Using enrichment planting to test for environmental filtering and niche differentiation in grassland communities

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Summary

Many grassland communities have suffered diversity loss through land-use intensification. Landscape fragmentation and a general decline of grasslands caused by abandonment or conversion from grassland to arable land lead to dispersal limitation of many plant species. Many grassland communities are therefore not saturated with species and there is the potential that new species could become established. Adding new species to existing grassland communities can give insight into the mechanisms and assembly rules behind plant community formation. The process of niche differentiation is supposed to favor plant species with dissimilar traits, whereas the process of environmental filtering is assumed to select plant species with similar traits. However, knowledge to which degree both processes impact the assembly of plant species under increasing land-use intensity is still missing.

The aim of the present thesis is to investigate how similar or dissimilar new species need to be in traits in order to become established at grassland sites under varying land-use intensity. To answer the raised questions two experiments were established within the framework of this thesis: An enrichment planting experiment set up in existing grassland communities and a common garden experiment.

The enrichment planting experiment was conducted on 54 grassland sites in three different regions of Germany (Schwäbische Alb, Hainich and Schorfheide) within the network of the Biodiversity Exploratories. Young transplants of 130 vascular plant species were raised in the greenhouse and planted into the experimental grasslands according to four different enrichment planting scenarios. The species of the *Random* scenario were selected randomly from a regional species pool. The *Dissim* and *Sim* scenarios represented species with most dissimilar and most similar traits respectively compared to the resident communities. These two trait-based scenarios were used to quantify the influence of niche differentiation and environmental filtering processes along the gradient of land-use intensity. The *Beals* scenario contained species with high probability of co-occurrence to the resident communities. Species of this scenario are supposed to exhibit the degree of trait similarity that reflects the searched impact of niche differentiation and environmental filtering in a community, because they grow in similar community constellations under natural conditions.

The common garden experiment was set up in the Botanical Garden of the Martin Luther University of Halle-Wittenberg. The same species as in the enrichment planting experiment grew in a threefold repetition without influences of land-use and communities. Both experiments resulted in three papers presented in chapter 2 – 4 of this thesis. Chapter 2 and 3

of this thesis are based on the enrichment planting experiment and investigate the influence of scenario and land-use intensity on species establishment success. Hereby, chapter 2 focuses on survival rates and changes in community mean trait distances brought about by adding the transplant species to the experimental subplots. Chapter 3 examines the growth of transplant individuals in three different vegetation periods. Chapter 4 compares the performance of the same species grown in the enrichment planting and in the common garden experiment; hereby, species-specific trait-performance relationships are analyzed.

In the first hypothesis H1 of this thesis it is assumed that the investigated grassland communities were not saturated with species, thus new species can become established. The enrichment planting experiment showed that new species achieved a high total survival rate (44.6%) until the end of the experiment after two years and that the investigated grassland communities seemed not to be saturated. However, the short duration of the experiment hinders the prediction of the long-term colonization success of transplants.

The second hypothesis H2 suggests that species differences, reflected in traits, are connected with survival and performance. Species effects explained high proportions of variance in the investigated analyzes and interspecific rankings for performance parameters were significantly correlated between the two experiments. However, trait-performance relationships were different between the two experiments. Thus, the second hypothesis of this thesis can only be confirmed partly: Performance seems to be highly species-specific, but trait-performance relationships depend on the environment.

Hypothesis H3 presumes that the scenario, according to which a transplant species was selected, has impact on its establishment success. Significant scenario effects were only found for survival rates but not for performance. However, the performance of the *Beals* scenario was positively correlated with trait-based functional diversity measures of the community. This showed that survival rates and growth parameters may be independent and not always correspond similar to environmental gradients.

Sub-hypothesis H3a postulates that species of the *Random* scenario have a low establishment success under all conditions. Species of the *Random* scenario had low survival rates, but the species of the *Dissim* scenario had even lower rates. In chapter 2 it was found that the species of the *Random* scenario were also more dissimilar compared to the resident communities, which indicates that dissimilarity in traits is less advantageous.

Sub-hypothesis H3b assumes that the species of the *Dissim* scenario have higher establishment success compared to the *Sim* scenario under low land-use intensity conditions.

This hypothesis has to be rejected. The species of the *Dissim* scenario had lowest survival rates under all conditions, suggesting lower impact of niche differentiation. However, traits that are supposed to be influenced stronger by niche differentiation as for example regeneration-, phenology- and root-traits, were not investigated, which could have led to the observed results.

Sub-hypothesis H3c supposes that species of the *Sim* scenario have higher establishment success under high land-use intensity conditions. This hypothesis is rejected as survival rates of the species of the *Sim* scenario did likewise to those of all other scenarios decrease with increasing land-use intensity. However, the survival rates of the *Sim* scenario were second highest under all conditions compared to the other scenarios, indicating a general higher impact of environmental filtering.

Sub-hypothesis H3d presumes that species of the *Beals* scenario have highest establishment success and highest survival rates under all conditions. In comparison to the *Dissim* and *Sim* scenarios the mean trait distances of the *Beals* scenario were constantly composed of about 30% dissimilar and about 70% similar traits. This relationship did not change along the gradient of land-use intensity. A higher impact of environmental filtering is therefore suggested. However, 30 % dissimilarity as well as positive correlations of growth of the *Beals* scenario with trait-based functional diversity measures might point to some influence of niche differentiation or at positive biotic interactions.

The fourth hypothesis H4 suggests that land-use intensity has the strongest influence on transplant growth compared to trait characteristics of the communities. This is confirmed by the results. Land-use intensity explained growth in the three different vegetation periods investigated most often.

In conclusion, this thesis has highlighted the role of combining trait-based with co-occurrence-based approaches. The main finding of the thesis is that the *Beals* scenario had highest survival rates, positive growth response to trait-based functional diversity of communities and in comparison to the *Dissim* and *Sim* scenario the mean trait distance of species of this scenario were constantly about 70 % similar and 30% dissimilar along the land-use intensity gradient. The scenarios *Beals* and *Sim*, which contained species that were more similar in traits compared to the resident communities, were in general more successful than the two scenarios *Random* and *Dissim*, which contained species that were more dissimilar in traits. This implies a higher impact of environmental filtering compared to niche differentiation.

Zusammenfassung

Viele Grünlandgesellschaften haben auf Grund von Landnutzungsintensivierung einen Diversitätsverlust erlitten. Fragmentierung der Landschaft, Bewirtschaftungsaufgabe oder Konvertierung von Grünland zu Ackerland haben zu einem generellen Rückgang an Grünländern geführt, was zur Folge hat, dass viele Grünlandarten eine Ausbreitungslimitierung erfahren. Viele Grünlandgemeinschaften sind daher nicht mit Arten gesättigt und potentiell könnten sich noch neue Arten ansiedeln. Das Einfügen von fehlenden Pflanzenarten in bestehende Grünlandgemeinschaften kann darüber Aufschluss geben, welche Mechanismen und Regeln hinter der Bildung von Pflanzengemeinschaften wirken. Man nimmt an, dass Nischendifferenzierung zu Merkmalsunterschieden bei Pflanzenarten führt, während Umweltfilter Pflanzenarten mit ähnlichen Merkmalen selektieren. Es ist aber unklar, wie stark diese beiden Prozesse bei steigender Intensität der Landnutzung auf die Bildung von Pflanzengemeinschaften wirken.

Ziel der vorliegenden Arbeit ist es, zu erforschen wie ähnlich oder unähnlich neue Pflanzenarten in ihren Merkmalen sein müssen um sich erfolgreich in Grünländern mit unterschiedlicher Landnutzungsintensität zu etablieren. Um den aufgeworfenen Fragen nachzugehen wurden innerhalb dieser Doktorarbeit zwei Experimente – ein Artenanreicherungsexperiment in bestehenden Grünlandgemeinschaften und ein Gartenexperiment – durchgeführt.

