 3.1. and the R-packages *lme4*, *pkbrtest* and *ape*.

3.3 Results

The majority of the investigated traits were correlated to each other, while in most cases the relationships were similar for both species (see Appendix B3). The most significant correlations included plant height, being positively correlated to generative traits (mean and total seed mass, number of flowers and seeds), and specific leaf area, being negatively correlated with plant height, number of seeds and flowers.

Our study species responded differently to the precipitation gradient (Table 3.2). *Geropogon hybridus* showed significant trends in generative traits along the precipitation gradient. The species produced a higher number of seeds and mean seed mass decreased with aridity (Figure 3.2). Moreover, the production of seed types changed along the precipitation gradient. Both the proportion of pappus seeds and the seed mass ratio increased towards the Southern study sites (Figure 3.2). Plant height did not change along the precipitation gradient for this species. In contrast, *C. crupinastrum* showed a decrease of plant height towards the South (Figure 3.3). All considered generative traits of this species appeared to be independent of the precipitation gradient (see Appendix B4), though plant height had a positive effect on number of seeds and flowers as well as on mean seed mass (Table 3.2). Both species showed no trend in total seed mass or number of flowers along the gradient (Table 3.2). Leaf traits showed no consistent trend along the precipitation gradient, although land unit had a significant effect on specific leaf area for both species and leaf N-content in *G. hybridus*. In the central land unit, plants of both species had on average the highest specific leaf areas and the lowest leaf N-contents (Figure 3.3).

The variance decomposition revealed that most of the observed trait variation remained unexplained by the nested random effects model, indicating that most trait variation (51 – 98%) existed within populations (Table 3.3, see also Figure 3.2 and Figure 3.3). Both predictors, land unit and the population within the land unit, explained on average similar proportions of trait variations (range 0 – 41%, Table 3.3), though it strongly depended on the species and trait under consideration. The population level explained consistently more variation in *C. crupinastrum* compared to *G. hybridus*, whereas the latter consisted more trait variation within the population. As expected, the proportion of the variance explained by the land unit was in general higher for traits that showed significant trends along the precipitation gradient compared to traits that were not influenced by the land unit. However, in all models the within-population trait variability was higher than the trait variability between populations and along the precipitation gradient.

Table 3.2. Effect of precipitation gradient (land unit) on functional traits of *C. crupinastrum* and *G. hybridus*. The linear mixed effects models included study site as random effect and land unit as categorical fixed effect with three levels (north, central, south). Models of generative traits included additionally plant height as covariate. Trend signifies whether traits significantly increase (↗) or decrease (↘) towards north or show no clear trend (∩). Significance of the fixed effects was determined with a F-test via Kenward-Roger approximation. All traits were log-transformed prior to analyses, except of Prop. pappus seeds, which was arcsine root-transformed. Significant effects ($p<0.05$) of land unit are bold typed.

Trait	***C. crupinastrum***					***G. hybridus***				
	Trend	**Land unit**		**Plant height**		**Trend**	**Land unit**		**Plant height**	
		F	p	F	p		F	p	F	p
Seed release height	↗	**17.80**	**<0.001**				3.73	0.052		
Canopy height	↗	**10.85**	**0.002**				2.92	0.090		
Specific leaf area	∩	**6.93**	**0.009**			∩	**5.49**	**0.019**		
Leaf N-content		0.82	0.463			∩	**9.65**	**0.003**		
Leaf P-content		0.56	0.585				2.18	0.156		
Total seed mass		0.18	0.840	19.47	<0.001		3.65	0.055	88.21	<0.001
Numb. flowers		2.77	0.084	108.21	<0.001		3.35	0.066	37.49	<0.001
Numb. seeds		0.76	0.480	38.83	<0.001	↘	**9.13**	**0.003**	32.64	<0.001
Mean seed mass		0.33	0.721	12.42	<0.001	↗	**7.83**	**0.006**	25.23	<0.001
CV seed mass		0.52	0.601	2.15	0.145		1.03	0.384	5.89	0.017
Prop. pappus seeds						↘	**7.43**	**0.007**	16.77	<0.001
Seed mass ratio						↘	**16.77**	**<0.001**	<0.01	0.985

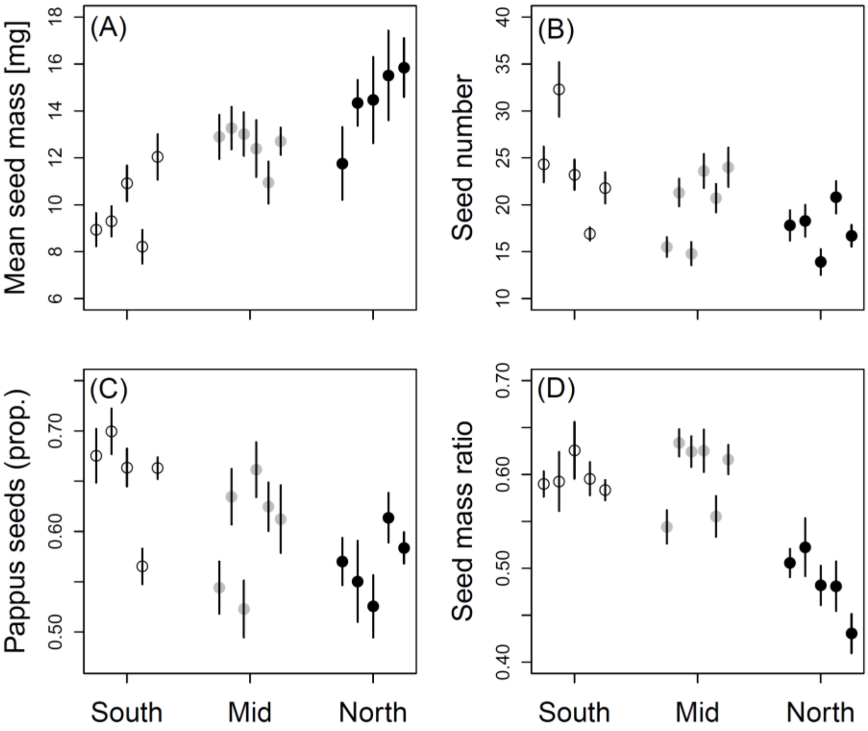

Figure 3.2. Generative traits of *Geropogon hybridus* along the precipitation gradient with increasing annual precipitation from south to north. Each point represents the mean trait value (±SE) of one study site. (A) mean seed mass, averaged across both seed types (see Methods), (B) number of seeds in the capsula, (C) proportion of pappus seeds, (D) seed mass ratio between the two seed types (mean seed mass pappus seed/mean seed mass trident seed). The statistical analyses included also plant height as covariate (see Table 3.2).

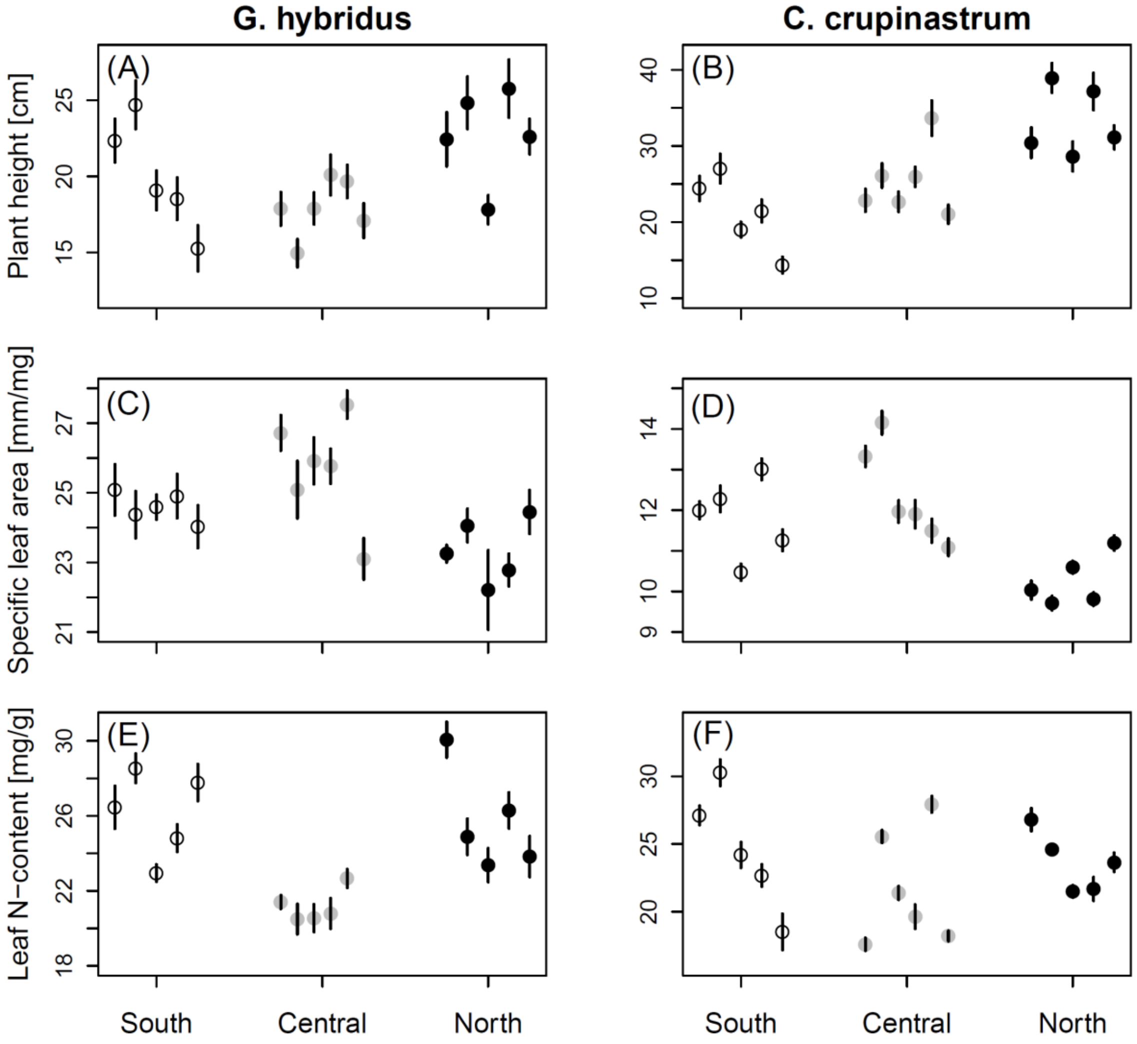

Figure 3.3. Vegetative trait responses of *G. hybridus* (A, C, E) and *C. crupinastrum* (B, D, F) along the precipitation gradient with increasing precipitation amounts towards north. Points indicate the mean trait value of one study site (±SE). Plant height refers to the seed release height.

Table 3.3. Variance decomposition for each trait and for both species. The table shows the proportion (%) of the trait variation explained by the nested factors land unit and population. The third column (within) gives the trait variation which remains unexplained, i.e. is found within populations. The analyses were conducted with hierarchically nested linear mixed-effects models. CV_{tot} refers to the coefficient of variation within the whole study region of the untransformed trait. CV_{pop} refers to the average trait variability (coefficient of variation) within populations.

	C. crupinastrum					*G. hybridus*				
	Land unit	**Population**	**within**	**CV_{tot}**	**CV_{pop}**	**Land unit**	**Population**	**within**	**CV_{tot}**	**CV_{pop}**
Seed release height	20.10	17.42	62.48	0.42	0.34	5.15	11.80	83.05	0.40	0.36
Canopy height	16.74	14.39	68.87	0.39	0.32	1.06	12.68	86.27	0.35	0.32
Specific leaf area	28.46	20.29	51.25	0.15	0.11	8.79	1.52	89.69	0.14	0.13
Leaf N-content	0.00	36.76	63.24	0.23	0.17	22.02	5.39	72.59	0.22	0.18
Leaf P-content	0.00	35.45	64.55	0.30	0.24	2.47	0.79	96.74	0.30	0.24
Total seed mass	0.00	18.70	81.30	0.38	0.35	7.57	10.17	82.26	0.52	0.46
Numb. flowers	16.35	19.71	63.94	0.47	0.41	8.94	0.00	91.06	0.47	0.32
Numb. seeds	11.96	8.06	79.98	0.74	0.62	21.21	2.58	76.21	0.41	0.35
Mean seed mass	8.98	35.22	55.80	0.21	0.17	25.15	13.00	61.85	0.33	0.27
CV seed mass	0.00	1.15	98.85	0.98	0.77	0.45	3.29	96.26	0.42	0.38
Prop. pappus seeds						13.12	5.46	81.42	0.17	0.15
Seed mass ratio						41.45	7.83	50.72	0.18	0.12
Average	**10.26**	**20.72**	**69.03**			**13.12**	**6.21**	**80.68**		

3.4 Discussion

Decreasing precipitation in the Mediterranean basin increases environmental stress for plants. As a result, plant species should show shifts from competitive ability towards stress tolerance along natural precipitation gradients. In this study, we observed that a) two Mediterranean annuals showed contrasting trait responses towards aridity and b) most of the observed trait variation was found within populations.

Trait responses along the precipitation gradient

Geropogon hybridus responded in generative traits and showed a trade-off between seed mass and seed number (Westoby *et al.* 2002). Seed mass decreased with aridity, while seed number increased, in agreement with findings at the community level in the same study system (May *et al.* 2013a). Larger seed mass might be an adaptation to a more competitive environment in mesic conditions (Harel *et al.* 2011). However, Ben-Hur and Kadmon (2015) showed that the competitive hierarchy was not related to seed mass in Mediterranean annuals, which was supported by similar findings from other ecosystem studies (Ben-Hur and Kadmon 2015). An alternative explanation for the observed shifts in seed mass and seed number is that plants under the stressful and unpredictable conditions of arid environments increase their dispersal ability (Siewert and Tielbörger 2010). A higher number of seeds in combination with lower seed mass and higher proportion of pappus seeds should increase the dispersal ability under arid conditions in *G. hybridus*. Similarly, *Catananche lutea*, another heterocarpic annual, increased the dispersal ability towards aridity in the same study region by producing a higher proportion of aerial flower heads at the expense of subterranean flower heads (Gemeinholzer *et al.* 2012). Moreover, *G. hybridus* showed a higher seed diversification under dry conditions, as the seed mass ratio between pappus and trident seeds increased in the southern land units. While *G. hybridus* increases its dispersal ability with pappus seeds under dry conditions (see above), the heavier trident seeds may guarantee the establishment of at least a few seedlings near the mother plant, which is a suitable site ("mother-plant theory"; Zohary 1937). Hence, *G. hybridus* has a diversified bet-hedging dispersal strategy, which is more developed under dry conditions. Interestingly, the proportion of heterocarpic annuals slightly increased with aridity in our study system (land unit north=16.4%, central=17.6%, south=18.3%; data taken from Giladi *et al.* 2011), which goes in line with the intraspecific findings on *G. hybridus* and supports the expectation that seed heterocarpy is associated with unpredictable environments (Imbert 2002). Certainly, seed heterocarpy may increase the fitness in unpredictable environments also through other mechanisms that are not related to dispersal, e.g. contrasting germination behavior between seed types (Venable 1985). However, the seed trait responses of *G. hybridus* indicate an adaptation to deal with increasing unpredictability due to the spatial and temporal variation in environmental conditions. A recent genetic study revealed genetic differentiation in the same populations of *G. hybridus* along the precipitation gradient (Müller *et al.* 2017), indicating that precipitation selects for different ecotypes in the study region. Indeed, a common garden experiment revealed that onset of flowering was accelerated with increasing aridity of the source population in G. hybridus (Bergholz, unpublished data), which is a common response to aridity (e.g. Hänel and Tielbörger 2015). However, the experiment failed to show significant shifts of generative traits as observed along the precipitation gradient in the field study.