Das Artenanreicherungsexperiment wurde auf 54 Grünländern in drei verschiedenen Regionen Deutschlands (Schwäbische Alb, Hainich und Schorfheide) innerhalb der Biodiversitäts-Exploratorien durchgeführt. Für das Artenanreicherungsexperiment wurden Jungpflanzen von 130 verschiedenen Gefäßpflanzenarten im Gewächshaus angezogen, und unter Anwendung vier verschiedener Anreicherungs-Szenarien in die Grünländer eingebracht. Die Arten des *Random* Szenario wurden zufällig aus dem vorhandenen regionalen Artenpool ausgewählt (engl. random = zufällig). Die Szenarien *Dissim* und *Sim* repräsentieren Arten, die jeweils am unähnlichsten, bzw. am ähnlichsten in ihren Merkmalen (engl. dissimilar/similar = unähnlich/ähnlich) im Vergleich zu den Arten der bestehenden Grünlandgemeinschaften sind. Diese beiden merkmalbasierten Szenarien wurden dazu genutzt den Einfluss von Nischendifferenzierung und umweltfilterbasierten Prozessen entlang des Landnutzungsintensitätsgradienten zu quantifizieren. Das *Beals* Szenario umfasst Arten, die mit hoher Wahrscheinlichkeit gemeinsam mit den Arten der bestehenden Grünlandgemeinschaften vorkommen. Es wird angenommen, dass diese Arten den Grad an

Ähnlichkeit in ihren Merkmalen aufweisen, der dem gesuchten Einfluss von Nischendifferenzierung und Umweltfilterprozessen in einer Gemeinschaft entsprechen, da diese Arten in ähnlichen Gemeinschaftsgefügen unter natürlichen Bedingungen wachsen.

Das Gartenexperiment wurde im Botanischen Garten der Martin-Luther-Universität Halle-Wittenberg durchgeführt. Die gleichen Arten wie im Artenanreicherungsexperiment wuchsen hier in einer dreifachen Wiederholung ohne Einflüsse von Landnutzung und ohne gemeinschaftsbedingte Einflüsse. Die Ergebnisse beider Experimente wurden in drei Publikationen zusammengefasst, die in den Kapiteln 2 – 4 vorgestellt werden. Kapitel 2 und 3 dieser Arbeit basieren einzig auf dem Artenanreicherungsexperiment und erforschen den Einfluss der verschieden Szenarien und der Landnutzungsintensität auf den Etablierungserfolg der verpflanzten Arten. Hierbei liegt der Schwerpunkt im 2. Kapitel auf den Überlebensraten und der Änderung der errechneten mittleren Merkmalsdistanz einer Pflanzengemeinschaft, die durch das Hinzufügen der neuen Arten der verschiedenen Szenarien in die Flächen des Artenanreicherungsexperiments entstanden. Kapitel 3 untersucht die Wachstumsleistungen der verpflanzten Individuen in drei verschiedenen Vegetationsperioden. Kapitel 4 vergleicht die Wachstumsleistungen der gleichen Arten des Artenanreicherungsexperiments mit denen des Gartenexperiments, dabei werden artspezifische Zusammenhänge zwischen Merkmalen und Wachstumsleistungen analysiert.

Hypothese H1 dieser Arbeit formuliert die Annahme, dass die untersuchten Grünlandgemeinschaften nicht mit Arten gesättigt sind, weshalb sich neue Arten etablieren können. Das Artenanreicherungsexperiment zeigte, dass hohe Überlebensraten (44,6%) bis zum Ende des Experiments nach 2 Jahren erreicht wurden und die untersuchten Grünlandgemeinschaften nicht mit Arten gesättigt zu sein scheinen. Durch die kurze Dauer des Experiments lässt sich aber nicht auf den dauerhaften Kolonisationserfolg der Arten in der Zukunft schließen.

Die zweite Hypothese H2 postuliert, dass Unterschiede zwischen den Arten, die sich in deren Merkmalen widerspiegeln, mit dem Überleben und der Wachstumsleistung verknüpft sind. Artspezifische Effekte erklärten hohe Anteile an Varianz in den durchgeführten Analysen und artspezifische Rangfolgen der Wachstumsparameter waren signifikant zwischen den beiden Experimenten korreliert. Zusammenhänge zwischen Merkmalen und Wachstumsleistungen waren aber zwischen den beiden Experimenten verschieden. Daher kann die zweite Hypothese nur teilweise bestätigt werden, da Wachstumsleistungen stark artspezifisch zu sein scheinen, doch Zusammenhänge zwischen Merkmalen und Wachstumsleistungen von der Umwelt abhängen.

Hypothese H3 besagt, dass das Szenario Auswirkungen auf den Etablierungserfolg einer Art hat. Ein Szenarien-Effekt wurde nur für Überlebensraten, nicht aber für Wachstumsleistungen gefunden. Die Wachstumsleistungen des *Beals* Szenario waren aber positiv mit der merkmalbasierten „Funktionellen Diversität" der Gemeinschaften korreliert. Dies zeigt, dass Überlebensraten und Wachstumsparameter unabhängig voneinander sein können und nicht immer gleich auf Umweltgradienten reagieren.

Sub-Hypothese H3a formuliert die Erwartung, dass die Arten des *Random* Szenario den geringsten Etablierungserfolg unter allen Bedingungen haben. Arten des *Random* Szenario hatten geringe Überlebensraten, die Arten des *Dissim* Szenario hatten jedoch noch geringere. Da die Arten des *Random* Szenario ebenfalls aus mehr unähnlichen Arten bestanden, wie im 2. Kapitel herausgefunden wurde, scheint Unähnlichkeit in Merkmalen weniger vorteilhaft zu sein.

Sub-Hypothese H3b postuliert, dass die Arten des *Dissim* Szenarios höheren Etablierungserfolg im Vergleich zum *Sim* Szenario bei geringer Landnutzungsintensität haben. Diese Hypothese muss abgelehnt werden. Die Arten des *Dissim* Szenario hatten unter allen Bedingungen die niedrigsten Überlebensraten, was einen niedrigeren Einfluss von Nischendifferenzierung vermuten lässt. Allerdings wurden Merkmale, für die angenommen wird, dass sie stärker von Nischendifferenzierung beeinflusst werden, wie etwa Fortpflanzungs-, Phänologie- und Wurzel-Merkmale, nicht in die Untersuchungen mit einbezogen, was zu den beobachteten Ergebnissen geführt haben könnte.

Sub-Hypothese H3c nimmt an, dass die Arten des *Sim* Szenario einen höheren Etablierungserfolg bei starker Landnutzungsintensität haben. Diese Hypothese lässt sich nicht bestätigen. Die Überlebensraten der Arten des *Sim* Szenario verringerten sich, wie bei allen anderen Szenarien auch, mit steigender Landnutzungsintensität. Jedoch waren die Überlebensraten des *Sim* Szenario am zweithöchsten unter allen Bedingungen im Vergleich zu den anderen Szenarien, was auf einen höheren Einfluss umweltfilterbedingter Prozesse hinweist.

Sub-Hypothese H3d vermutet, dass die Arten des *Beals* Szenario den höchsten Etablierungserfolg unter allen Bedingungen haben. Arten des *Beals* Szenarios hatten unter allen Bedingungen die höchsten Überlebensraten. Im Vergleich zum *Dissim* und *Sim* Szenario bestand die mittlere Merkmalsdistanz des *Beals* Szenario aus konstant ca. 70% ähnlicher und ca. 30% unähnlicher Merkmale. Dieses Verhältnis änderte sich entlang des Landnutzungsgradienten nicht. Umweltfilterbedingte Prozesse scheinen einen höheren Einfluss zu haben. 30% Unähnlichkeit sowie die positiven Korrelationen des Wachstums der *Beals*-Arten mit der merkmalbasierten „Funktionellen Diversität“ der Gemeinschaften könnten auf einen geringen Einfluss von Nischendifferenzierung oder auf positive biotische Interaktionen hindeuten.

Die vierte Hypothese H4 postuliert, dass die Landnutzungsintensität den stärksten Einfluss auf das Wachstum der verpflanzten Arten im Vergleich zu Merkmalscharakteristika der Gemeinschaften hat. Dies bestätigte sich, da die Landnutzungsintensität das Wachstum in den drei verschiedenen Vegetationsperioden am häufigsten erklärte.