In contrast to the generative responses of *G. hybridus*, *C. crupinastrum* showed predominantly a decrease in plant height under drier conditions. This pattern reflects the decreasing productivity coupled with lower competition for light (May *et al.* 2013). Furthermore, the shorter growing season under dry conditions leads to an acceleration of phenology (Hänel and Tielbörger 2015). As a result, plants invest less time in vegetative growth and therefore reach smaller plant height at the end of the growing season.

Surprisingly, none of the species showed a clear trend of leaf traits along the precipitation gradient, as predicted by theory (Westoby 1998) and observed at the community level (May *et al.* 2013). Similarly, Albert *et al.* (2010) revealed that intraspecific responses of leaf traits along environmental gradients were highly species-specific, partly hump-shaped and idiosyncratic. Although studies showed that precipitation affects intraspecific responses of leaf traits in semi-arid environments (Ramírez-Valiente *et al.* 2010, Carlson *et al.* 2016, Baruch *et al.*, 2017), these studies analyzed evergreen woody plants, whose leaves have to endure long dry seasons. In contrast, leaves of annuals in our study region withered at the end of the rainy season. As a result, these species may not show stress tolerance in foliar leaf traits towards aridity.

Trait variation across scales

The variance decomposition analysis revealed a high proportion of within-population variability (51 – 98%) within populations. Both species under study showed a typical within-population trait variability for annuals in the study region (see Appendix B5). In comparison to woody plant communities (Bastias *et al.* 2017) and subalpine grasslands (Albert *et al.* 2010), we observed a similar within-population trait variability in leaf traits and plant height. However, our analyses revealed further that both land unit and population level explained only a limited (to negligible) amount of trait variation. Hence, sources of intraspecific trait variability within populations seem to be more important than differences in precipitation amounts or other factors that differ between populations. Our study system is characterized by a high degree of small-scale spatial environmental heterogeneity due to the presence of shrubs and perennial grass tussocks, bare rocks and varying soil depths (Giladi *et al.* 2011, Bergholz *et al.* 2017). These structures modulate water and light availability for annual plants (Luzuriaga *et al.* 2012, Segoli *et al.* 2012). As a result, varying environmental conditions should favor different phenotypes and therefore maintain a large variation of genotypes within a population (Ravenscroft *et al.* 2014). For instance, the higher water availability of deep-soil hollows should favor large individuals with high growth rates, i.e. high specific leaf area. In contrast, dry slopes should select for small individuals. Therefore, small-scale heterogeneity may, in particular, be important for buffering negative effects of climate change, as it fosters populations having individuals with different traits (Fridley *et al.* 2011, Ravenscroft *et al.* 2014). Moreover, the study system features a substantial variation of precipitation amounts between years (CV ~0.35). This temporal variability may additionally maintain diversity in genotypes within populations, with genotypes that are adapted to different water availability, e.g. dry and wet years. Our study was conducted in a particularly dry year, in which the most northern sites received precipitation equaling that at the most Southern site in an average year. Surprisingly, the reproductive output, measured as total seed mass and number of flowers, remained constant along the precipitation gradient. This pattern may reflect the high adaptability of populations at the margin of their distribution, indicating that even in a particular dry year the most southern populations are able to successfully reproduce. Therefore, future decrease in average precipitation may not have a large effect on species performance, since species in this region are adapted to large differences in precipitation and small-scale heterogeneity (Tielbörger *et al.* 2014). However, it should be noted that this study did not investigate other important measures to predict survival chance under climate change, such as survival until maturity and population sizes.

Conclusions

Our study revealed that species with similar ecological preferences may respond differently to decreasing precipitation, which impedes the prediction of general intraspecific trait responses under climate change (Cochrane *et al.* 2015). Moreover, variance decomposition showed that at the scale under study, precipitation explains only a limited amount of trait variation. Therefore, we encourage researchers to quantify and compare the effects of precipitation gradients that correspond to predicted precipitation gradients and evaluate local environmental factors on key functional traits in order to better understand how predicted climate change influences species performance and distribution.

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Link to chapter IV

Both previous chapters investigated how a natural precipitation gradient affect plant traits at the community and species level. These studies used key functional traits, which are known to correlate well with important niche dimensions within the life-cycle of plants. However, one single plant trait may correlate with various processes (Violle *et al.* 2008), which makes a detailed understanding of observed trait pattern often difficult. One of the best examples is seed mass that is strongly correlated to the ability to establish. However, seedling establishment a complex process, which consists of four main components: seedling emergence, time of seedling emergence, seedling survival and seedling growth. All these processes had been shown to be affected by seed mass and may be further mediated by the specific environmental conditions. Detailed analyses of how seed mass influences the four components and how this relationship is mediated by certain environmental factors, may help to understand observed seed mass-environment relationships. In particular, the relationship between seed mass and soil fertility remains unclear, since studies found a positive, negative or no correlations. On the one hand, increasing soil fertility leads to an increase of competition for light (and litter). On the other hand, environmental stress due to nutrient deficiency should also select for large seed mass. Since most studies investigated how *indirect* effects of soil fertility, i.e. competition, shade, litter, affects seed mass and seedling establishment there is little known how soil fertility *directly* affects seed mass and seedling establishment. This is in particular important to understand biodiversity loss in context of human induced Nitrogen-deposition.

In the next chapter, I disentangle nutrient availability as *direct* and competition as *indirect* effect of soil fertilization on seedling establishment of species differing in seed mass. For this purpose, I used an experiment with 22 perennial dry grassland species from Eastern Brandenburg (Germany). Specifically, I analyze interacting effects of seed mass, nutrient availability and competition on the four key components seedling emergence, time of seedling emergence, seedling survival and seedling growth. This experiment builds the basis for a conceptual model that predicts seed mass relation along a gradient of soil fertility.

Chapter IV

Fertilization affects the establishment ability of species differing in seed mass via direct nutrient addition and indirect competition effects[3]

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[3] An article with equivalent content was published as: **K. Bergholz**, F. Jeltsch, L. Weiss, J. Pottek, K. Geißler, M. Ristow (2015). Fertilization affects the establishment ability of species differing in seed mass via direct nutrient addition and indirect competition effects. *OIKOS*, *124,* 1547–1554. doi: 10.1111/oik.02193

Summary

Fertilization causes species loss and species dominance changes in plant communities worldwide. However, it still remains unclear how fertilization acts upon species functional traits, e.g. seed mass. Seed mass is a key trait of the regeneration strategy of plants, which influences a range of processes during the seedling establishment phase. Fertilization may select upon seed mass, either directly by increased nutrient availability or indirectly by increased competition. Since previous research has mainly analyzed the indirect effects of fertilization, we disentangled the direct and indirect effects to examine how nutrient availability and competition influence the seed mass relationships on four key components during seedling establishment: seedling emergence, time of seedling emergence, seedling survival and seedling growth. We conducted a common garden experiment with 22 dry grassland species with a two-way full factorial design that simulated additional nutrient supply and increased competition. While we found no evidence that fertilization either directly by additional nutrient supply or indirectly by increased competition alters the relationship between seed mass and (time of) seedling emergence, we revealed that large seed mass is beneficial under nutrient-poor conditions (seedlings have greater chances of survival, particularly in nutrient-poor soils) as well as under competition (large-seeded species produced larger seedlings, which suffered less from competition than small-seeded species). Based on these findings, we argue that both factors, i.e. nutrient availability and competition intensity, ought to be considered to understand how fertilization influences seedling establishment and species composition with respect to seed mass in natural communities. We propose a simple conceptual model, in which seed mass in natural communities is determined by competition intensity and nutrient availability. Here, we hypothesize that seed mass shows a U-shaped pattern along gradients of soil fertility, which may explain the contrasting soil fertility-seed mass relationships found in the recent literature.

4.1 Introduction

Fertilization causes plant species loss and changes the dominance of species in grasslands worldwide (Bobbink *et al.* 2010, Borer *et al.* 2014). Still, there is an ongoing discussion about the mechanisms that are responsible for these fertilization-induced community changes (e.g. Cleland and Harpole 2010, Dickson and Foster 2011, Stevens *et al.* 2011). Numerous studies have shown that the increased biomass production caused by the additional nutrient supply increases aboveground competition for light (e.g. Hautier *et al.* 2009, Borer *et al.* 2014), while there is some evidence that also belowground competition for soil resources is increased (e.g. Rajaniemi *et al.* 2003, Dickson and Foster 2011). In particular, seedlings should suffer in this high competition, as they are sensitive to adverse conditions (Westoby *et al.* 2002). Indeed, fertilization reduces seedling establishment (Tilman 1993, Foster and Gross 1998, Wilson and Tilman 2002, Stevens *et al.* 2004), which is considered to be an important cause of fertilization-induced species loss (Tilman 1993, Stevens *et al.* 2004).

Seed mass plays a central role during the establishment phase of seedlings, as the internal amount of seed resources, e.g. lipids and carbohydrates, positively influences the success of seedling establishment (Westoby *et al.* 2002, Moles and Westoby 2004). However, there is conflicting evidence for how fertilization affects the species composition with respect to seed mass. While some studies reported a positive relationship between soil fertility and seed mass (Marañón and Grubb 1993, Grubb and Coomes 1997, Manning *et al.* 2009), other studies found no relationship (e.g. Pakeman *et al.* 2008, Azcárate *et al.* 2010) or even a negative one (Lee and Fenner 1989, Parolin 2000, Dainese and Sitzia 2013). This contradiction may arise because fertilization influences seedling establishment via at least two different mechanisms. Fertilization increases competition (see above), while simultaneously increasing the nutrient availability for seedlings. These two factors, competition and nutrient availability, may influence the relationships between seed mass and various processes during the establishment phase, thus favoring species with a specific seed mass through different mechanisms. Increased competition should favor large-seeded species (Manning *et al.* 2009), since they better tolerate competition due to higher growth rates (Leishman 1999) and survival rates (Burke and Grime 1996). Moreover, intense competition should suppress and delay the seedling emergence of small-seeded species, because they have a higher light requirement for germination (Milberg *et al.* 2000, Jensen and Gutekunst 2003). Delayed seedling emergence may result in lower seedling growth and adult fecundity (Verdú and Traveset 2005) and could therefore disadvantage small-seeded species under increased competition. In contrast, increasing nutrient availability as direct effect of fertilization should favor small-seeded species. Small-seeded species are known to have lower survival rates (Jurado and Westoby 1992) and partly slower growth rates (Hanley *et al.* 2007) under nutrient deprivation, which leads to a lower abundance of small-seeded species in habitats with low soil fertility (Dainese and Sitzia 2013). Increasing nutrient availability should ameliorate this disadvantage and promote small-seeded species, as they produce higher amounts of seeds, which increases the chances of colonizing suitable microhabitats (Ehrlén and Eriksson 2000). High nutrient concentrations have also been shown to positively influence seedling emergence (Baskin and Baskin 2000) and shorten the time of seedling emergence (Violle *et al.* 2009), but it has not yet been tested, whether such effects depend on seed mass.

So far, research has primarily focused on competition and other indirect effects of fertilization on seedling establishment, like shade or litter, but has not sought to disentangle direct nutrient addition from the indirect competition effects of fertilization. Hence, there is surprisingly little known about how nutrient availability affects the establishment ability of species and whether this is mediated by seed mass (see Hanley *et al.* 2007, Manning *et al.* 2009). Therefore, it needs to be understood how fertilization directly, by additional nutrient supply, and indirectly, by increased competition, affects the potential effect of seed mass during seedling establishment. These findings may provide valuable insights into seedling establishment under fertilization and allow general conclusions to be drawn regarding how fertilization affects the species composition of natural communities.

In this study, we investigated the interacting effects of seed mass, nutrient availability and competition on four key components of seedling establishment, i.e. seedling emergence (including germination), time of seedling emergence, seedling survival and seedling growth. For this purpose, we conducted a common garden experiment that incorporated a full factorial design with two treatments: 1. competition from already established plants (yes/no) and 2. nutrient availability (natural soils / fertilized soils). We sowed seeds of 22 perennials of a dry grassland community with a large seed mass variation between species and measured seedling emergence, time of seedling emergence, seedling survival and seedling growth. Specifically we hypothesize:

a) Seedling emergence of small-seeded species is reduced under competition, since small-seeded species have a higher light requirement for germination than large-seeded species.
b) Time of seedling emergence, i.e. number of days after sowing, increases under competition, particularly for small-seeded species, due to their higher light requirement.
c) Seedling survival increases with seed mass. This relationship should be strengthened under competition and weakened under fertilized conditions.
d) Seedling growth increases with seed mass, whereas competition suppresses growth particularly in small-seeded species. In contrast nutrient addition weakens the positive seed mass effect on growth.

4.2 Methods

Study system and seed collection

Our seedling establishment experiment is based on dry grassland communities which are located in the north-eastern part of the federal state of Brandenburg (Germany) along the River Oder (centered 52°28' N, 14°28'E). These communities are referred to as *Potentillo arenariae-Stipetum capillatae* (Hueck) Libbert, *Sileno otitae-Festucetum brevipilae* Libbert corr. Kartzert & Dengler and *Festuco psammophilae-Koelerietum glaucae* Klika (Ristow *et al.* 2011). The climate in this area exhibits continental influences, with a low annual precipitation of 450 – 500 mm, hot summers and cold winters. Dry grasslands in this area are mainly found on calcareous, sandy and sandy-loamy soils with low nutrient concentrations (medians of 67 soil samples across the study area: pH=7.39, N_{min}=5.7 mg/kg, P_{min}=9.1 mg/kg, Bergholz 2010). This low nutrient availability makes the dry grasslands an appropriate study system to study the impact of fertilization.

We selected 22 perennial species with large variations in seed mass between species and a tolerance to low nitrogen environments (low Ellenberg indicator values for nitrogen), which are typical of dry grassland communities (Table 4.1). Seeds of the species were collected from different individuals of healthy populations from July to October 2009. 20 seeds of each species were weighed without appendages to determine the species' mean seed mass (about 92% of the single seed mass variation was explained by the species' identity).

Experimental design

We conducted the experiment outdoors in the botanical garden of Potsdam, Germany. The experiment featured a two-way factorial design with two treatments: competition and nutrient availability. The set-up was conducted from 29 to 31/3/2010. In order to simulate natural conditions for the seeds, we used soil that was taken from a dry grassland slope in the referred study region (pH=7.99, N_{min}=6.7 mg/kg, P_{min}=12 mg/kg). This soil was filled into plastic pots (9 cm × 9 cm × 9 cm). For the treatment of increased nutrient availability, soil was enriched with horn meal (Planta vital®, 13% N, 0.6% P, 42% C, 89% organic matter). Horn meal is slowly decomposed by soil organisms and guarantees constant nitrogen fertilization of soils (Fischer and Schmitz 2000). We added 2 g of horn meal per liter of soil to the plots, which is equivalent to 23.4 N and 1.2 P mg/m². We confirmed that the mineral nitrogen content (NO_3 and NH_4) significantly differed between the fertilized (F+) and unfertilized (F-) soils throughout the experiment (mean±SD across two time points; NH_4 (F+)=11.49±2.19 mg/kg, NH_4 (F-)=4.66±0.96 mg/kg; NO_3 (F+)=9.40±3.01 mg/kg, NO_3 (F-)=1.78±0.57 mg/kg; see Appendix C1 for details). For the competition treatment, we planted four *Festuca brevipila* tussocks (diameter 3 cm) taken from a dry grassland near the botanical garden in each pot, one at each site (Figure 4.1). This grass is a typical matrix species of the dry grasslands in the study area. We observed no considerable growth differences in *F. brevipila* tussocks between the two fertilization treatments. Hence, our experiment constitutes two additional treatments. Three weeks after these preparations (23–24/04/2010), seeds of the target species were planted at five different positions in the pots. At each corner and in the middle of the pot, we placed three seeds of the same species, approximately one centimeter apart (Figure 4.1). We buried the seeds approximately five millimeters into the soil to guarantee that they would not be blown away by the wind. For each species and treatment we used five pots as replicates (i.e. 440 pots in total). Pots were arranged in a randomized block design and were carefully watered every second day if the soil surface was dry. The experiment was secured with a coarse meshed net to prevent seed predation and disturbance by birds.