Zusammenfassend hebt die vorliegende Arbeit die Rolle des Zusammenspiels merkmalbasierter Untersuchungen und solcher, die Informationen über das gemeinsame Vorkommen von Arten verwenden, hervor. Die Haupterkenntnis der Arbeit ist, dass das *Beals* Szenario die höchsten Überlebensraten aufwies, mit positivem Wachstum auf die „Funktionelle Diversität“ an Merkmalen der Gemeinschaft reagierte, und im Vergleich zum *Dissim* und *Sim* Szenario aus konstant ca. 70% ähnlichen Merkmalen und ca. 30% unähnlichen Merkmalen entlang des Landnutzungsgradienten bestand. Die beiden Szenarien *Beals* und *Sim*, die aus einer größeren Zahl ähnlicher Arten im Vergleich zu den Grünlandgesellschaften bestehen, waren im Hinblick auf den Etablierungserfolg der Arten allgemein erfolgreicher als die Szenarien *Random* und *Dissim*, die aus mehr Arten mit unähnlichen Merkmalen bestanden. Daher wird davon ausgegangen, dass umweltfilterbedingte Prozesse einen größeren Einfluss haben als Nischendifferenzierung.

Chapter 1 – Introduction

1.1 General Introduction

About 3.8 billion years of evolution (Mojzsis et al. 1996) have pushed the formation of species diversity to approximately 300,000 different vascular plant species known nowadays (Christenhusz & Byng 2016). Despite this huge potential of possible species combinations to form communities, many species are restricted to certain sections of environmental gradients (Whittaker 1956; Brown 1984; MacArthur 1984; Osmond et al. 1987) and grow in structured communities with certain abundance patterns (Whittaker 1965; Grime 1998). This leads to the questions how species coexist, what factors drive species distribution and abundance patterns and which mechanisms regulate community assembly.

Neutral theory, and in particular “The Unified Neutral Theory of Biodiversity and Biogeography” proposed by Hubbell and based on observations of species-rich tropical rainforest tree communities, follow the idea that there are no differences between species concerning the chance of reproduction and death within a community (Hubbell 2001; Volkov et al. 2003; Rosindell et al. 2011). Therefore, neutral theory assumes that species abundance varies randomly (Hubbell 2001; Volkov et al. 2003; Rosindell et al. 2011). Furthermore, it is assumed that local species diversity is at equilibrium and extinction rates are balanced by speciation and immigration of new species from a larger metacommunity (Hubbell 2001; Volkov et al. 2003; Rosindell et al. 2011). This theory implies functional equivalence for species traits (Hubbell 2005). Moreover, Hubbell argues that dispersal and recruitment limitation as well as differences in the biotic and abiotic microenvironments are the factors that prevent competitive exclusion of functional similar species (Hubbell 2005).

In contrast, the principle of competitive exclusion postulates that two species with the same ecological resource requirements cannot coexist (Gause 1934; Hardin 1960). Competition is assumed to be a main driver for species coexistence in niche models. Hutchinson (1957) distinguishes a fundamental from a realized niche, whereby the fundamental niche is set by the environmental factors under which a species is able to exist; the realized niche is a subset of the fundamental niche reduced by competition (Hutchinson 1957; Hutchinson 1959; Holt 2009). However, not only competition but also other biotic interactions should be considered in the context of a species niche (Colwell & Fuentes 1975). Biotic interactions such as facilitation, herbivory and the presence or absence of pollinators, pathogens or symbionts were all shown to be important factors for species distribution (Wisz et al. 2013). As resources are limited per definition (Chapin et al. 1987), niche theory assumes therefore that species specialize their way of resource use in order to avoid competitive exclusion (MacArthur & Levins 1964). However, plant species share the same few resources (light, CO_2, water and nutrients), but have the capacity to differently tolerate shortages or oversupply of these resources (Blom & Voesenek 1996; Grubb 1998; Liancourt et al. 2005). Moreover, environmental heterogeneity creates sites and microhabitats that are more favorable for one species than for another (Stein et al. 2014). Evolution generated specialization of species to particular abiotic and biotic conditions, which are reflected by species differences in morphological and physiological traits. Adaptations of plant species to a wide range of environmental conditions, for example along gradients of water availability, light intensity or temperature, have generated pronounced interspecific trait differences. Great examples are adaptations to harsh environmental conditions: Some plant species can stand shade whereas others prefer intense light, some tolerate extreme high, others low temperatures, some get along with low water availability, others even live in water. In general, all traits of a species can be used to describe the niche of that species, because they reflect the species' adaptations to environmental factors, and at the same time are connected with certain ecological functions of a species in a community (Violle et al. 2007). Traits are widely used to investigate the mechanisms of species coexistence and the underlying rules of community establishment and species assembly.

Neutral theory does not consider trait differences between species such as for example physiological tolerances, habitat preferences, energy usages, growth patterns, reproductive strategies or dispersal abilities (Gaston & Chown 2005), while niche-based concepts integrate such differences among species. MacArthur & Levins (1967) described that increasing competition is one of the factor resulting in limiting similarity in traits. One important process of community assembly that is based on the rule of limiting similarity is niche differentiation. This process describes the capacity of species to avoid competition by using the available resources differently. Examples for niche differentiations were found in many studies: for example interspecific differences in rooting depths (Berendse 1979; Casper & Jackson 1997; Mueller et al. 2013) or phenology (Rathcke & Lacey 1985; Fargione & Tilman 2005; Elzinga et al. 2007). In these studies, it was found that sharing the resources of different space or in varying time spans enhanced species coexistence and led to increased species richness. Niche differentiation can also result in a more efficient exploitation of resources (Loreau & Hector 2001), which would also be an explanation for the observed increased productivity of communities with higher plant diversity (Hector et al. 1999; Cardinale et al. 2007). Moreover, niche differentiation was found to stabilize diversity, because rare species with specialized traits are not excluded by competition (Chesson 2000; Wilson 2011).

Another major idea is that communities are organized by environmental filtering. Environmental filtering describes the process of filtering species by their adaptations to certain environmental conditions before they become established at new locations. Whether a species can pass the abiotic or biotic filters in order to become established at a new site, is the result of how well the species is adapted to the conditions (Keddy 1992). Relationships between environmental filters and species-specific morphological and physiological traits are widely investigated (Díaz et al. 1998; Dwyer & Laughlin 2017). Abiotic filters concern geographical and geological conditions, which are connected with climatic conditions like light intensity, temperature, precipitation, water availability and soil conditions, and further human induced conditions like land-use management regimes. An example for abiotic filtering is that on regularly mown grasslands woody species are excluded because they do not tolerate cutting (Hansson & Fogelfors 2000), therefore only species with defoliation tolerance or avoidance strategies will pass the filter and become established on grazed or cut sites (Briske 1996). Biotic filters are interactions that are brought about by other plant species of the community like e.g. competition or facilitation. Furthermore, all kinds of interactions with other trophic levels as for example interactions with herbivores, pollinators, pathogens or symbionts also represent biotic filters. Examples for biotic filtering are the occurrence of special mycorrhizal fungi or pollinators that are obligate for a species' establishment or reproduction (Richardson et al. 2000). Beside abiotic and biotic filtering also seed, dispersal or recruitment limitation can exclude a species from settling within a community (Tilman 1997; Ehrlen & Eriksson 2000; Zobel et al. 2000; Foster & Tilman 2003).

Environmental filtering and niche differentiation are supposed to be contrasting processes that differently influence the establishment of species. Strong environmental filtering is assumed to select species with similar functional traits, which leads to trait convergence on the community level over time (Le Bagousse-Pinguet et al. 2017; Bruelheide et al. 2018). Studies in this context showed that there is a trade-off between plant growth and resource conservation under high vs. low nutrient availability (Ryser & Lambers 1995; Ordoñez et al. 2009). It was found that under fertile conditions species tend to have high specific leaf area (SLA) whereas under nutrient-poor conditions species preferably have scleromorphic, evergreen leaves with high leaf dry matter content (LDMC) (Wright et al. 2004; Ordoñez et al. 2009). This relationship is called the leaf economic spectrum which differentiates between fast and slow growing species under different nutrient availability (Wright et al. 2004). In contrast, the rule of limiting similarity, which leads to niche differentiation in order to avoid competition, is supposed to create communities of species with trait differences (trait dissimilarity or trait divergence) (MacArthur & Levins 1967; Pacala & Tilman 1994). However, as competition can also act as a biotic filter it is important to keep in mind that competition may also lead to trait convergence, by excluding species with extreme trait values (Mayfield & Levine 2010; Gerhold et al. 2013; Loughnan & Gilbert 2017). Although environmental filtering and niche differentiation can act in contrasting ways concerning trait convergence and divergence respectively, both processes simultaneously and jointly form the structure of a community (Weiher et al. 1998; Maire et al. 2012; Spasojevic & Suding 2012; Gross et al. 2013). On the one hand species must be similar to some degree in order to pass the environmental filters, on the other hand they must be dissimilar to some degree in order to avoid competition (Díaz et al. 1998; Wilson 2007). Still there remains the question of the relative strengths of these two processes. To answer this question traits are a useful tool: They can give insight on filtering processes or niche differentiation processes via measuring the trait similarity (or dissimilarity) between communities (Cornwell & Ackerly 2009). The more similar species are in their traits, the lower are the trait distances among them. If two species do not differ in a trait (e. g. leaf anatomy; both species have mesomorphic leafs), the species trait distance will be zero for this trait. However, if one species has mesomorphic leaves and the other species has scleromorphic leaves, than the trait distance between these two species for the trait "leaf anatomy" will be one. Distances between different types of traits of two species can be used to calculate a mean trait distance (Pavoine et al. 2009). Based on the mean trait distances of all species in a community a community's mean trait distance can be calculated (Pavoine et al. 2009). When the different contributions of each individual species to the whole community are considered (Grime 1998) abundance-weighted mean trait distances can be calculated. Functional trait diversity (FD) calculated after Rao (1982) is an abundance-weighted measurement that represents the trait attributes of a community by taking trait distances of one or more traits (multi-trait FD) into account (Botta-Dukát 2005).