Table 4.1. Species used in the experiment with the corresponding mean seed mass (±SD), the percentages of emerged seedlings in the experiment and Ellenberg's indicator value for nitrogen (EIV N).

Index	Species	Family	Seed mass [mg]	Emergence [%]	EIV N
A	*Agrostis capillaris*	*Poaceae*	0.05 (±0.02)	0.71	4
B	*Armeria elongata*	*Plumbaginaceae*	0.75 (±0.24)	0.47	2
C	*Campanula persicifolia*	*Campanulaceae*	0.04 (±0.02)	0.04	3
D	*Corynephorus canescens*	*Poaceae*	0.05 (±0.02)	0.24	2
E	*Dianthus carthusianorum*	*Caryophyllaceae*	0.40 (±0.16)	0.74	2
F	*Dianthus deltoides*	*Caryophyllaceae*	0.19 (±0.06)	0.48	2
G	*Galium verum*	*Rubiaceae*	0.40 (±0.18)	0.43	3
H	*Helichrysum arenarium*	*Asteraceae*	0.04 (±0.06)	0.31	1
I	*Hypericum perforatum*	*Hypericaceae*	0.10 (±0.02)	0.37	4
J	*Knautia arvensis*	*Dipsacaceae*	3.63 (±1.46)	0.18	4
K	*Peucedanum oreoselinum*	*Apiaceae*	3.72 (±1.32)	0.59	2
L	*Phleum phleoides*	*Poaceae*	0.11 (±0.05)	0.43	2
M	*Pimpinella nigra*	*Apiaceae*	1.01 (±0.35)	0.34	1
N	*Rumex thyrsiflorus*	*Polygonaceae*	0.67 (±0.28)	0.70	4
O	*Scabiosa canescens*	*Dipsacaceae*	0.57 (±0.11)	0.78	3
P	*Seseli annuum*	*Apiaceae*	0.57 (±0.19)	0.29	2
Q	*Silene chlorantha*	*Caryophyllaceae*	0.14 (±0.03)	0.42	2
R	*Solidago virgaurea*	*Asteraceae*	0.25 (±0.15)	0.21	4
S	*Stipa capillata*	*Poaceae*	4.77 (±1.52)	0.76	2
T	*Thalictrum minus*	*Ranunculaceae*	1.10 (±0.59)	0.10	3
U	*Thymus pulegioides*	*Lamiaceae*	0.10 (±0.03)	0.22	1
V	*Veronica spicata*	*Plantaginaceae*	0.05 (±0.02)	0.42	2

Seedling emergence and survival were recorded every second to third day until most species showed no further seedling emergence (63 days). If more than one seedling emerged at one position (i.e. two or three), the smaller seedling or the seedling, which emerged later was pulled out in order to avoid interspecific competition between seedlings. After 68 days, the growth of the surviving seedlings was quantified with four morphological traits: height (highest point in cm), diameter (greatest distance of leaves in cm), length of the longest leaf (cm) and number of leaves.

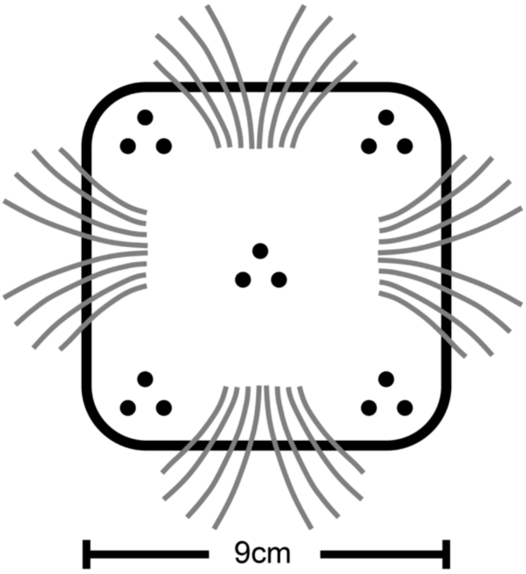

Figure 4.1. Experimental design. The figure shows the view of a pot from above, which included competition by four *Festuca brevipila* tussocks at the sides of the pot. Three seeds of the same species were put at five positions (four corners and mid) in the pot.

Statistical analyses

We analyzed the interacting effects of seed mass, competition and nutrient availability on the four key components of seedling establishment: (i) seedling emergence (yes/no), (ii) time of seedling emergence (days since planting), (iii) seedling survival (yes/no) and (iv) seedling growth. Survival defines whether a seedling survived until the end of the experiment (68 days after seeds were sown). The analyses of survival included only those seedlings that had never had a direct seedling neighbor at the position in the pot, because the removal of neighboring seedlings may have influenced the seedlings' chances of survival. The seedling growth was estimated by means of the four measured traits (height, diameter, leaf length and number of leaves). Since leaf length and number of leaves are species specific characteristics and therefore independent of species seed mass, full analyses of these two traits are based on standardizations, where for each species each trait was expressed relative to the species mean value. Therefore, analyses of these two traits reveal only intraspecific differences.

All statistical models included species mean seed mass, competition and nutrient availability, and the two-way interactions between species mean seed mass and the treatments as fixed effects. The models of seedling performance (iii, iv) additionally included the day of seedling emergence as covariate. These models incorporated pot nested within species as random effect to correct for the nested design of the study. The models of seedling emergence and time of seedling emergence (i,

ii) included the position within the pot nested in pot nested in species as random effect. Seedling emergence (i) and survival (iii) were analyzed with general linear mixed-effects models (function *glmer*, R-package *lme4*, Bates *et al.* 2015), with binomial error distribution. All other analyses were carried out with linear mixed-effects models (function *lmer*). The same models were also conducted without the interaction terms of the fixed effects to reveal the individual effects of seed mass, competition and nutrient availability.

All models were simplified with a step-wise backward selection, removing non-significant ($p > 0.05$) terms to obtain the minimal adequate model as described by Crawley (2007). Because classical likelihood-ratio tests are known to produce biased p-values (Pinheiro and Bates 2000), we used parametric bootstrapping tests (function *PBmodcomp*, R-package *pbkrtest*, Højsgaard 2013) to assess the significance of predictors, as recommended by Bates *et al.* (2015). Performance traits, time of seedling emergence and seed mass had to be log-transformed prior to analyses in order to meet statistical assumptions. Analyses were carried out with R Version 3.0.3 (R Core Team 2014).

4.3 Results

Seedling emergence

In total, 2759 seedlings (~42%) emerged within 68 days. During the final week of the experiment *Thalictrum minus* was the only species which showed emergence (four seedlings). As no further seedling emergence events were recorded during the final week, we suspect that the time the experiment ended did not influence our main results. Species showed highly differing emergence rates (Table 4.1), but neither seed mass nor treatments had a significant effect on seedling emergence (i) (Table 4.2). Time of seedling emergence (ii) was only affected by the competition treatment (Table 4.2). Seedlings appeared significantly earlier in the presence of competition (on average 17.46 days after sowing) compared to the control (18.73 days). Hence, competition accelerated the emergence of seedlings irrespective of seed mass.

Seedling performance

Seedling survival (iii) was analyzed for 643 seedlings that had never grown directly next to a neighboring seedling at the same position in the pot. 63% of those seedlings survived until the end of the experiment. As hypothesized, the survival chance increased along with seed mass (Table 4.3), confirming that large-seeded species have a higher chance of survival during the establishment phase. However, under fertilized conditions the positive effect of seed mass on seedling survival was weakened, as indicated by the significant interaction between seed mass and fertilization treatment (Table 4.2, Figure 4.2). In other words, the positive effect of seed mass on seedling survival depends on the nutrient status of the soils. This indicates that in natural, nutrient-poor dry grassland soils large seeds are able to better compensate for nutrient deficiency, thus promoting the survival chance of seedlings. In fertilized soils, the seed mass benefit becomes less apparent, since the increased overall nutrient availability enhances the survival chance of small-seeded species.

We measured the growth of 1086 seedlings, more than that used in the survival analysis as some had neighboring seedlings for a short period of time. Preliminary analyses revealed that this circumstance did not affect our main results. The four growth traits (iv) of the seedlings were moderately correlated to each other with correlation coefficients ranging from 0.35 to 0.66 (Appendix C2). However, the effects of seed mass, nutrient availability and competition on all traits were similar. Large-seeded species produced larger seedlings, measured in height and diameter (Table 4.3). Competition reduced seedling growth (Table 4.3), though seedlings with increasing seed mass suffered less from competition, as indicated by the significant interaction between seed mass and the competition treatment (Table 4.2, Figure 4.3).

Table 4.2. Parameter estimates of the minimal adequate models and the respective significance of the fixed effects as well as random effects variances with the respective number of groups in brackets. The maximal models included the interactions of log-transformed seed mass with the nutrient availability and competition as well as the corresponding single effects. Estimates of the intercept refer to the control treatment (C-N-). Please note that the values of the parameter estimates of nutrient availability and competition are defined as differences to the intercept. Similarly, parameter estimates of interactions refer to the difference of the seed mass effect. Significant predictors ($p<0.05$) are in bold. 'n.s.' indicates not significant. Growth traits and time of seedling emergence were log-transformed. Additionally, leaf length and number of leaves were standardized for the species. [a] Terms in significant interactions. Significance of these terms was not estimated (see Table 4.3). * $p<0.05$, ** $p<0.01$, *** $p<0.001$, **** $p<0.0001$.

	Seedling emergence (i)	**Time seedl. emer.$_{log}$ [d]** (ii)	**Survival** (iii)	**Height$_{log}$ [cm]** (iv)	**Diameter$_{log}$ [cm]** (iv)	**Std. leaf length$_{log}$** (iv)	**Std. # leaves$_{log}$** (iv)
Fixed effects							
Intercept (C-N-)	-0.45	2.93	3.97	2.52	2.77	0.08	0.06
Seed mass$_{log}$ [mg] (SM)	n.s.	n.s.	1.26^a	0.28^a	0.20^a	-0.01^a	-0.02^a
Nutrients	n.s.	n.s.	-0.80^a	**0.45******	**0.42******	**0.44******	**0.34******
Competition	n.s.	**-0.07******	n.s.	-0.44^a	-0.38^a	-0.46^a	-0.32^a
SM: Nutrients	n.s.	**n.s.**	**-0.53****	n.s.	n.s.	n.s.	n.s.
SM: Competition	n.s.	n.s.	n.s.	**0.09****	**0.17******	**0.11******	**0.13******
SM: Nutr: Comp	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Time seedl. emer.	-	-	**-0.07*****	**-0.01******	**-0.01******	**-0.01*****	**-0.01*****
Random effects variances							
Species	1.35 (22)	0.12 (22)	1.07 (22)	0.32 (21)	0.05 (21)	0.01 (21)	0.01 (21)
Species/pot	0.31 (439)	0.01 (415)	1.03 (342)	0.06 (355)	0.06 (355)	0.06 (355)	0.06 (355)
Species/pot/position	0.23 (2195)	0.004 (1516)	-	-	-	-	-

These two findings, therefore, indicate that fertilization may indirectly by increased competition favor large-seeded species, as large-seeded species are better able to tolerate competition due to their larger internal resources. Although nutrient addition had a positive effect on the four traits, which confirms that the growth was nutrient-limited, the effect was independent of the seed mass (Table 4.2). Thus, we found no indication that species with a specific seed mass grew better in fertilized soils. It should be noted that all the results of seedling performance were independent of whether the time of seedling emergence was included in the statistical models, or whether analyses were performed on standardization for species differences (Appendix C3 and C4).

Table 4.3. Parameter estimates of the minimal adequate models, which were obtained from maximal models that did not include interactions. See Table 4.2 for specifics and the results for seedling emergence and time of seedling emergence.

	Survival	**Height$_{log}$ [cm]**	**Diameter$_{log}$ [cm]**	**Std. leaf length$_{log}$**	**Std. # leaves$_{log}$**
	(iii)	(iv)	(iv)	(iv)	(iv)
Fixed effects					
Intercept (C-N-)	3.41	2.57	2.85	0.13	0.12
SM$_{log}$ [mg]	**0.97******	**0.32****	**0.30******	**0.05***	**0.05***
Nutrients	n.s.	**0.45******	**0.41******	**0.44******	**0.34******
Competition	n.s.	**-0.52******	**-0.53******	**-0.56******	**-0.44******
Time seedl. emer.	**-0.07*****	**-0.01******	**-0.01******	**-0.01*****	**-0.01*****
Random effects variances					
Species	1.03 (22)	0.33 (21)	0.04 (21)	0.01 (21)	0.01 (21)
Species/pot	1.09 (342)	0.07 (355)	0.08 (355)	0.07 (355)	0.07 (355)

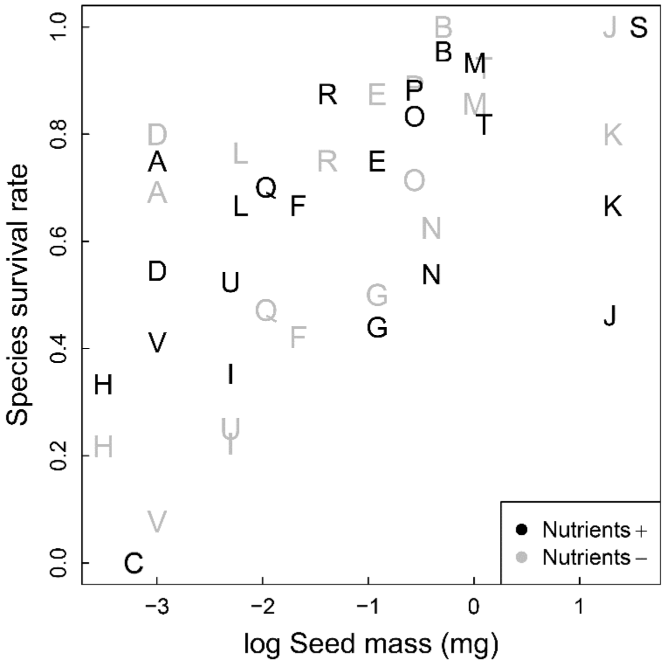

Figure 4.2. Species survival rates of seedlings depending on seed mass and nutrient availability. Each letter stands for the survival rate of one species (see Index in Table 4.1) in natural soils (Nutrient–) and in soils with nutrient addition by horn meal (Nutrient+). The minimal adequate model of seedling survival (iii) predicts a positive effect of seed mass, which is weakened under nutrient addition (see Table 4.2 and 4.3). Please note that the statistical analyses were conducted for individual seedlings and not for survival rates of species as presented here.

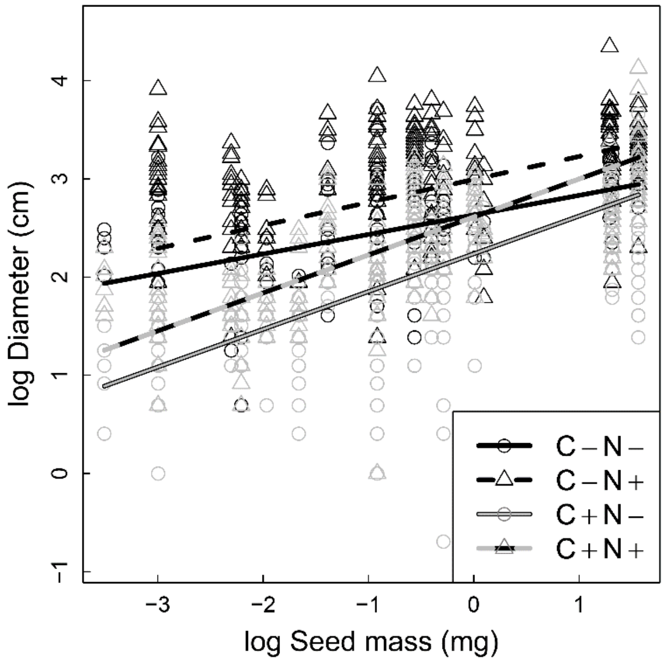

Figure 4.3. Fitness of the seedlings (quantified by diameter) in relation to species mean seed mass and the four different treatments in the study (C = competition, N = nutrient availability). Lines mark significant predictions of the minimal adequate model (see Table 4.2).

4.4 Discussion

Our experiment supports the view that seed mass plays an important role during seedling establishment. The strength of the seed mass effect, however, was impacted by the nutrient availability and competition treatments, which represented the direct addition of nutrients and indirect competition effects of fertilization. In the following, we first discuss our findings for seedling emergence and seedling performance and compare these to findings from other studies. Finally, we introduce a conceptual model and discuss how soil fertilization affects species composition with respect to seed mass in natural communities.

Seedling emergence

Seedling emergence was not related to seed mass. There is still conflicting evidence for whether seed mass already has an effect on the appearance of seedlings. While Moles and Westoby (2004) found no correlation in a meta-study, Ben-Hur *et al.* (2012) showed for Mediterranean annuals that seedling emergence was positively correlated to seed mass independent of the germination ability and viability of seeds. Since laboratory experiments have also shown contrasting seed mass effects on seed germination (e.g. Wang *et al.* 2009, Koutsovoulou *et al.* 2013), the seed mass-seedling emergence relationship seems to be highly context specific and may change with the environmental conditions and species investigated. We hypothesized (a), but could not confirm that increased competition in particular reduces seedling emergence of small-seeded species, since they have a higher light requirement to germinate (Milberg *et al.* 2000). As light availability decreases drastically in soils within the first millimeter (Ciani *et al.* 2005), we conclude that our competition treatment did not significantly reduce the light availability to our shallow buried (five millimeters) seeds.

Contrary to hypothesis (b), we observed an acceleration of seedling emergence under competition. This pattern has been interpreted as an adaptation to deal with competitive environments (Dyer *et al.* 2000, Tielbörger and Prasse 2009), since early emergence increases seedling survival and fecundity (Verdú and Traveset 2005). While our study supports this hypothesis, we question whether early emergence under competition is actually an adaptation to deal with competition. Neighboring plants may modulate the environmental conditions for seeds in many different ways, such as decreasing light availability, but also increasing soil temperature and moisture (Fayolle *et al.* 2009). Hence, it remains speculative whether the seeds actually 'sense' the competitors and germinate faster because this is beneficial, or whether seeds germinate faster under competition just because higher soil temperature and moisture mediated by neighboring plants increase the metabolic activity of seeds. More importantly, the effect of competition on the time of seedling emergence was independent of seed mass.

Seedling performance

In accordance with our hypothesis (c), seed mass did have a positive effect on seedling survival. Furthermore, we showed that the increased survival chances due to seed mass were less pronounced in fertilized soils. This pattern confirms that nutrient deficiency in natural dry grassland soils is a critical factor during the establishment phase, which large-seeded species are more able to tolerate. If nutrient availability increases, the internal resource benefit of large-seeded species is diminished. Hanley *et al.* (2007) found a positive effect of seed mass on seedling growth for Australian species under nutrient deprivation, whereas British species showed no correlation. The authors suggested that these results 'indicate that seed mass is not a consistent predictor of plant response to nutrient deprivation'. However, this study was based on a very small sample size (seven British and eight Australian species of the family *Fabaceae*). In comparison to the global seed mass distribution (Kattge *et al.* 2011), the species included in the study of Hanley *et al.* (2007) were generally large-seeded (1.1 – 23.7 mg), while our study comprises a wide range of seed masses including small-seeded species (0.04 – 4.77 mg). Notably, our experiment represents the global seed mass distribution of herbaceous plants quite well (see Kattge *et al.* 2011, e.g. global mean seed mass with SD of C3-herbs =0.77±0.82 mg, C3-grasses =0.61±0.70 mg). Further, Hanley *et al.* (2007) only analyzed the effect on seedling growth, but not on seedling survival. In contrast, our study provides strong support for the notion that large-seeded species benefit under nutrient-poor conditions, as both seedling survival and growth were positively affected by seed mass.

Competition did not influence the chances of survival, but decreased seedling growth, as observed by Schiffers and Tielbörger (2006). As we hypothesized (d), particularly small-seeded species suffered from competition through a disproportional decrease in growth (see also Leishman 1999). As small-seeded species already produced smaller seedlings, it can be assumed that these seedlings are inherently vulnerable to competition in later growth phases. Metz *et al.* (2010), for instance, showed that small-seeded species also have lower survival rates long after the establishment phase. Hence, small-seeded species should have problems persisting in environments with high productivity, due to reductions in their growth during the establishment phase.

Effect of soil fertility on seed mass in natural communities

In natural plant communities, fertilization increases both the nutrient availability for seedlings as well as competition. It should be mentioned that fertilization also increases litter production (Foster and Gross 1998), which has similar effects to competition on seedling establishment. Litter lowers the light availability for seedlings and thus favors the establishment of large-seeded species (Jensen and Gutekunst 2003, Loydi *et al.* 2013). While most experimental studies have focused on such indirect effects of fertilization (i.e. competition, shade, litter), we also analyzed how nutrient availability influences the establishment ability of species. We found evidence that large-seeded species fared better under nutrient deficiency (higher survival chance) and competition (larger seedlings suffered less from competition than small-seeded species). Based on these findings, we argue that both factors have to be considered in order to understand how fertilization affects seedling establishment and species composition with respect to seed mass. To achieve this goal, we developed a simple conceptual model, in which the average seed mass in plant communities is determined by competition intensity and nutrient deficiency along a gradient of soil fertility (Figure 4.4). When nutrients are scarce and competition is low, large-seeded species have an advantage due to an inherently higher chance of survival under nutrient deprivation (our study, Jurado and Westoby 1992). An increase of nutrient availability diminishes the benefit of large-seeded species (our study). Thus, small-seeded species should eventually dominate the community, as they produce higher amounts of seeds, which increases the chance of colonizing a suitable microsite (Ehrlén and Eriksson 2000). A further increase in soil fertility leads to increased competition (and litter production), which suppresses the establishment of small-seeded species (see above). Fertilization could, therefore, either positively or negatively affect seed mass, depending where the study system is set along the soil fertility gradient and whether competition or nutrient deficiency predominantly affects seedling establishment. This model provides an explanation for why previous studies found either a positive or a negative relationship between soil fertility and seed mass, or no consistent correlation at all (see references in the Introduction).

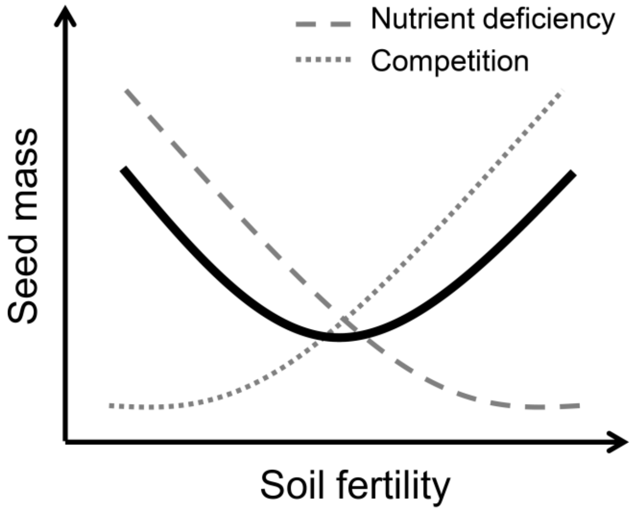

Figure 4.4. Model of the hypothesized relationship between soil fertility and mean community seed mass in relation to competition and nutrient deficiency.

The proposed model is a first attempt to resolve the contradicting patterns of soil fertility – seed mass relationships in the literature, but it definitely requires further verification by experimental field studies. We chose a study system with low soil fertility, which corresponds to the left side in Figure 4, and showed that increasing fertility weakens the positive seed mass-effect on seedling survival. However, in mesic or eutrophic study systems, it remains speculative whether the additional supply of nutrients affects seedling establishment. Another important aspect is how different management regimes influence the seed mass – soil fertility relationship. A recent global experiment showed that herbivory lowers competition for light in plant communities and thereby lowers fertilization induced-species loss (Borer *et al.* 2014). Furthermore, large herbivores also enhance the availability of open microsites through trampling (Bullock *et al.* 1995), which may positively affect the seedling establishment of small-seeded species even in nutrient rich habitats. Hence, the effect of competition on seed mass related processes might be lower in pastures compared to meadows. Finally, it has to be noted that the seed mass variation is quite large in communities (e.g. Westoby *et al.* 2002) and that fertilization incorporates a variety of further mechanisms that influence the species composition such as plant-soil feedbacks, ammonium toxicity and acidification (Stevens *et al.* 2011). These mechanisms are not necessarily linked to seed mass and may obscure any possible relationships between soil fertility and seed mass. Despite the limitations of the model, this highlights the interplay of nutrient availability, competition and seed mass for seedling establishment. In the face of global increases in N-deposition and eutrophication with subsequent species loss, it remains surprising that the role of nutrient availability in structuring plant communities is still not fully understood.

Chapter V
General Discussion

Predicting species compositions of plant communities along environmental gradients and in the context of future environmental change remains a key challenge in plant ecology. In this thesis, I used three empirical approaches to investigate how functional traits can elucidate the underlying mechanisms that drive species compositions in plant communities. In the following text, I first synthesize the findings of the previous three chapters and discuss how traits can help to distinguish between abiotic, biotic and neutral processes. Afterwards, I place my findings in the broader context of whether local or regional processes maintain species diversity, and discuss the critical aspect of scale-dependency. Next, I assess the prospects and pitfalls of the usage of intraspecific trait variability and phylogeny in trait-based community ecology, as both have been controversial topics of discussion in recent publications. Finally, I offer my view of trait-based plant ecology in the future based on the previous discussion.

5.1 Differentiating between abiotic, biotic and neutral processes with the help of traits

Trait-based approaches were highlighted as powerful tools to differentiate between 'Schimper world' (environmental effects) and 'Hubbell world' (neutral effects) in Westoby and Wright (2006). In other words, traits help to distinguish between niche-based and neutral processes (Kraft *et al.* 2008). In the second chapter, I showed that species with similar traits tend to co-occur within the same microsite, indicating that specific environmental conditions favor species with similar traits (trait convergence). In Chapter III, I analyzed whether two Mediterranean species showed trait responses along a precipitation gradient. Although the responses were species-specific and considerable variation remained unexplained, this study highlighted that, even at relatively low precipitation gradients, plant species respond to changing environmental conditions. In chapter IV, I investigated how seedling establishment, a key process during the life cycles of plants, is affected by seed mass in combination with competition and nutrient availability. The experiment showed that the strength of the positive effect of seed mass is mediated by specific environmental conditions. Taken together, these three studies underline how environmental conditions select upon traits and, therefore, the results clearly support Schimper's view on plant communities, in which niche-based processes structure the assembly of species. These findings are consistent with numerous trait-based studies (e.g., Cornwell and Ackerly 2009, Jung *et al.* 2010, Bernard-Verdier *et al.* 2012, Kraft *et al.* 2015, de Bello *et al.* 2015).

The separation of niche-based processes into abiotic environmental filtering and filtering due to biotic interactions is more complex because both can restrict ecological strategies (Mayfield and Levine 2010, de Bello *et al.* 2012, Kraft *et al.* 2015). Classic examples of abiotic environmental filtering include underwater germination ability in submerged plant communities (Van der Valk

1981) or freezing tolerance in alpine regions. Such cases have been widely cited to illustrate environmental filtering based purely on abiotic factors. However, most investigated environmental gradients simultaneously influence biotic interactions; e.g., increasing productivity leads to higher competition for light (Grime 2001, Hautier *et al.* 2009, Borer *et al.* 2014). In chapter II, I discussed how differences in environmental conditions between microhabitats can be used to detect trait convergence; i.e., species with similar traits tend to co-occur. Microhabitats with low water availability (e.g., slopes with a thin soil layer) may be inhabited by stress-tolerant species. By contrast, microsites with high water availability, such as deep-soil hollows, likely favor strong competitors. However, it remains unclear whether the segregation of species with different traits is a result of abiotic environmental filtering (i.e., species cannot survive under particular conditions) or biotic filtering (i.e., species with dissimilar traits are outcompeted by species that are better adapted to particular conditions). The challenge of distinguishing between abiotic and biotic filtering has been outlined in recent publications (Mayfield and Levine 2010, de Bello *et al.* 2012, Kraft *et al.* 2015, Gerhold *et al.* 2015). From my perspective, in vivo experiments that exclude competitors cannot truly separate abiotic and biotic factors in plant communities (Kraft *et al.* 2015) because the exclusion of competitors also changes the abiotic factors, such as local temperature and wind speed. Further, microorganisms that interact with plants are omnipresent in all habitats and cannot be separated from the abiotic environment (Aguilar-Trigueros *et al.* 2017). Distinguishing between abiotic and biotic filtering is further complicated by temporal variability in environmental conditions. For example, Mediterranean annual plant communities experience considerable interannual variability in precipitation. In dry years, abiotic filtering may be the determining process that structures species assembly, since abiotic stress increases under dry conditions. By contrast, in wet years, competition may be more important for species assembly. It should also be kept in mind that both abiotic and biotic filtering are processes that may take several years even in annual communities. For example, the focal species may survive under local conditions, but not be able to produce sufficient seeds for a viable population. Under these considerations, it is critical to ask if there is a clear separation between biotic and abiotic filtering, or if they often act together. A recent review found that clear evidence for abiotic filtering is fairly rare (Kraft *et al.* 2015). However, in my opinion, it is more important to understand why species with particular traits have a fitness advantage under certain conditions rather than trying to disentangle abiotic and biotic components of environmental filtering. Although there has been considerable research investigating the relationships between traits and processes, it is (surprisingly) often unclear which plant traits are correlated with fitness (Hortal *et al.* 2015, Laughlin *et al.* 2018). In chapter IV, I analyzed how nutrient availability and competition mediate the presumably positive effect of large seed mass on seedling establishment, and found that this effect is particularly strong in nutrient-poor soils. By contrast, the positive effect of seed mass on seedling growth was particularly high under competition, but was not altered by nutrient availability. Therefore, the fitness advantage of seed mass depends on specific abiotic and biotic conditions and may act via different processes. Hence, assessing how fitness is related to traits across habitat types and along environmental gradients may also help to elucidate abiotic and biotic filtering processes.