High FD values indicate high trait distances between those species that contribute most to the community. FD can be used to distinguish between trait convergence and divergence compared to a random expectation and therefore indirectly may point to environmental filtering or niche differentiation processes (Cornwell et al. 2006; Ricotta & Moretti 2011; Mason & de Bello 2013). Another abundance-weighted measurement is the community-weighted mean (CWM) of one trait for a whole community, which can be used for example to explain trait changes of communities along environmental gradients (Ricotta & Moretti 2011). Grime (2006) doubted the concept of niche differentiation as a driver for trait divergence. Instead of competition he proposed disturbance to be the main driver of trait divergence (Grime 2006). Disturbances are known to cause reduction or damage of plants biomass, and thus, can change competitive relationships between species, causing not always the dominant competitor to survive (Huston 1979; Kempel et al. 2015). The "Intermediate Disturbance Hypothesis" (Connell 1978) predicts that species richness is highest at intermediate disturbance intensity. Under high disturbance intensity species richness is limited by harsh conditions, while under very low disturbance intensity competition eliminates species that are weak competitors (Grime 2006; Fraser et al. 2016). Under high disturbance regimes competition is assumed to have little impact, and species are very similarly specialized to cope with the stressful environment (Grime 2006; Fraser et al. 2016). This leads to high trait convergence under the extreme conditions of high and low disturbance, whereas intermediate levels of disturbance lead to trait divergence (Grime 2006; Fraser et al. 2016). In grassland communities most disturbances are caused by land-use (Díaz et al. 1999; Austrheim et al. 1999; Laliberté et al. 2010). However, land-use has very different impacts as different management regimes, disturbance intensities and amounts of fertilizer are involved (Socher et al. 2012; Socher et al. 2013). Under a grazing regime, species not only have to recover from being eaten but also have to tolerate trampling (Van Wieren 1995). In general, grazing is more selective and irregular and causes heterogeneity (Adler et al. 2001; Rook et al. 2004), whereas mowing causes the same damage for all species at the same time and is supposed to create less disturbances and milder conditions compared to grazing, though enhancing species richness (Fischer & Wipf 2002). Different land-use management regimes can therefore favor different traits (Díaz et al. 2007; Catorci et al. 2011). Disturbance intensity in grazed or mown systems depends on the duration and density of stocking as well as on the frequency of the disturbance events (Blüthgen et al. 2012). Furthermore, different amounts of applied fertilizer lead to different productivity of the grasslands (Hejcman et al. 2010; Socher et al. 2012). In order to combine various aspects of land-use, Blüthgen et al. (2012) established a quantitative land-use intensity index (LUI) which jointly considers fertilization, mowing and grazing intensity (for calculation details see chapter 2.3).

In addition, land-use intensity acts as an environmental filter (Díaz et al. 1999). Favorable traits under high land-use intensity are connected with quick compensation, regrowth and recovery of biomass loss or damage after disturbances (Vesk et al. 2004), high relative growth rates (Poorter 1989), high SLA (McIntyre 2008) or traits that are connected with the species ability to rapidly colonize newly formed gaps by vegetative reproduction or clonal growth (Klimešová et al. 2008; Wellstein & Kuss 2010; Klimešová et al. 2016; Klimešová et al. 2018). The input of high amounts of fertilizer to increase yields of intensively managed grasslands cause, on the one hand, higher disturbance levels, and on the other hand, higher competition between species (Plantureux et al. 2005; Socher et al. 2012). Intensive land-use leads to species loss and homogenization of the community and therefore also to trait convergence (Flynn et al. 2009; Allan et al. 2015; Gossner et al. 2016; Chisté et al. 2018). At present, many ecosystems are influenced by land-use intensification and are threatened to change or to be destroyed (Sala et al. 2000; Gossner et al. 2016). Changes of ecosystems also concern ecosystem functions and ecosystem services, which are of major interest for human beings (Costanza et al. 1997; Foley et al. 2005). Moreover, dispersal limitation contributes to species loss (Ozinga et al. 2009). However, species invasions show that communities are not saturated with species and that there is potential that new species can become established (Loreau 2000; Stohlgren et al. 2003; Stohlgren et al. 2008). Seed addition experiments were used to investigate the establishment of potential species, to gain more insight in invasion biology, but also to test for dispersal limitations of local species (Burke & Grime 1996; Buckland et al. 2001; Foster & Tilman 2003). Species that potentially co-occur within existing communities but are absent because of dispersal limitation or species loss, have been defined as “dark diversity” (Pärtel et al. 2011; Pärtel 2014). Bennett & Pärtel (2017) used the concept of “dark diversity” to test assembly rules via a seed addition experiment. However, Clark et al. (2007) criticized seed addition experiments, because they were found to have little success and the conditions of the microhabitats mostly had more influence on the establishment of plants from seeds than the amount of seeds used. Another approach to test the establishment of potentially occurring species is the use of already germinated plant individuals for transplantation instead of seeds. This approach is called enrichment planting and is mostly used in forestry to restore degraded forests (Millet et al. 2013; Schweizer et al. 2013). Using young transplants raised in the greenhouse instead of seeds has the advantage to avoid high mortality rates due to unfavorable abiotic or biotic conditions during germination (Chambers & MacMahon 1994), thus allowing to focus on the adult life stage.

1.2 Objectives of the thesis

The central idea of this thesis is to use an enrichment planting experiment to test if missing species of the local species pool, i.e. all species that potentially can co-occur in a given habitat, follow certain assembly rules in order to become established, taking different land-use intensities and functional trait characteristics of communities into account.

In particular, this thesis studies the role of species traits for the establishment and growth of 130 different vascular plant species in different German grassland communities under varying conditions of land-use intensity. I tested whether missing plant species can be established by using an enrichment planting experiment with young transplant species. Particularly, I asked whether the establishment success depends on environmental filtering or niche differentiation. In order to know whether traits are important indicators in the assembly of communities and if they can distinguish between environmental filtering and niche differentiation processes, four enrichment planting scenarios were developed.

First, following neutral theory and ignoring interspecific trait differences for establishment success, the “Random Scenario” was designed by using a random selection of transplant species.

The second and third scenarios were called “Dissim” and “Sim”. Both scenarios were trait-based and were used to differentiate between niche differentiation and environmental filtering processes.

The “Dissim Scenario” was created using species with the most dissimilar traits compared to the resident community to test for niche differentiation processes. Under high competition pressure the rule of limiting similarity predicts species to be more dissimilar, which will be the case under low land-use intensity, where conditions are less harsh but more favorable and competition is supposed to be stronger.

In contrast, the “Sim Scenario” was designed to represent transplant species with the most similar traits compared to the resident community in order to test for environmental filtering. Under high environmental filtering and, in addition, high land-use intensity species are supposed to have similar traits to the residents in order to survive the harsh conditions.