5.2 Importance of local heterogeneity for species coexistence

Scale-dependency is critical for understanding species assembly because environmental filters, interaction with other species, and neutral processes presumably act at different spatial scales (HilleRisLambers *et al.* 2012, Götzenberger *et al.* 2012, Chase 2014). A central debate in community ecology is whether the coexistence of species is driven by regional or local processes (Ricklefs 2008, May *et al.* 2013b, Weiss *et al.* 2014). For example, Ricklefs (2008) proposed casting aside the concept of communities because species assemble based on large-scale, regional processes; therefore, high diversity at small spatial scales is just an 'epiphenomenon.' However, a question remains: how important are regional processes for the species composition in plant communities at a given site? A modeling study (May *et al.* 2013b) investigated the same semi-arid system examined in chapters II and III and showed that species compositions within habitat patches behaved like isolated islands rather than meta-communities or mainland–island structures. Further support for isolation of habitat patches comes from two genetic studies that revealed strong genetic differentiation between populations of closely situated habitat patches in the same study system (Gemeinholzer *et al.* 2012, Müller *et al.* 2017). Additionally, in central European dry grasslands, there is increasing evidence that habitat patches are indeed quite isolated (Weiss *et al.* 2014, Müller *et al.* 2014). Therefore, I suspect that the coexistence of species within both study systems is mainly driven by local processes. In chapter II, I showed that species with similar traits tend to co-occur in the same microsites, indicating that species are spatially separated according to their environmental preferences. With increasing heterogeneity, species diversity and functional diversity also increased. Therefore, small-scale heterogeneity can be considered a central stabilizing factor that allows species to coexist and communities to harbor species with diverse traits. For instance, seed mass ranged from 0.008 mg to 113.2 mg at the local scale (15 m × 15 m). Similar variations in seed mass were also observed in other study systems, such as dry grasslands (chapter IV). Muller-Landau (2010) postulated that spatial heterogeneity in resource availability may maintain species with different seed masses in the community because stressful microhabitats are colonized by large-seeded species and mesic microhabitats by small-seeded species that produce more seeds. In the semi-arid environment (chapters II and III), different structures like large bushes and exposed rocks provided microhabitats with different resources and environmental conditions. In central European dry grasslands, large herbivores create environmental heterogeneity and alter soil nutrient availability with their droppings, and affect local competition for light by grazing and trampling (Olff and Ritchie 1988, Adler *et al.* 2001). In chapter IV, I showed that large-seeded species particularly benefit during seedling establishment in nutrient poor soils as well as under high competition. Therefore, large herbivores may foster the coexistence of species with differing seed masses. This is particularly interesting because the positive effect of grazers on plant species diversity is often attributed solely to a reduction in competition for light without acknowledging the role by herbivores in spatial resource heterogeneity (Borer *et al.* 2014). In conclusion, coexistence of plant species seem to be triggered by local factors rather than determined by regional propagule exchange in the investigated plant communities. Hereby, further experiments should assess how small-scale heterogeneity affects fitness differences between species with different traits (compare Adler *et al.* 2013).

5.3 Resolving conflicting trait–environment relationships

Conflicting trait–environment relationships can be the result of scale-dependency. In chapter IV, I developed a conceptual model for how seed mass should respond along a soil fertility gradient to resolve inconsistent reports of seed mass–soil fertility relationships. In this model, two factors—nutrient availability and competition—determine seed mass in a u-shaped pattern. This model may be extended to any stress–productivity gradient. As is the case with soil fertility–seed mass relationships, clear empirical evidence for an aridity–seed mass relationship is lacking. At the community level, studies have variously reported positive (Azcarate *et al.* 2010) or negative relationships (Harel *et al.* 2011, May *et al.* 2013a), or none at all (Pakeman *et al.* 2008, Nunes *et al.* 2017). In addition, Cochrane *et al.* (2015) summarized inconsistent seed mass–aridity relationships at the population level (see also Kurze *et al.* 2017). In the Southern Judean Lowlands, where the studies from chapters II and III were conducted, seed mass increased with precipitation at the community level (May *et al.* 2013a) and within at least one of two species (chapter III). In the context of the conceptual model developed in chapter IV, this study system would be further right along the stress–productivity gradient, where seed mass increases with productivity. This seem unlikely, since the same pattern was observed along a broad precipitation gradient in Israel (mean annual precipitation: 90–780 mm), including a desert site (Harel *et al.* 2011). Therefore, it cannot be expected that seed mass would increase further under even drier conditions, as the model from chapter IV would predict. One fundamental reason for inconsistent precipitation–seed mass relationships may be due to the multidimensionality of precipitation gradients. The precipitation gradient in Israel is almost ideally suited for study, since there is a substantial increase over a relatively short distance moving from south to north, (e.g., May *et al.* 2013a, Kurze *et al.* 2017), and many other confounding parameters remain constant, including temperature and altitude.

However, towards the arid end of the precipitation gradient, the growing season is shorter and the predictability of rainfall decreases (Kurze *et al.* 2017). These factors might not necessarily vary in other study regions (or in other dimensions), but they may act as an independent selecting factor. A shorter vegetation period favors earlier flowering and smaller plants (Kigel *et al.* 2011), which generally produce lighter seeds (Westoby *et al.* 2002, Diaz *et al.* 2016). Unpredictability of rain events should increase bet-hedging strategies to minimize interannual variability in survival chance. Indeed, an extensive field study within Israeli annual plant communities revealed that large seed mass maximizes survival chances from year to year, indicating that it is beneficial under unpredictable environment conditions (Metz *et al.* 2010). Therefore, variation in precipitation may act as a selecting factor, particularly in arid environments when annual precipitation becomes increasingly unpredictable (Siewert and Tielbörger 2010, Kurze *et al.* 2017). An alternative strategy for coping with unpredictable conditions is to increase dispersal ability (Venable and Brown 1988), e.g., with a higher number of smaller seeds. As a result, species in arid environments should have on average a lower seed mass and increased number of seeds. Thus, the observed seed-mass trends along the Israeli precipitation gradient may not be an adaptation to aridity *per se*, but to unpredictability or a shorter vegetation period. This multidimensionality complicates the resolution of trait–environment relationships and may help to explain why studies find apparently inconsistent relationships, given that second or third confounding factors were not considered in these analyses.

Understanding trait–environment relationships at larger scales (e.g., along precipitation gradients) may also help to elucidate assembly patterns at small scales (chapter II). I assumed that the same selective pressures (i.e., water availability) that structured plant communities across the landscape also structured species co-occurrence at small spatial scales. One main drawback of chapter II is that environmental conditions of the microsites where vegetation was sampled were not properly characterized due to the tremendous effort that would have been required (972 microsites). Therefore, I can only assume that drier microsites due to shallower soils drive the convergence of seed mass, plant height, and specific leaf area, as observed in Mediterranean grasslands (Bernard-Verdier *et al.* 2012). However, since the observed large-scale trait patterns are not easy to interpret (see above), a more detailed analysis is needed to investigate how differences in microhabitats select for specific traits at local scales, particularly for how small-scale heterogeneity affects species assembly (see above).

5.4 Intraspecific trait variability in community ecology

Intraspecific trait variability (ITV) was previously neglected in plant community studies. This situation changed when empirical studies revealed that a substantial proportion of trait variation is actually found within species (Messier *et al.* 2010, Siefert *et al.* 2015) and new conceptual frameworks began to incorporate ITV into community ecology (Jung *et al.* 2010, Violle *et al.* 2012, De Bello *et al.* 2012, Laughlin *et al.* 2012, Carmona *et al.* 2016). In this thesis, neither community study (chapters II and IV) explicitly considered ITV. In chapter IV, 92% of variation in single-weighted seed masses was explained by the species identity, indicating that in this case study ITV was indeed negligible compared with interspecific trait variation. In chapter II, I expect that the environmental conditions at a microsite would select for the same traits at both the intraspecific and interspecific levels (e.g., Westoby 1998). This is supported by the comparison of intraspecific and community responses along the precipitation gradient (May *et al.* 2013a, see chapter III). Therefore, I suspect that the observed pattern within chapter II would have strengthened or remained constant, but would most certainly not have changed, if ITV had been included. Although the incorporation of ITV might be beneficial in specific cases (e.g., Jung *et al.* 2010), I do not think it is a general necessity to incorporate ITV into community studies for two main reasons. First, chapter III revealed that intraspecific responses along environmental gradients are highly species-specific (see also Albert *et al.* 2010). Such studies ask whether there are common intraspecific responses, which impedes the inclusion of ITV. A thorough examination of ITV requires that the sampling effort increases substantially, meaning that only easily measured traits are realistic to include. Thus, although accuracy is gained for specific traits, other niche dimensions that are more time-consuming to measure are ignored. Certainly, it is no coincidence that almost all community ITV studies use easily measured foliar traits and plant height (e.g., Albert *et al.* 2010, Messier *et al.* 2010, Siefert *et al.* 2015, Baruch *et al.* 2017). However, coexistence and community assembly act according to various niche dimensions (Kraft *et al.* 2015), so a sufficient number of niche dimensions should be guaranteed. Second, it remains questionable whether the measured ITV equals the ‘true’ ITV. Measurement errors may inflate ITV (Kraft *et al.* 2009) and studies that reported an apparently high ITV within communities analyzed single traits separately (Siefert *et al.* 2015). These one-dimensional analyses show that trait values are not limited to a particular species, but rather overlap between species. However, this trait overlap will certainly decrease in a multidimensional trait space because species that are similar in one trait will differ in other traits despite of certain trait syndromes (Diaz *et al.* 2016). Therefore, the importance of ITV decreases if the ecological behavior of the ‘whole’ species (rather than single niche dimensions) is considered. In conclusion, the advantages of including ITV often do not outweigh the disadvantages; i.e., a reduction in the number of sampled traits, thus including ITV, may hamper our understanding of how environmental gradients and biotic interactions shape species co-occurrence.

5.5 Phylogeny in community ecology

Phylogenetic relationships between species can be used to better understand species assembly. Since the introduction of community phylogenetics by Webb *et al.* (2002; see also Webb 2000), there has been an ongoing, lively debate on the merits, pitfalls and prospects of detecting community assembly processes with the help of phylogeny (Cavender-Bares *et al.* 2009, Gerhold *et al.* 2015, de Bello *et al.* 2015, Cadotte *et al.* 2017). In general, it is assumed that closely related species share similar traits (trait conservatism) because they have the same ancestor (Webb *et al.* 2002). However, critical reviews have pointed out that the associations between traits and phylogenies are often weak (Losos 2008) and depend on the scale under consideration (Cavender-Bares *et al.* 2009). Additionally, in the same species set, some traits may have been conserved while others have diverged (i.e., closely related species have different traits) (Gerhold *et al.* 2015, Cavender-Bares *et al.* 2009). Therefore, the interpretation of observed phylogenetic patterns in communities can be impeded or even impossible. In chapter II, I used the three most fundamental and widely used functional traits in plant ecology: seed mass, specific leaf area and plant height. All traits showed some degree of phylogenetic signal (i.e., traits were phylogenetically conserved), which has been observed in other ecosystems (e.g., Kraft and Ackerly 2010, Bernard-Verdier *et al.* 2012). Furthermore, a series of other traits (not measured in chapter II) have been shown to be phylogenetically conserved, e.g., root traits (Valverde-Barrantes *et al.* 2015, Bergmann *et al.* 2017, Wang *et al.* 2018), germination traits (Cao *et al.* 2017) and the ability to fix nitrogen. Therefore, I expected to find that closely related species tend to co-occur, since the functional approach consistently detects trait convergence. However, in the second null model analysis of chapter II, I detected phylogenetic overdispersion of individuals; i.e., species abundances at the microsites were more regularly distributed across the phylogenetic tree than expected by chance. There are two ways to interpret these results. Either the traits are phylogenetically convergent, which seems very unlikely (see above and discussion of chapter II) or the traits were phylogenetically conserved but the species assembly has opposing effects on the traits. In this case, some traits show convergence, while others show divergence (Grime 2006, Spasojevic and Suding 2012). The phylogenetic approach therefore indicates that other processes may have caused divergence in this study. Such conclusions remain obscure, however, if the phylogenetic approach is not employed. Therefore, the criticism of phylogenetic approaches is reminiscent of that concerning trait-based approaches because the selection of traits has a strong impact on the results. It must be remembered that researchers' selection of traits is mostly driven by the resources available rather than by the specific research question. This is particularly problematic because the standardization of functional traits (Cornellissen *et al.* 2003) and databanks (Kattge *et al.* 2011) lead to plant ecologists usually working with the same handful of traits. In conclusion, I believe that the simultaneous usage of functional and phylogenetic approaches (chapter II) is a compelling example for how phylogenetic approaches may contribute to our understanding of species assembly and may lay the foundation for future research. Of course, the interpretation of phylogenetic patterns should be approached with care, as the underlying mechanisms remain vague. However, careful interpretation is also needed for trait-based analyses.

5.6 Trait-based research – where do we go from here?

The identification of key functional traits (Grime *et al.* 1997, Westoby 1998, Weiher *et al.* 1999, Westoby *et al.* 2002) and the following standard protocols for measurements (Cornellisen *et al.* 2003, Perez-Higuary *et al.* 2013) helped plant ecologists to 'speak a common language.' These fundamental works standardized study approaches and facilitated cross-scale and global analyses of plant communities (e.g., Wright *et al.* 2004, Siefert *et al.* 2015, Diaz *et al.* 2016, Butler *et al.* 2017, Le Bagousse-Pinguet *et al.* 2017). However, after 20 years of trait-based plant-community research, ecologists should ask themselves whether it is always appropriate to use the same functional traits from a core list. The predictive power is often quite low and a lot of variation remains unexplained (e.g., Kraft and Ackerly 2009, Hortal *et al.* 2015). In addition, although some generalities have emerged, contradictory patterns are far from the exception (chapters III and IV, Cochrane *et al.* 2015, Moles 2018). Most likely, this is because the commonly used traits, although easily measured, are only simple proxies for niche dimensions of species (Kraft *et al.* 2009, Hortal *et al.* 2015). In recent years, it has been argued that the incorporation of intraspecific trait variability would increase the predictive power of trait-based analyses, leading to a better understating of community assembly and ecosystem services (Violle *et al.* 2012, Laughlin *et al.* 2012). I would agree that the inclusion of ITV is necessary for some research questions (see above). However, I think that measuring both intra- and interspecific trait variability risks leading to a serious reduction in the trait dimensions being investigated. Therefore, I advocate going beyond the commonly used key traits and investigate traits that (a) are more tailored to the specific study system and research question and (b) have mostly been neglected in plant community studies. In a recent common garden experiment, Kurze *et al.* (2017) showed that the annual grass *Brachypodium hybridum* showed no ecotypic differentiation in key functional traits (specific leaf area, seed mass and plant height) along a large precipitation gradient. However, strong trends were observed in phenology and belowground traits, such as root biomass and root:shoot ratio. Therefore, it seems very likely that plant coexistence and species assembly will be also influenced by these traits (Laughlin 2014, de la Riva 2018). While most trait-based research focused on traits that are correlated with the ability to exploit light and produce biomass, traits correlated with the ability to acquire water have been studied far less (Kattge *et al.* 2011, Laughlin 2014). Furthermore, it is clear that belowground traits are not correlated with aboveground traits (Bergmann *et al.* 2017). In particular, belowground traits should be acknowledged in plant studies conducted in study systems in which water is a main limiting resource. Although community-wide sampling of such traits requires a huge effort, it will certainly strengthen our understanding of the underlying mechanisms of species assembly and coexistence. Otherwise, we are neglecting a large part of species separation, which seems risky, since species coexistence is likely triggered by multidimensional trait variation, rather than single trait dimensions (Kraft *et al.* 2015, see also Laughlin 2014).

In 2011, Weiher *et al.* wrote in an influential review stating that “the formal description of trait–environment relationships remains surprisingly rare”. Due to the overwhelming amount of recent trait-based studies, this situation has changed at least for plant communities. However, the underlying mechanisms of observed patterns remain often unclear; some studies have found contradictory trait–environment relationships, and it is often not clear why a species with specific traits has a fitness advantage (see above). Potential reasons for inconsistent trait–environment relationships are varied; scale-dependence, poor trait selection, or the multidimensionality of environmental gradients are all possible. To understand apparently contradictory trait–environmental relationships, I propose experimentally quantifying the correlation between traits and fitness along environmental gradients (e.g., Laughlin *et al.* 2018). Preferably, such experiments should be conducted in study systems where inconsistent trait–environment relationships have been previously observed.

Since the early days of Alexander von Humboldt, numerous studies have shown species-sorting along environmental gradients, although the underlying mechanisms often remain unclear (see above). Far less is known about the importance of environmental differences at small spatial scales for maintaining species diversity. As outlined above, I argue that it is crucial to focus on local processes to understand species coexistence and why so many species may co-occur at small spatial scales. Although new experiments are impacting how modern coexistence theory is tested in annual plant communities (Godoy *et al.* 2014, Kraft *et al.* 2015), these experiments have failed to incorporate environmental heterogeneity. The results of chapter II indicate that environmental differences at microsites favor species with specific traits, leading to environmental filtering at small spatial scales. As a result, more species may persist in heterogeneous habitats than in homogenous ones. Additionally, the findings of chapter IV indicate that heterogeneity in soil and competition may lead to the coexistence of species with differing seed masses (compare Muller-Landau 2010). Another body of studies highlights heterogeneity in time as a stabilizing factor for species coexistence (e.g., Adler *et al.* 2013). In particular, for annuals in semi-arid environments, variation in annual precipitation is an important factor for survival, and studies have shown that dormancy or high seed mass increases fitness and may act as bet-hedging strategies (Metz *et al.* 2010, Venable *et al.* 2014). However, due to a lack of long-term studies, it remains unclear how important temporal variability is for coexistence in these annual communities. An assessment of the importance of both temporal and spatial heterogeneity can be conducted in pot community experiments that simulate microhabitats with varying spatial heterogeneity, e.g., soil depth, temporal heterogeneity, and water availability between growing seasons. The species composition should be manipulated simultaneously within the experiment so that pots contain species that are functionally (and phylogenetically) similar and dissimilar to each other, as well as random assortments. Furthermore, systematic manipulation of seed placement in the pots would help to elucidate the importance of dispersal among microsites and neutral processes.

5.7 Concluding remarks

Trait-based research is very much guided by the question, “Are there general laws in ecology?” asked by Lawton (1999), who stated that community ecology is a mess (McGill *et al.* 2006). In this thesis, I aimed to improve our understanding of how environmental gradients shape plant communities based on functional traits. At the end of my thesis, I would like to respond to Lawton’s question: “Yes, there are laws in plant communities, but they are sometimes very well hidden.” Despite all the criticism, trait-based approaches have indeed identified generalities; observed inconsistencies do not necessarily mean that different processes took place. Different assembly pattern between studies may be resolved if scale-dependence is addressed (chapter II). Species that show different trait responses along gradients may show the same responses in other traits (chapter III). Studies reporting Inconsistent trait–environment relationships may be the result of different locations along environmental gradients (chapter V). Therefore, I am confident that trait-based approaches are an essential tool to further improve our understanding of how environmental gradients and future environmental change will affect plant distributions.

Supplementary Material

Appendix A - Supplementary Material to chapter II

Appendix A1

Construction of the phylogenetic tree of the annual plants in the Southern Judean Lowlands. The phylogenetic tree was constructed in two steps. At first, we built a tree of the respective plant families, which bases on the proposed phylogeny of the Angiosperm Phylogeny Group (APG 2009). Notes and branch lengths of this tree were adjusted to divergence times estimated by molecular data, which were calibrated to known fossil ages (Bell *et al.* 2010). We used divergence times of the exponential model of gene evolution, as it more appropriate than the log-normal model, if paleontological information is inadequate. The relationships between species within families were resolved manually with the help of 39 publications (see References). Divergence times within families were unfortunately not always available and had to be guessed. Unclear relationships between species remained as polytomies. The tree used in this study is given in Newick format and as figure.

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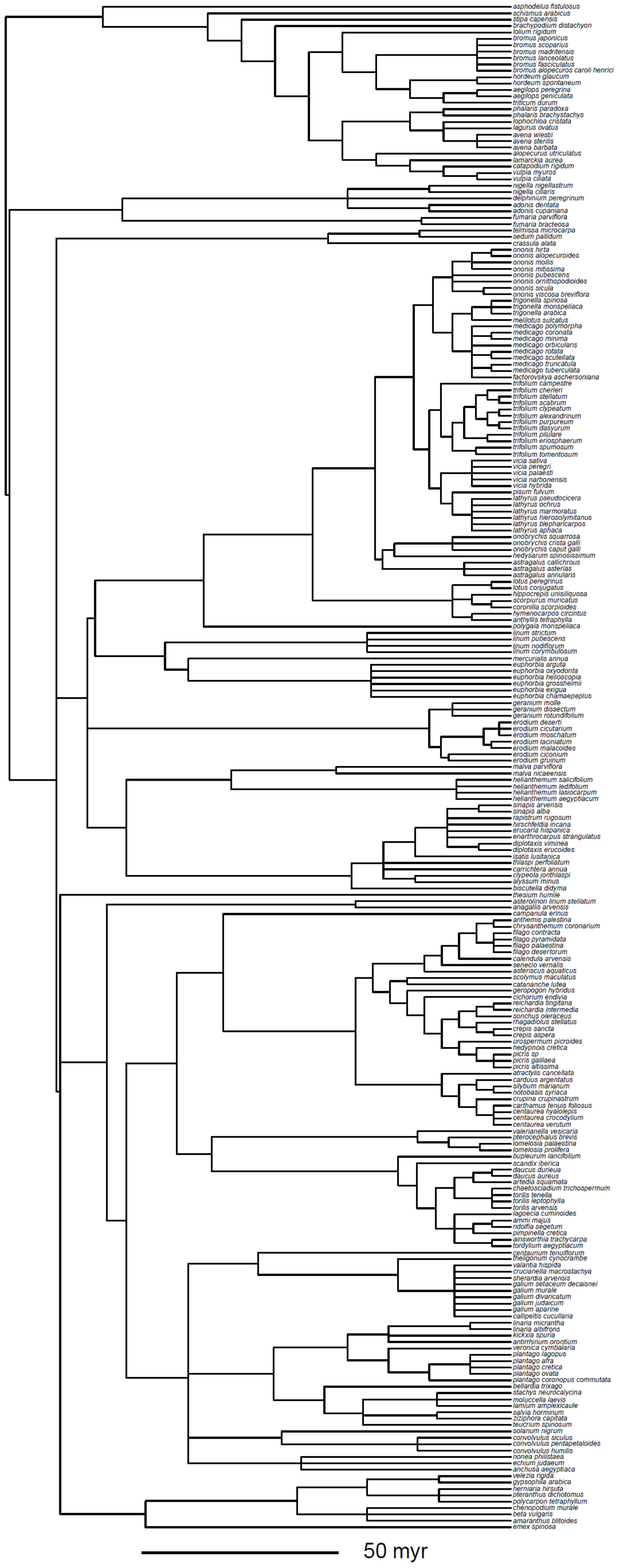
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bromus alopecuros caroli henrici
hordeum glaucum
hordeum spontaneum
aegilops peregrina
aegilops geniculata
triticum durum
phalaris paradoxa
phalaris brachystachys
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lagurus ovatus
avena wiestii
avena sterilis
avena barbata
alopecurus utriculatus
lamarckia aurea
catapodium rigidum
vulpia myuros
vulpia ciliata
nigella nigellastrum
nigella ciliaris
delphinium peregrinum
adonis dentata
adonis cupaniana
fumaria parviflora
fumaria bracteosa
telmissa microcarpa
sedum pallidum
crassula alata
ononis hirta
ononis alopecuroides
ononis mollis
ononis mitissima
ononis pubescens
ononis ornithopodioides
ononis sicula
ononis viscosa breviflora
trigonella spinosa
trigonella monspeliaca
trigonella arabica
melilotus sulcatus
medicago polymorpha
medicago coronata
medicago minima
medicago orbicularis
medicago rotata
medicago scutellata
medicago truncatula
medicago tuberculata
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trifolium tomentosum
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vicia peregri
vicia palaesti
vicia narbonensis
vicia hybrida
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lathyrus ochrus
lathyrus marmoratus
lathyrus hierosolymitanus
lathyrus blepharicarpos
lathyrus aphaca
onobrychis squarrosa
onobrychis crista galli
onobrychis caput galli
hedysarum spinosissimum
astragalus callichrous
astragalus asterias
astragalus annularis
lotus peregrinus
lotus conjugatus
hippocrepis unisiliquosa
scorpiurus muricatus
coronilla scorpioides
hymenocarpos circintus
anthyllis tetraphylla
polygala monspeliaca
linum strictum
linum pubescens
linum nodiflorum
linum corymbulosum
mercurialis annua
euphorbia arguta
euphorbia oxyodonta
euphorbia helioscopia
euphorbia grossheimii
euphorbia exigua
euphorbia chamaepeplus
geranium molle
geranium dissectum
geranium rotundifolium
erodium deserti
erodium cicutarium
erodium moschatum
erodium laciniatum
erodium malacoides
erodium ciconium
erodium gruinum
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malva nicaeensis
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helianthemum ledifolium
helianthemum lasiocarpum
helianthemum aegyptiacum
sinapis arvensis
sinapis alba
rapistrum rugosum
hirschfeldia incana
erucaria hispanica
enarthrocarpus strangulatus
diplotaxis viminea
diplotaxis erucoides
isatis lusitanica
thlaspi perfoliatum
carrichtera annua
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alyssum minus
biscutella didyma
thesium humile
asterolinon linum stellatum
anagallis arvensis
campanula erinus
anthemis palestina
chrysanthemum coronarium
filago contracta
filago pyramidata
filago palaestina
filago desertorum
calendula arvensis
senecio vernalis
asteriscus aquaticus
scolymus maculatus
catananche lutea
geropogon hybridus
cichorium endivia
reichardia tingitana
reichardia intermedia
sonchus oleraceus
rhagadiolus stellatus
crepis sancta
crepis aspera
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hedypnois cretica
picris sp
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picris altissima
atractylis cancellata
carduus argentatus
silybum marianum
notobasis syriaca
crupina crupinastrum
carthamus tenuis foliosus
centaurea hyalolepis
centaurea crocodylium
centaurea verutum
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pterocephalus brevis
lomelosia palaestina
lomelosia prolifera
bupleurum lancifolium
scandix iberica
daucus durieua
daucus aureus
artedia squamata
chaetosciadium trichospermum
torilis tenella
torilis leptophylla
torilis arvensis
lagoecia cuminoides
ammi majus
ridolfia segetum
pimpinella cretica
ainsworthia trachycarpa
tordylium aegyptiacum
centaurium tenuiflorum
theligonum cynocrambe
valantia hispida
crucianella macrostachya
sherardia arvensis
galium setaceum decaisnei
galium murale
galium divaricatum
galium judaicum
galium aparine
callipeltis cucullaria
linaria micrantha
linaria albifrons
kickxia spuria
antirrhinum orontium
veronica cymbalaria
plantago lagopus
plantago afra
plantago cretica
plantago ovata
plantago coronopus commutata
bellardia trixago
stachys neurocalycina
moluccella laevis
lamium amplexicaule
salvia horminum
ziziphora capitata
teucrium spinosum
solanum nigrum
convolvulus siculus
convolvulus pentapetaloides
convolvulus humilis
nonea philistaea
echium judaeum
anchusa aegyptiaca
velezia rigida
gypsophila arabica
herniaria hirsuta
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polycarpon tetraphyllum
chenopodium murale
beta vulgaris
amaranthus blitoides
emex spinosa
50 myr

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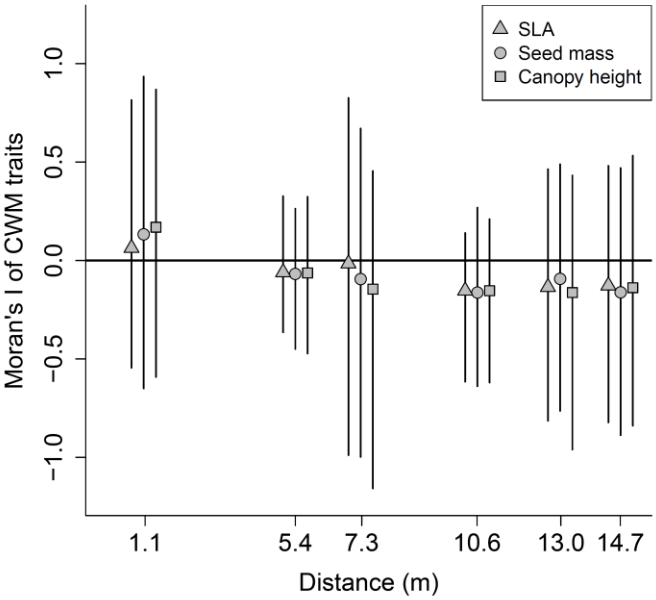
Appendix A2

Spatial autocorrelation of community weighted mean (CWM) traits within 15 m × 15 m plots. The CWM traits were calculated for the small microsites (0.06 m²) and included the abundance of species. Moran's I was calculated for six distance-classes with an equal number of observations. Symbols mark mean values with the respective 95%-confidence interval.



Appendix A3

Effect of environmental heterogeneity (Het) and land unit (LU) on the standardized effect sizes (SES) of both null models. The linear models included also the functional diversity (FD) and the number of species (SD) of the null model, since both have a strong effect on the magnitude of SES (see Methods). For analyses of null model 2, mean species and functional diversity of plots (15 m × 15 m) were taken. The table shows F-values of single-term deletions with respective p-values. Analyses were conducted only for null models, in which SES was significantly different from zero (see Table 2.1). ‘#’ signifies term in significant interaction. Significant ($p<0.05$) effects of predictors are bold-typed.

Null model	**Trait**	**Grain size [m²]**	**Het : LU**		**Het**		**LU**		**SD**		**FD**	
			F	p	F	p	F	p	F	p	F	p
1	LHS	0.06	0.14	0.87	0.03	0.86	0.19	0.82	0.25	0.61	0.05	0.83
	Seed mass		0.71	0.49	0.01	0.91	0.27	0.77	0.02	0.88	0.91	0.34
	Canopy height		2.28	0.11	1.37	0.25	0.24	0.78	0.43	0.52	0.11	0.74
	LHS	1	0.13	0.88	0.38	0.54	1.7	0.19	**4.9**	**0.03**	0.28	0.6
	Seed mass		0.36	0.69	1.07	0.3	1.49	0.23	0.86	0.36	0.05	0.83
	Canopy height		0.41	0.81	1.1	0.3	1.13	0.33	2.76	0.1	0.3	0.58
	Phylogeny		0.04	0.96	2.8	0.098	1.07	0.35	0.17	0.68	0.07	0.8
2	LHS	0.06	1.84	0.17	0.61	0.44	0.69	0.51	**12.59**	**0.0007**	**70.65**	**>0.0001**
	Seed mass		0.21	0.81	1.13	0.29	0.35	0.7	**5.02**	**0.03**	**24.09**	**>0.0001**
	Canopy height		0.98	0.38	1.89	0.17	2.64	0.08	0.005	0.95	**8.13**	**0.006**
	Specific leaf area		**3.13**	**0.049**	#		**#**		**22.22**	**>0.0001**	**42.68**	**>0.0001**
	Phylogeny		1.84	0.17	0.31	0.58	2.99	0.57	3.51	0.07	0.71	0.4