The fourth scenario, the “Beals Scenario” referred to an index developed by E. Beals (1984). This index describes the probability of co-occurrence of a missing species to a resident community. This scenario was solely statistically derived and did not include traits. The underlying data basis for selecting species with highest probability of co-occurrence was the German Vegetation Reference Database (GVRD), which at the time when the project was developed comprised 111,928 vegetation records of Germany (Jandt & Bruelheide 2012). In contrast to the other scenarios, in the "Beals Scenario" information of the environment (habitat conditions and biotic interactions) is indirectly included, because species with highest probability of co-occurrence are supposed to already coexist in other communities under certain abiotic and biotic conditions. Species of the "Beals Scenario" grow together in similar community constellations at other sites under natural conditions. Therefore, the "Beals Scenario" is supposed to represent the degree between environmental filtering and niche differentiation that is actually observed in a community. Comparing the "Beals Scenario" to the Dissim and Sim scenarios might allow deriving the relative importance of trait divergence and convergence in a community and how niche differentiation and environmental filtering act in the assembly of existing grassland communities along the gradient of land-use intensity.

The study was conducted within the Biodiversity Exploratories. The Biodiversity Exploratories are a network of forest and grassland sites differing in land-use intensity and species composition. This network comprises three different regions of Germany (Schwäbische Alb, Hainich and Schorfheide) where interdisciplinary research teams investigate the effect of land use on biodiversity and the role of biodiversity for ecosystem processes (a description and maps of the study area are given in the following section 1.3 of this chapter). Chapters 2 and 3 of this thesis are exclusively based on enrichment planting experiments within the Biodiversity Exploratory network (experimental design is described in chapter 2), whereas chapter 4 additionally includes a common garden experiment set up in the Botanical Garden of the Martin Luther University Halle-Wittenberg (experimental design is described in chapter 4). The enrichment planting experiment within the Biodiversity Exploratories was conducted in 54 grassland plots, with 18 each per region (information of plots are provided in Table 1.1 in the following section 1.3 of this chapter).

All four enrichment planting scenarios contained a set of six transplant species which were plot-specific, thus differed between plots depending on the species composition of the resident community. Furthermore, all scenarios were replicated once per plot, resulting in 8 subplots per plot (for detailed information of the experimental design see chapter 2).

In order to identify the missing species and to develop the plot-specific enrichment planting scenarios, vegetation records of the resident communities were recorded and trait information of all species was gathered in 2011 (for detailed information on vegetation surveys and measurements of traits as well as the calculation procedure to construct the four different plot-specific enrichment planting scenarios see chapter 2). Seeds were collected and raised in the greenhouse in 2011. In spring 2012, a total of 2592 young plant individuals of 130 different species were transplanted into 54 plots of different German grassland communities within the

Biodiversity Exploratories network. At the same time, three replicates of each of the 130 species were also planted in a common garden experiment in the Botanical Garden of the Martin Luther University Halle-Wittenberg (for experimental design of the common garden experiment see chapter 4).

The performance of all transplanted individuals (survival rates and relative growth rates of different parameters) was regularly monitored over two years and aboveground biomass, SLA and LDMC were determined after the harvest of plants at the end of all experiments in September 2013. Relationships between survival and performance of the transplants and land-use intensity, scenario dependency, trait properties of species as well of the communities (mean trait distances, FD and CWM) were investigated.

In accordance with the chronology of the three written papers within this thesis (chapters 2 to 4), the structure of this thesis is as follows.

The main objective of chapter 2 was to analyze the change of community mean trait distances caused by adding the four enrichment planting scenarios (Random, Dissim, Sim and Beals) to the different subplots along the gradient of land-use intensity. A further aim of chapter 2 was to investigate the survival of the transplants belonging to the different scenarios along the gradient of land-use intensity. Both studied aspects of this chapter aimed at revealing differences based on scenario levels.

Chapter 3 addressed the question which predictors could best explain the performance (mainly relative growth rates and final biomass production) of the transplanted individuals in the different vegetation periods. Predictors considered in this context were land-use intensity (LUI), certain trait characteristics of the community (FD or CWM), climate (temperature and moisture of air and soil) as well as factors given by the experimental setting (exploratory identity, plot identity, subplot identity, scenario identity and species identity).

The aim of chapter 4 was to evaluate species-specific trait–performance relationships by comparing the performance of the species transplanted into plots of the Biodiversity Exploratories within the enrichment planting experiment under realistic management conditions (in this study called field experiment) to the species planted into a common garden of the Martin Luther University Halle-Wittenberg without differences in land-use management and community effects (in this study called common garden experiment). This included analyses of performance variables (relative growth rates (RGR), aboveground biomass and survival) of the same species under different environmental settings and comparisons of changes in the relationships of species traits to performance under both conditions. This chapter investigated the effects of species' identities and therefore all performance parameters were averaged at the species level.

The tested hypotheses in this thesis are as following:

H1 Grassland communities are not saturated with species, and therefore, new species can become established.

H2 Species differences, which were reflected in trait differences, are connected with growth, survival and performance (investigated in chapter 3 and 4).

H3 The scenario, according to which a species was selected, has the most prominent impact on survival and performance of the transplants (investigated in chapters 2 and 3). This resulted in the following sub-hypotheses:

H3a The chance to fit into the different grassland communities with varying land-use intensity is low for transplant species of the Random scenario, because the underlying assembly processes environmental filtering and niche differentiation are supposed to act differently along the gradient of land-use intensity, which is not considered in a random selection. Species of the Random scenario are chosen randomly and irrespective of traits. Traits are supposed to be important for growth, therefore species of the Random scenario will have a lower establishment success reflected in lower survival and performance, as compared in particular to the trait based scenarios Dissim and Sim (see Fig. 1.1; investigated in chapters 2 and 3).

H3b Because of niche differentiation under higher competition regimes, species of the Dissim scenario will have higher establishment success under low land-use intensity. Survival and performance of the species of the Dissim scenario are supposed to increase with decreasing land-use intensity, and thus being superior in survival and performance to the most similar species of the Sim scenario under low land-use intensity conditions (see Fig. 1.1; investigated in chapters 2 and 3).

H3c Due to environmental filtering, species of the Sim scenario will have a higher establishment success under high land-use intensity, which will be reflected in higher survival and performance with increasing land-use intensity, and thus being superior in survival and performance to the most dissimilar species of the Dissim scenario under high land-use intensity conditions (see Fig. 1.1; investigated in chapters 2 and 3).

H3d Species of the Beals scenario show the highest establishment success, reflected in higher survival and performance compared to all other scenarios, because species of this scenario are found in real co-occurrence constellations in nature (see Fig. 1.1; investigated in chapters 2 and 3).

H4 Land-use intensity is supposed to be the strongest environmental filter in grassland communities and therefore the LUI will have highest impact on species growth, whereas trait characteristics of the community like FD will have lower impact (chapter 2).

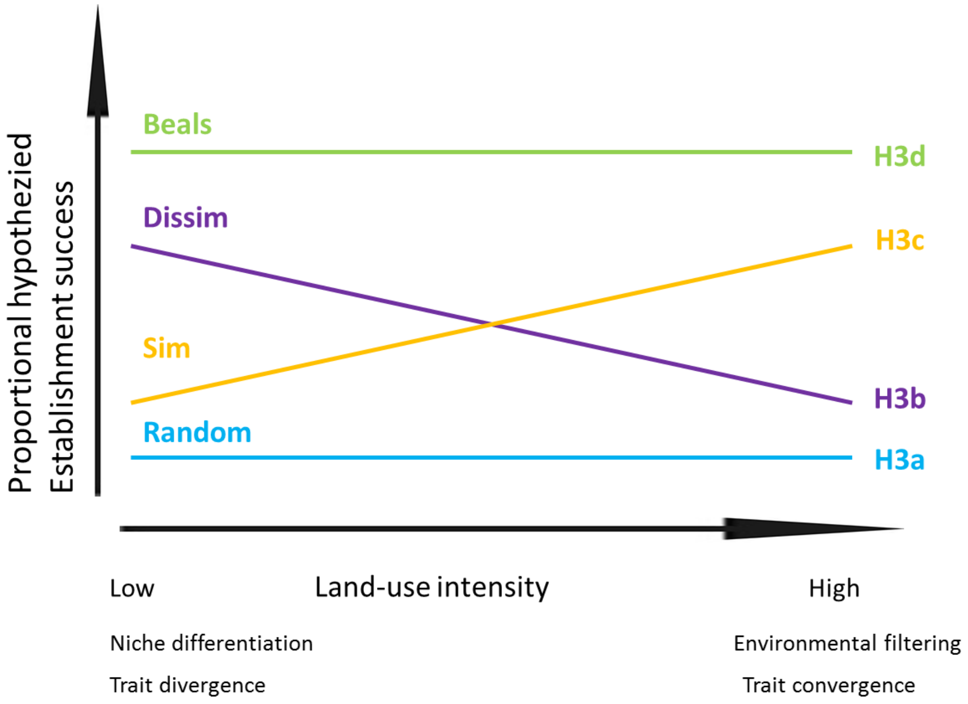

Figure 1.1 The proportional hypothesized establishment success of transplant species of the four different enrichment planting scenarios Random, Dissim, Sim and Beals along the gradient of land-use intensity and the assembly processes niche differentiation and environmental filtering which are supposed to be involved behind as stated in the hypotheses of this thesis (H3a – H3d).