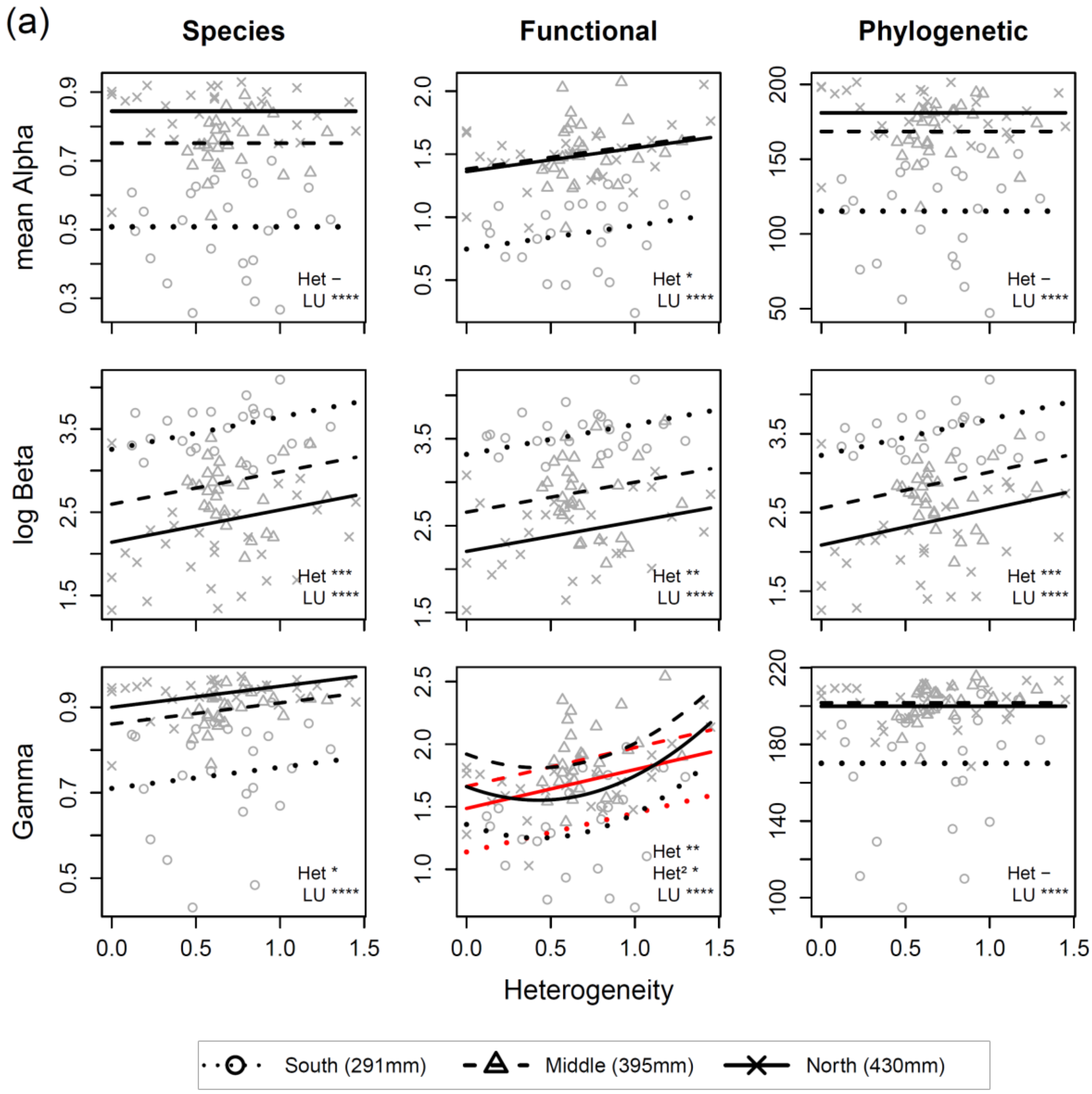
Appendix A4

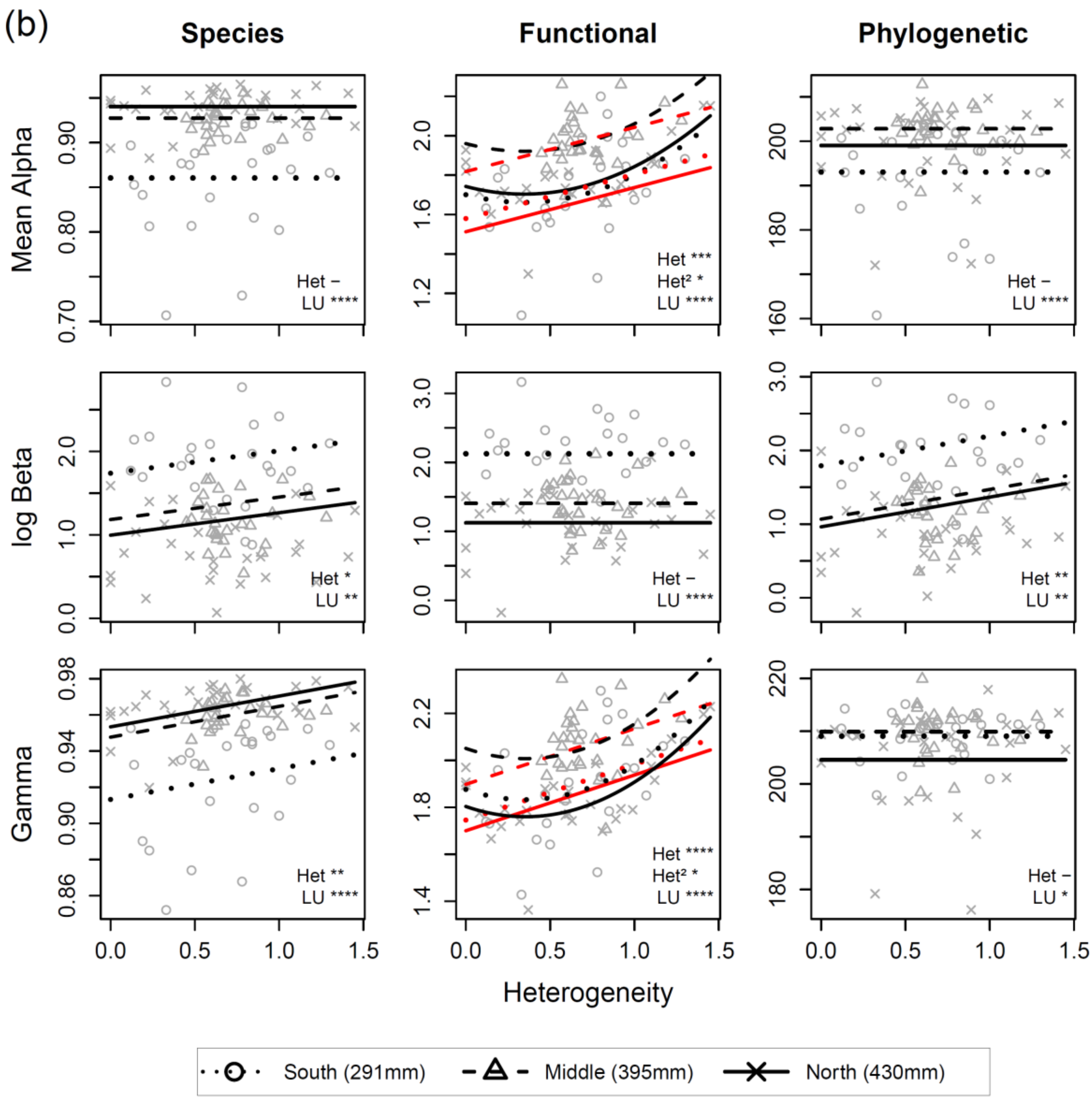
Correlation coefficients between species (SD), functional (FD) and phylogenetic (PD) diversities for different grain sizes (0.06 m², 1 m²) based on presence-absence data. Significant correlations are in bold font ($p<0.05$).

Diversity	**Grain size [m²]**	**SD/FD**	**SD/PD**	**FD/PD**
Mean Alpha	0.06	**0.86**	**0.97**	**0.87**
	1	**0.54**	**0.66**	**0.55**
Beta	0.06	**0.94**	**0.99**	**0.94**
	1	**0.94**	**0.97**	**0.95**
Gamma	0.06	**0.71**	**0.91**	**0.74**
	1	**0.34**	0.05	**0.33**

Appendix A5

Effect of environmental heterogeneity (Het) and land unit (LU) on mean alpha, beta and gamma diversity of 15 m × 15 m plots. The analyses were conducted separately for species, functional and phylogenetic diversity at two different grain sizes (a) 0.06 m^2 and (b) 1 m^2. Analyses were conducted with presence-absence data (see Table 2.2). Black lines indicate significant ($p<0.05$) predictions of minimal adequate models. Red lines indicate predictions of models that did not include the quadratic term of the heterogeneity index. Please note that the models of beta diversity additionally included species richness as covariate. For the graphical illustration, number of species was set to the medians of the land units. ****<0.0001, *** $p<0.001$, ** $p<0.01$, * $p<0.05$, '–' indicates not significant ($p>0.05$).

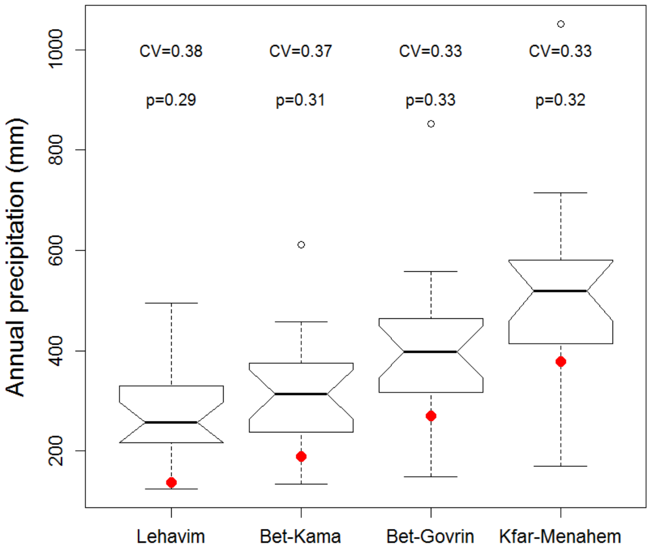



(b)
Species
Functional
Phylogenetic
Mean Alpha
log Beta
Gamma
0.70
0.80
0.90
1.2
1.6
2.0
160
180
200
0.0
1.0
2.0
3.0
0.86
0.90
0.94
0.98
1.4
1.8
2.2
220
Het –
LU ****
Het ***
Het² *
LU ****
Het –
LU ****
Het *
LU **
Het –
LU ****
Het **
LU **
Het **
LU ****
Het ****
Het² *
LU ****
Het –
LU *
0.0
0.5
1.0
1.5
Heterogeneity
South (291mm)
Middle (395mm)
North (430mm)

Appendix B - Supplementary Material to chapter III

Appendix B1

Precipitation of rainy seasons of four rain stations nearby the land unit. The rain stations are ordered from south to north and contain rain data from 25 consecutive years (1988 – 2013). The red dots mark the precipitation amount during the rainy season 2010-2011, when sampling was conducted. 'CV' refers to the coefficient of variation of annual precipitation amount. 'p' refers to the predictability of monthly precipitation amounts calculated after Colwell (1974). Both indices indicate that precipitation becomes increasingly unpredictable towards aridity.



Reference

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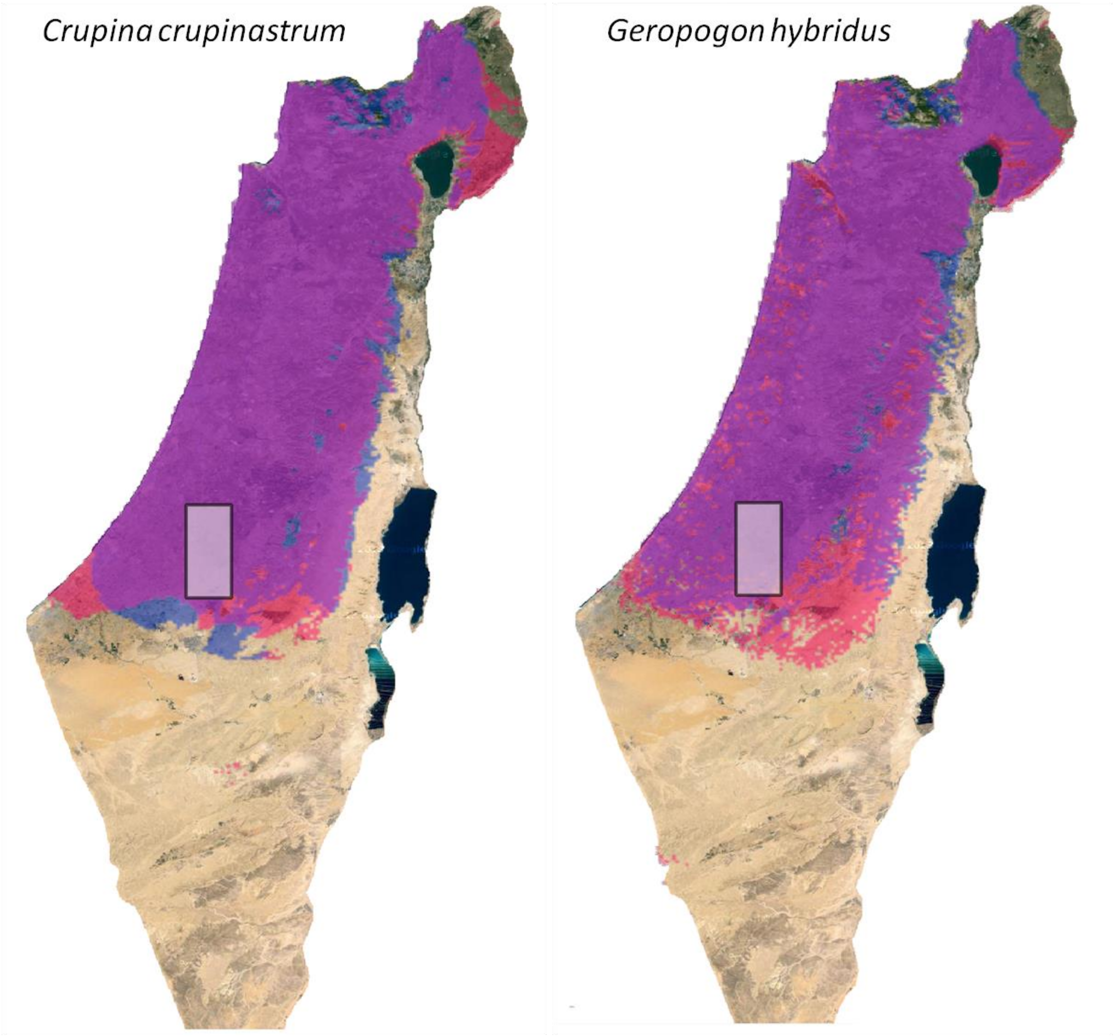
Appendix B2

Habitat models of both study species *Crupina crupinastrum* and *Geropogon hybridus*. Red areas mark potential areas identified by the ENFA (Ecological Niche Factor Analysis) model (Hirzel *et al.* 2002), blue areas by the Mahalanobis model (Farber and Kadmon 2003); purple areas define the overlap of both models. Habitat models base on 321 (*C. crupinastrum*) and 350 (*G. hybridus*) observations in Israel and four environmental factors: mean annual rainfall [mm], mean January temperature [°C], aspect [°] and seasonal temperature change [°C]. The models were conducted with BioGIS (2012) – Israel Biodiversity Information System. (http://www.biogis.huji.ac.il)