1.3 Study area

The enrichment planting experiment of this thesis was conducted on 54 experimental grassland plots of the Biodiversity Exploratories within the three German regions Schwäbische Alb, Hainich and Schorfheide (see Fig. 1.2, detailed information of all plots are provided in Table 1.1 and maps are shown in Figs. 1.3 – 1.5). The three regions Schwäbische Alb, Hainich and Schorfheide differ in climate, soil and vegetation characteristics.

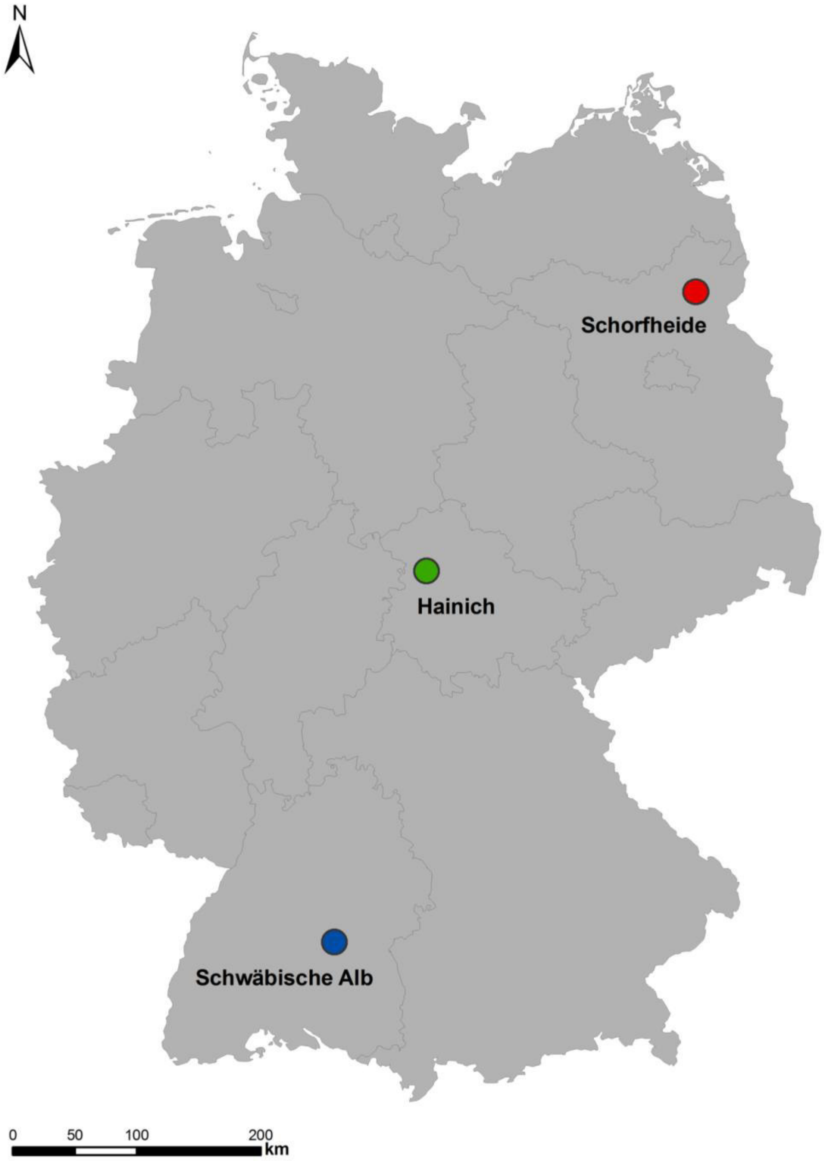

Figure 1.2 The three study regions in Germany. In each of the three regions, 18 grassland plots were selected, as shown in Figs. 1.3 – 1.5. This figure is also given on the attached CD in the Supporting Information of chapter 2.

The Schwäbische Alb is located in the south-west of Germany in Baden-Württemberg and belongs to a low mountain range with altitudes between 461 m and 823 m above sea level (Table 1.1). Compared to the other two regions, Hainich and Schorfheide, the relatively high elevation of the Schwäbische Alb is reflected in relatively low annual mean temperatures and relatively high annual mean precipitation with 6.5 °C and 963 mm, respectively (measured near Münsingen for the years 1961 – 1990, Deutscher Wetter Dienst (DWD 2018)).

Table 1.1 Main characteristics of the experimental plots within the three regions Schwäbische Alb (a), Hainich (b) and Schorfheide (c) of the Biodiversity Exploratories. Altitude was measured with GPS and is given in meter above sea level. Slope was estimated 2011 in degrees. Soil type (Soil WRB) after World Reference Base for Soil Resources (IUSS Working Group 2006) was characterized by the core team of the Biodiversity Exploratories in 2006 (Fischer et al. 2010). Land-use intensity (LUI) for the years 2006 to 2010 was calculated by Blüthgen et al. (2012). Information about land-use management was given by the respective management team of each region. Functional trait diversity (FD) was calculated with 8 traits (SLA, LDMC, height, leaf anatomy, leaf distribution, leaf persistence, physical defense and vegetative reproduction (for obtainment and measurements of traits see chapter 2)). The abundance measures required for FD calculation as well as species richness (SR) were obtained from vegetation records made in 2011.

Area a: Schwäbisch Alb

Plot ID	Location	Altitude	Slope	Soil WRB	Land-use management		LUI	FD	SR
AEG01	Kohlstetten	692	1	Leptosol	M	Fertilized, two cuttings	1.76	0.18	32
AEG02	Apfelstetten	756	9	Leptosol	M	Fertilized, three cuttings	3.12	0.17	23
AEG04	Marbach	658	11	Leptosol	M-P	Fertilized, one cut, cattle	1.69	0.17	21
AEG06	Grafeneck	716	1	Leptosol	M-P	Fertilized, one cut, cattle	2.47	0.16	36
AEG07	Sternberg	794	13	Leptosol	P	Not fertilized, sheep	0.58	0.22	49
AEG09	Hopfenburg	758	15	Leptosol	P	Not fertilized, sheep	0.65	0.23	56
AEG10	Sonnenbühl	753	10	Leptosol	M	Not fertilized, one cut	0.93	0.21	54
AEG15	Hengen	758	10	Leptosol	M	Not fertilized, three cuttings	2.59	0.14	21
AEG19	Grafeneck	719	4	Leptosol	M-P	Fertilized, one cut, cattle, horses	1.76	0.14	20
AEG20	Bad Urach	461	18	Leptosol	P	Fertilized, cattle	1.94	0.18	27
AEG30	Wittlingen	696	12	Leptosol	M-P	Not fertilized, sheep	1.41	0.21	36
AEG31	Wittlingen	737	10	Leptosol	M-P	Not fertilized, sheep	1.21	0.21	37
AEG38	Dottingen	823	2	Cambisol	M	Fertilized, two cuttings	1.38	0.21	33
AEG43	Böttingen	764	5	Cambisol	M-P	Fertilized, one cut, cattle	2.07	0.13	28
AEG44	Dapfen	685	15	Cambisol	P	Not fertilized, cattle	2.15	0.20	39
AEG45	Fauserhöhe	733	6	Cambisol	M	Not fertilized, two cuttings	1.31	0.18	25
AEG46	Grafeneck	679	2	Cambisol	P	Not fertilized, cattle, horses	1.77	0.17	29
AEG47	Dottingen	725	19	Cambisol	P	Not fertilized, , sheep	0.71	0.24	47

Continued

Area b: Hainich

Plot ID	Location	Altitude	Slope	Soil WRB	Land-use management		LUI	FD	SR
HEG04	Kammerforst	283	3	Stagnosol	M-P	Fertilized, cattle	2.08	0.17	19
HEG07	Horsmar	291	2	Stagnosol	P	Fertilized, cattle	1.65	0.15	19
HEG10	Eigenrode	320	1	Vertisol	M	Fertilized	1.23	0.14	24
HEG11	Eigenrode	363	0	Stagnosol	M	Fertilized	1.2	0.18	33
HEG14	Eigenrode	372	1	Stagnosol	M-P	Fertilized, sheep	2.04	0.15	35
HEG16	Hütschenroda	368	10	Stagnosol	P	Not fertilized, sheep	1.06	0.20	34
HEG18	Horsmar	311	1	Vertisol	P	Not fertilized, sheep	0.75	0.21	54
HEG23	Hallungen	317	14	Stagnosol	M-P	Not fertilized, cattle	1.48	0.18	35
HEG24	Wernershausen	340	5	Stagnosol	M-P	Not fertilized, cattle	1.63	0.22	37
HEG26	Zella	339	9	Cambisol	M	Fertilized	1.2	0.14	25
HEG27	Zimmern	233	9	Cambisol	M	Fertilized	1.74	0.14	27
HEG34	Pfaffenrode	310	10	Cambisol	M-P	Fertilized, cattle	2.11	0.15	23
HEG36	Behringen	328	5	Cambisol	M-P	Fertilized, sheep	2.09	0.16	28
HEG37	Behringen	320	8	Cambisol	M-P	Fertilized, sheep	2.13	0.20	29
HEG39	Hallungen/Naza	293	12	Cambisol	P	Not fertilized, cattle	1.33	0.19	33
HEG40	Melborn	308	5	Cambisol	P	Not fertilized, cattle	1.7	0.22	29
HEG41	Dörna	348	1	Cambisol	P	Not fertilized, sheep	0.66	0.20	58
HEG47	Zella	331	2	Cambisol	M-P	Not fertilized, cattle	1.58	0.19	29

Area c: Schorfheide

Plot ID	Location	Altitude	Slope	Soil WRB	Land-use management		LUI	FD	SR
SEG06	Milmersdorf	53	0	Histosol	M-P	Not fertilized, cattle	1.38	0.20	20
SEG07	Bruchhagen	20	0	Histosol	P	Not fertilized, cattle	1.35	0.19	13
SEG09	Milmersdorf	51	1	Histosol	P	Not fertilized, cattle	1.31	0.17	16
SEG15	Biesenbrow	20	0	Histosol	M-P	Not fertilized, cattle	1.18	0.17	22
SEG17	Milmersdorf	55	0	Histosol	M-P	Not fertilized, cattle	1.24	0.20	23
SEG18	Pfingstberg	35	0	Luvisol	M	Not fertilized	1.41	0.16	28
SEG22	Güntherberg	24	1	Gleysol	P	Not fertilized, cattle	1.39	0.19	18
SEG23	Biesenbrow	10	0	Histosol	M	Fertilized	1.75	0.14	16
SEG25	Milmersdorf	52	0	Histosol	M	Not fertilized	1.49	0.19	21
SEG29	Bruchhagen	17	1	Histosol	M	Not fertilized	0.94	0.19	21
SEG30	Voßberg	65	1	Albeluvisol	M	Not fertilized	1.33	0.09	12
SEG32	Voßberg	54	1	Luvisol	M	Not fertilized	1.33	0.14	17
SEG33	Neugrimnitz	72	10	Albeluvisol	M-P	Fertilized, cattle	1.94	0.16	27
SEG34	Neugrimnitz	75	8	Albeluvisol	M-P	Fertilized, cattle	2.23	0.16	29
SEG35	Neugrimnitz	90	1	Luvisol	M-P	Fertilized, cattle	2.24	0.18	23
SEG40	Steglitz	58	1	Luvisol	P	Fertilized, cattle	1.82	0.18	30
SEG49	Sperlingsherberge	79	2	Albeluvisol	P	Not fertilized, cattle	1.61	0.19	29
SEG50	Böckenberg	73	5	Cambisol	P	Not fertilized, cattle	1.43	0.20	25

The experimental plots of the Schwäbische Alb are located around Münsingen, Bad Urach and Gomadingen in the rural district of Reutlingen (N48°23 – N48°29, E009°12 – E009°32), see Fig. 1.3. Solid rock material of the Schwäbische Alb are calcareous bedrocks of the Jura with karst phenomena (Fischer et al. 2010). This geology in the Schwäbische Alb resulted in the development of mainly leptosol and some cambisol soils (Fischer et al. 2010) (see Table 1.1). The landscape of the Schwäbische Alb is very heterogeneous with small patches of forest, fields and grasslands; the latter were traditionally grazed by sheep (Plieninger et al. 2013). Nowadays, land-use intensity of grasslands ranges between extensively and intensively managed grasslands (Plieninger et al. 2013; Bieling et al. 2013). Moreover, many calcareous semi-dry grasslands have remained and are protected biotopes. An area of 85.000 ha around Münsingen has been declared UNESCO-Biosphere Reserve in 2009 (Plieninger et al. 2013; Bieling et al. 2013).

The Hainich is located in the federal state of Thüringen in Central Germany. The experimental plots are placed near Mühlhausen and Bad Langensalza (N50°58 – N51°17, E010°20 – E010°35), see Fig. 1.4. Elevation within the area ranges between 233 – 372 meter above sea level (Table 1.1) and an annual mean temperatures of 7.5 °C and an annual mean precipitation of 662.6 mm are achieved (measured near Leinefelde in the years 1961-1990, Deutscher Wetter Dienst (DWD 2018)). The landscape of the Hainich contains one of the largest undisturbed beech forests of Germany that has remained unmanaged for more than 30 years, because of military training activities, before parts of it were declared National Park in 1997 (Mölder et al. 2009). The Hainich forest is surrounded by an intensively used landscape formed by agriculture (Anthoni et al. 2004) on mostly calcareous bedrocks (Fischer et. al. 2010). Soil types of the experimental plots are cambisol, stagnosol and two plots with vertisols (Fischer et. al. 2010) (see Table 1.1).

The Schorfheide is located in the federal state of Brandenburg in the north-east of Germany. The experimental plots are located near Angermünde (N52°58 – N53°59, E013°36 – E014°01), see Fig. 1.5. The Schorfheide is a flat landscape at low altitudes between 10 and 90 meter above sea level (Table 1.1). Annual mean temperature and precipitation are 8.3°C and of 532.1 mm, respectively (measured in Angermünde for the years 1961 – 1990, Deutscher Wetter Dienst, (DWD 2018)). The glacial ice has arranged a moraine landscape with low hills, sandy areas, little lakes, swamps and wetlands (Schulzke 1995). Since 1990, parts of the area belong to the UNESCO-Biosphere Reserve Schorfheide-Chorin (Schulzke 1995). Soil conditions of the experimental plots in the Schorfheide are very diverse and include plots with mineral soils (e.g. cambisol and luvisol, Table 1.1) but, in contrast to the other two regions, also some plots that are characterized by stagnant moisture and soil wetness (histosol, Table 1.1) (Fischer et al. 2010).

The experimental plots in all regions were selected in order to represent a balanced mixture between the three land-use management regimes meadows (M), pastures (P) and meadow-pastures (M-P) and also between fertilized and non-fertilized plots (see Table 1.1), which however was not always achieved completely. Furthermore, I tried to cover a gradient of land-use intensity between less intensively and intensively managed grasslands for all plots in each region, identified by the LUI, which ranges between 0.58 (less intensively managed plots) and 3.12 (intensively managed plots) (Table 1.1). In the Schorfheide, land-use intensity was generally more homogenous, without semi-dry grassland plots with low LUI like in the Schwäbische Alb and the Hainich, resulting in a shorter land-use intensity gradient (Table 1.1). This trend is also obvious in the diversity of the vegetation seen in the range of species richness of vascular plants and their functional trait diversity in the plots (Table 1.1). For example, species richness in the Schorfheide is only between 12 and 30 vascular plant species per plot, whereas in the Schwäbische Alb and the Hainich species richness ranges between 20 and 56 and 19 and 58 per plot, respectively (Table 1.1). Moreover, there are strong regional differences in species composition. To account for differences between regions and plots, the experimental design variables (exploratory identity and plot identity) are used as random factors in the statistical analyses.