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Appendix B3

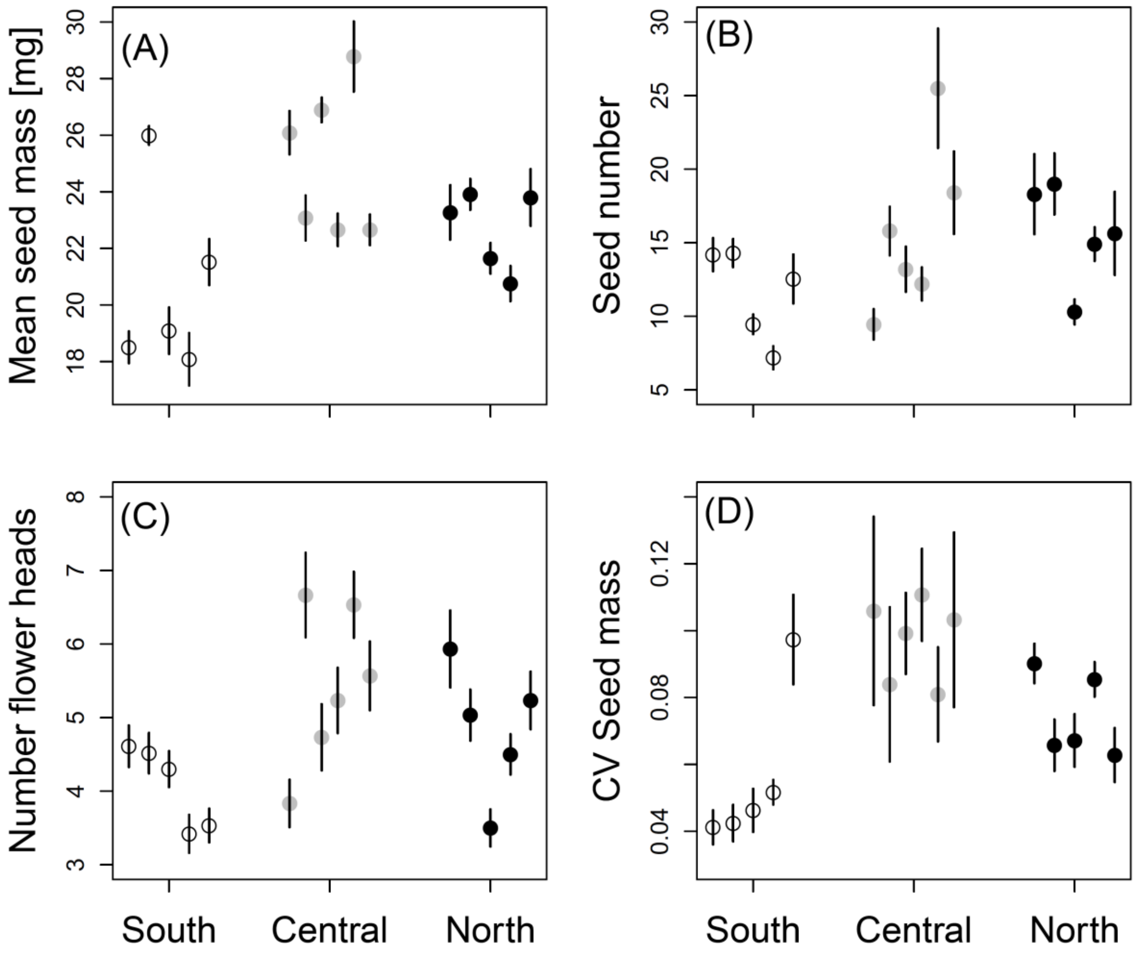
Pearson's correlation coefficients between traits, right-top corner *G. hybridus* (grey shaded), left-bottom *C. crupinastrum*. SRH = seed release height [cm], CH = canopy height [cm], SLA = specific leaf area [mg/mm²], N_{cont}/ P_{cont} = leaf N-/P-content [mg/g], SM_{tot} = total seed mass [mg], SM_{mean} = mean seed mass [mg], SM_{CV} = CV seed mass, % Pap = percentage of pappus seeds, SM_{ratio}= seed mass ratio between both seed types, # Seeds= number of seeds. All traits were log-transformed, except of % Pap, which was arcsine-square root transformed. Correlation between leaf and seed mass traits in *G. hybridus* was not available (see chapter 3.2). Significant correlations are bold typed, *** p<0.001, ** p<0.01, * p<0.05. Contrasting correlations between both species are italic.

	SRH	CH	SLA	N_{cont}	P_{cont}	SM_{tot}	SM_{mean}	SM_{var}	# Seeds	Flower
SRH	-	**0.96** ***	**-0.24** **	**0.33** ***	-0.15	**0.6** ***	***0.3*** ***	-0.15	**0.33** ***	**0.49** ***
CH	**0.91** ***	-	**-0.28** ***	**0.3** ***	***-0.19*** *	NA	NA	NA	**0.35** ***	**0.48** ***
SLA	**-0.36** ***	**-0.26** ***	-	-0.11	***0.34*** ***	NA	NA	NA	**-0.38** ***	**-0.46** ***
N_{cont}	**0.26** ***	**0.2** *	-0.11	-	**0.36** ***	NA	NA	NA	**0.17** *	**0.27** ***
P_{cont}	0.08	*0.12*	*0.06*	**0.53** ***	-	NA	NA	NA	***-0.25*** **	-0.15
SM_{tot}	**0.36** ***	**0.31** ***	**-0.28** ***	0.15	0.11	-	0.56 ***	*-0.24* **	**0.79** ***	**0.46** ***
SM_{mean}	*-0.07*	-0.01	-0.04	-0.03	0	**0.38** ***	-	-0.23 **	*-0.06*	***0.48*** ***
SM_{CV}	0.15	0.14	-0.11	0.03	0.08	0.12	**-0.22** **	-	*-0.11*	-0.13
# Seeds	**0.4** ***	**0.33** ***	**-0.27** ***	**0.2** *	***0.18*** *	**0.84** ***	***-0.19*** *	***0.28*** ***	-	**0.29** ***
Flower	**0.59** ***	**0.54** ***	**-0.28** ***	**0.31** ***	0.13	**0.32** ***	*0.02*	0.13	**0.31** ***	-

	SRH	SM_{tot}	SM_{mean}	SM_{CV}	# Seeds	Flower	SM_{ratio}
SM_{ratio}	-0,16 *	0.01	*-0.08*	**-0.24** **	0.07	-0.07	-
% Pap	**0.33** ***	**0.57** ***	-0.1	-0.09	**0.72** ***	0.11	**0.23** **

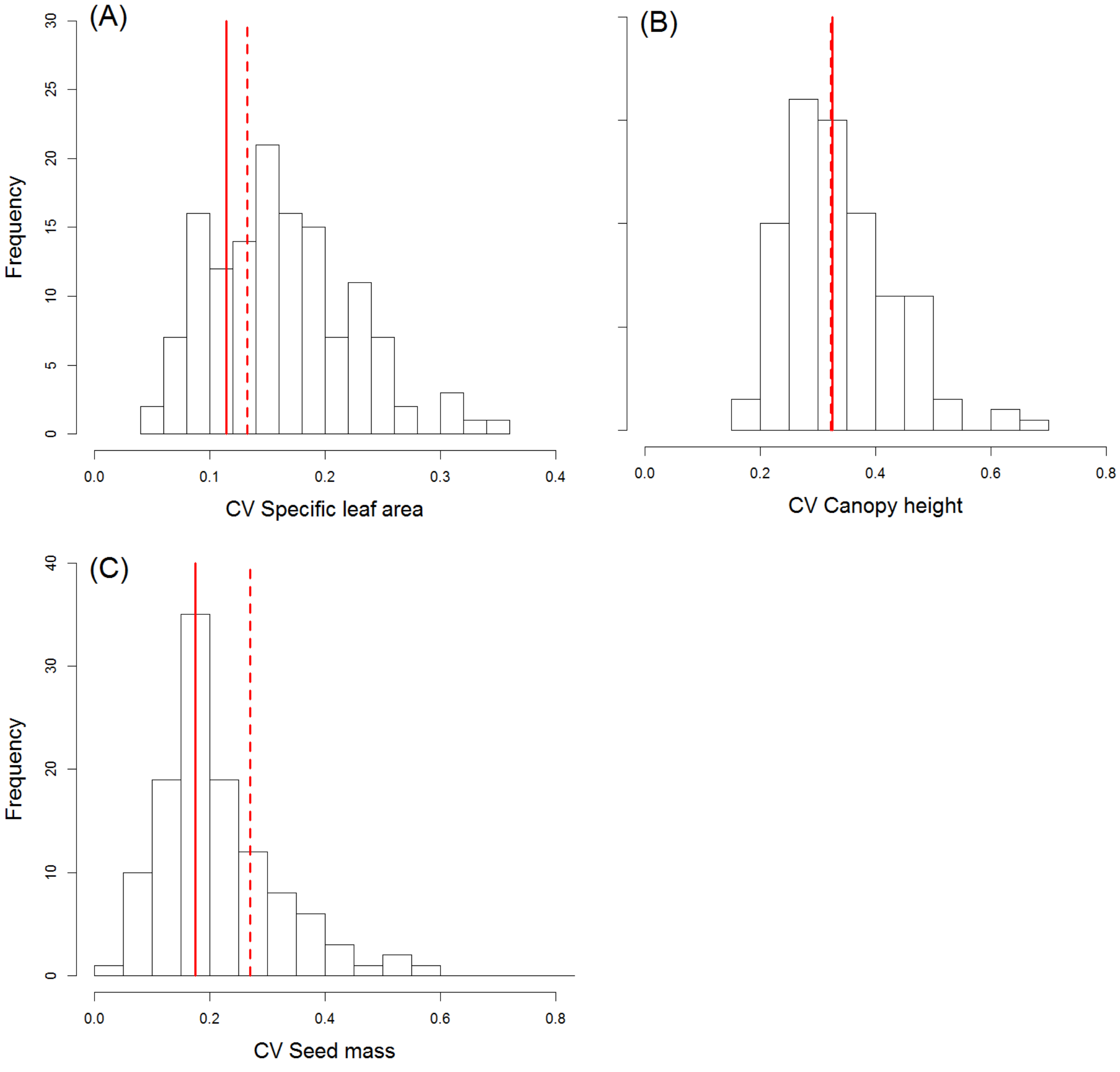
Appendix B4

Generative traits of *Crupina crupinastrum* along the precipitation gradient with increasing annual precipitation from south to north. Each point represent the mean trait value (±SE) of one study site. (A) mean seed mass, (B) total number of seeds, (C) number of flower heads, (D) Coefficient of variation (CV) of seed mass. Please note that the statistical analyses included also plant height as covariate (see Table 3.2).



Appendix B5

Intraspecific trait variability of annuals that were sampled within the same study region. The figures show histograms of the coefficient of variation (CV) observed for annuals: A) specific leaf area (number of species, n=135), B) canopy height (n=138) and C) seed mass (n=119). Data was taken from May *et al.* (2013) and Bergholz *et al.* (2017). From each species, ten (SLA, seed mass) or 25 individuals (canopy height) were sampled. The sampling was conducted mostly within one population. Only rare species were sampled in different populations (see May *et al.* 2013, Bergholz *et al.* 2017 for more details of sampling). The red lines mark average within-population trait variability of *G. hybridus* (dashed line) and *C. crupinastrum* (continuous line) observed in this study (see Table 3.2).



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Appendix C - Supplementary Material to chapter IV

Appendix C1

Comparison of mineral nitrogen (NO_3-N and NH_4-N) content between fertilized (F+) and unfertilized (F-) soils at two different time points. Significant differences in mineral nitrogen contents between fertilized and unfertilized soils were assessed with *ANOVA*. Degrees of freedom =5.

Date		**Fertilized (F+)** mg / kg dry soil mean (±sd)	**Unfertilized (F-)** mg / kg dry soil mean (±sd)	**F**	**p**
24/04/2010	NO_3-N	7.1 (±2.1)	2.2 (±0.5)	15.93	**0.016**
	NH_4-N	13.3 (±0.2)	5.5 (±0.5)	767.40	**<0.0001**
25/05/2010	NO_3-N	11.7 (±1.6)	1.4 (±0.2)	126.40	**0.0004**
	NH_4-N	9.7 (±1.4)	3.8 (±0.1)	54.85	**0.002**

Appendix C2

Correlation coefficients between the log-transformed growth traits of the seedlings. **** indicates p<0.0001.

	Height [cm]	**Diameter [cm]**	**Std. Leaf length**
Diameter [cm]	0.59****		
Std. Leaf length	0.56****	0.66****	
Std. Num. leaves	0.35****	0.6****	0.6****

Appendix C3

Parameter estimates of the minimal adequate models and the respective significance of the fixed effects as well as random effects variances with the respective number of groups in brackets. In contrast to the analyses presented in the main manuscript, the maximal models did not include the time of seedling emergence. Please note that leaf length and number of leaves were standardized. See Table 4.2 for specifics and the method section (chapter 4.2) for details.

Fixed effects	**Survival** (iii)	**Height$_{log}$ [cm]** (iv)	**Diameter$_{log}$ [cm]** (iv)	**Leaf length$_{log}$** (iv)	**# leaves$_{log}$** (iv)
Intercept (C-N-)	3.97	2.24	2.51	-0.01	-0.11
Seed mass$_{log}$ [mg] (SM)	1.26^{a}	0.24^{a}	0.17^{a}	-0.04^{a}	-0.04^{a}
Nutrients	-0.80^{a}	**0.45******	**0.41******	**0.44******	**0.34******
Competition	n.s.	-0.42^{a}	-0.36^{a}	-0.44^{a}	-0.31^{a}
SM: Nutrients	**-0.53***	n.s.	n.s.	n.s.	n.s.
SM: Competition	n.s.	**0.09*****	**0.18******	**0.11******	**0.14******
SM: Nutr: Comp	n.s.	n.s.	n.s.	n.s.	n.s.
Random effects variances					
Species	1.07 (22)	0.35 (21)	0.05 (21)	0.01 (21)	0.01 (21)
Species/pot	1.03 (342)	0.06 (355)	0.07 (355)	0.06 (355)	0.06 (355)

Appendix C4

Parameter estimates of the minimal adequate models and the respective significance of the fixed effects as well as random effects variances with the respective number of groups in brackets. The analyses were performed for response variables that were standardized by the species mean of the control treatment [log(y_i / $y_{\text{species mean- control treatment}}$)]. See Table 4.2 in the main manuscript for specifics and the method section (chapter 4.2) for details. Note that the analyses of the growth traits had to be conducted without the species *Thymus pulegioides* and *Veronica spicata*, since no individuals survived in the control treatment (C-N-). Hence, no species mean values of the control treatment could be calculated for these species.

Fixed effects	**Time seedl. emer.**	**Height**	**Diameter**	**Leaf length**	**# leaves**
Intercept (C-N-)	-0.02	0.17	0.17	0.20	0.17
Seed mass$_{\log}$ [mg] (SM)	n.s.	0.02^{a}	0.02^{a}	0.03^{a}	0.01^{a}
Nutrients	n.s.	**0.44******	**0.41******	**0.43******	**0.34******
Competition	**-0.067******	-0.43^{a}	-0.37^{a}	-0.46^{a}	-0.32^{a}
SM: Nutrients	n.s.	n.s.	n.s.	n.s.	n.s.
SM: Competition	n.s.	**0.08****	**0.17******	**0.10******	**0.14******
Time seedl. emer.	**-**	**-0.01****	**-0.01****	**-0.01*****	**-0.01****
Random effects variances					
Species	0.002 (22)	0.08 (19)	0.08 (19)	0.07 (19)	0.03 (19)
Species/pot	0.01 (415)	0.06 (332)	0.07 (332)	0.06 (332)	0.06 (332)
Species/pot/position	0.004 (1516)	-	-	-	-

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Declaration

This cumulative dissertation consists of three independent scientific articles that were published in peer-reviewed journals. Since these studies were published with co-authors, they are written in first-person plural.

As lead author, I designed the studies, developed the specific research questions, analyzed the data and wrote all parts of the three chapters. Therefore, the views expressed in the chapters are mine. All co-authors provided feedback on preliminary manuscript versions and during revisions. Additionally, the chapters contain suggestions from reviewers and editorial comments received during the peer-review process.

Chapter II comprises a large data set that was mainly compiled by Itamar Giladi (vegetation surveys), Felix May and Michael Ristow (trait measurements). I personally measured traits to a lesser extent and constructed the phylogenetic tree. I conducted the empirical work of chapter III myself. The empirical work described in chapter IV was a follow-up experiment to an experiment that I conducted for my Diploma Thesis (Bergholz 2009). I designed the follow-up experiment together with Michael Ristow, set up the experiment with Janine Pottek, and guided the data collection, which was mainly carried out by Janine Pottek, Lina Weiß and Katja Geissler. Preliminary results of the experiment were presented in the Master's Thesis of Janine Pottek "Einfluss von Konkurrenz und Stickstoff auf die Keimung und Etablierung verschiedener Arten aus basiphilen Trockenrasen".

Kolja Christoph Bergholz (PhD candidate)

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