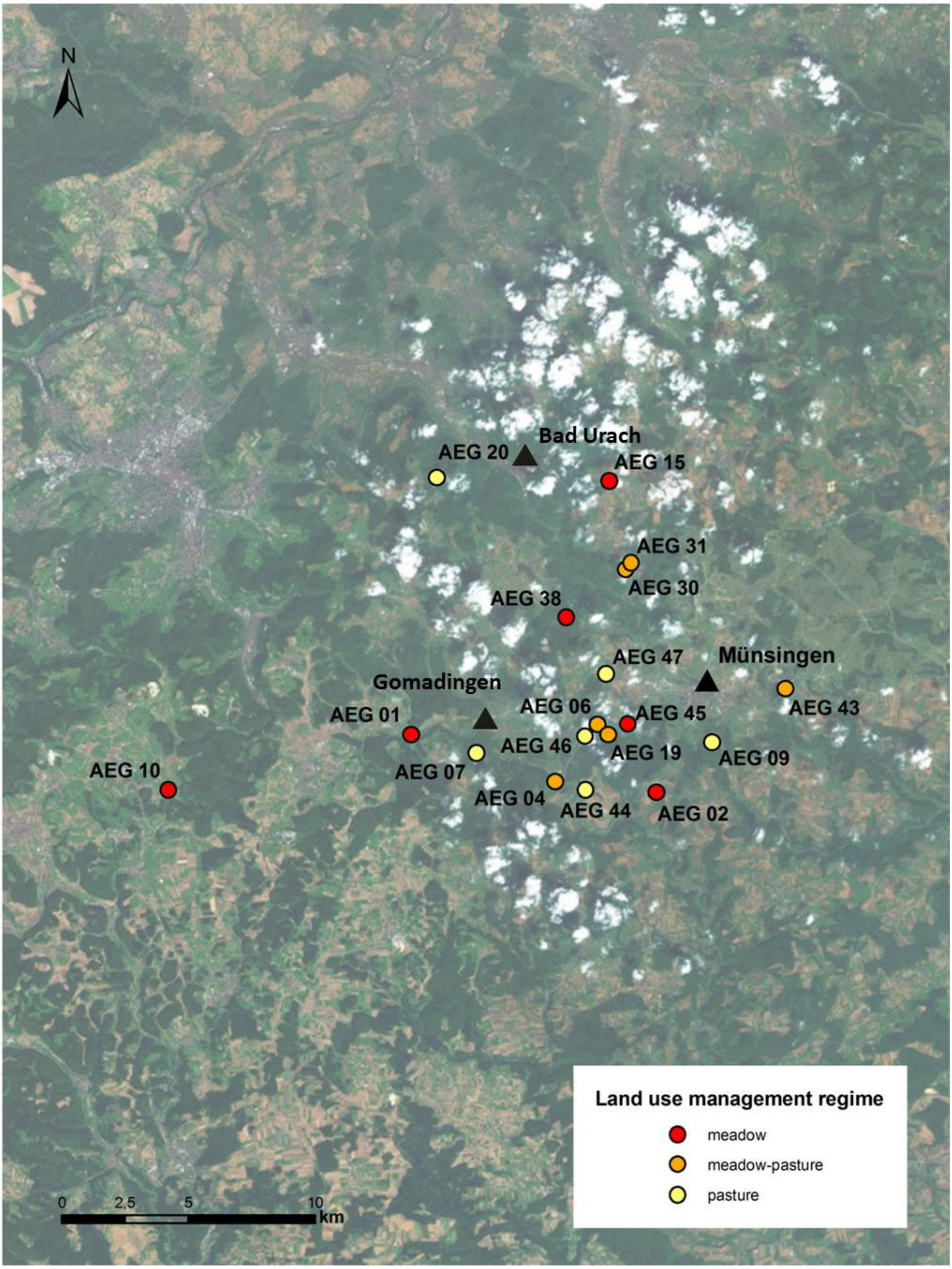

Figure 1.3 The distribution of 18 plots in the study region Schwäbische Alb near Münsingen (Baden-Württemberg). Meadows are shown in red, meadow-pastures in orange and pastures in yellow. This figure is also given on the attached CD in the Supporting Information of chapter 2.

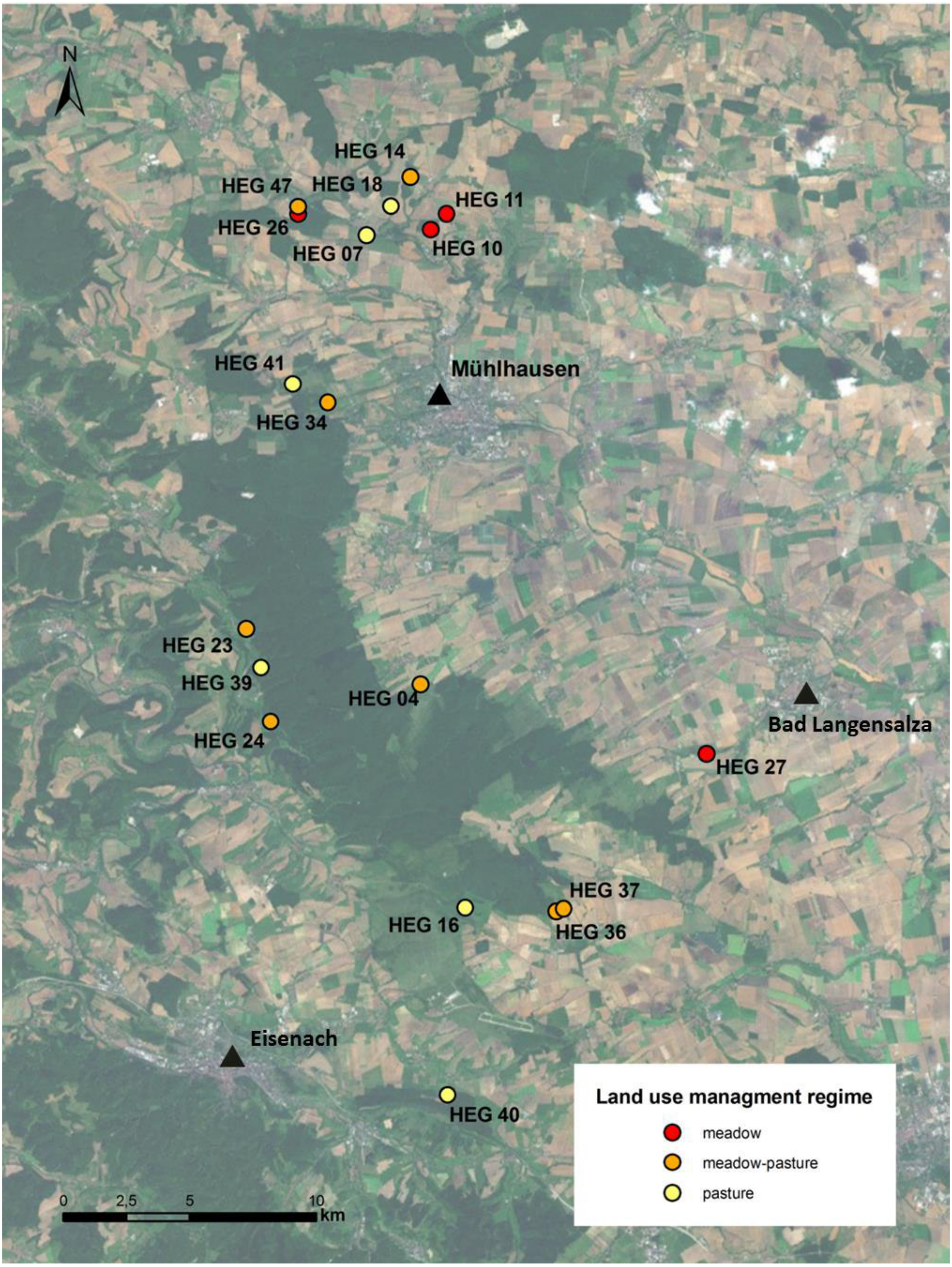

Figure 1.4 The distribution of 18 plots in the study region Hainich near Mühlhausen (Thüringen). Meadows are shown in red, meadow-pastures in orange and pastures in yellow. This figure is also given on the attached CD in the Supporting Information of chapter 2.

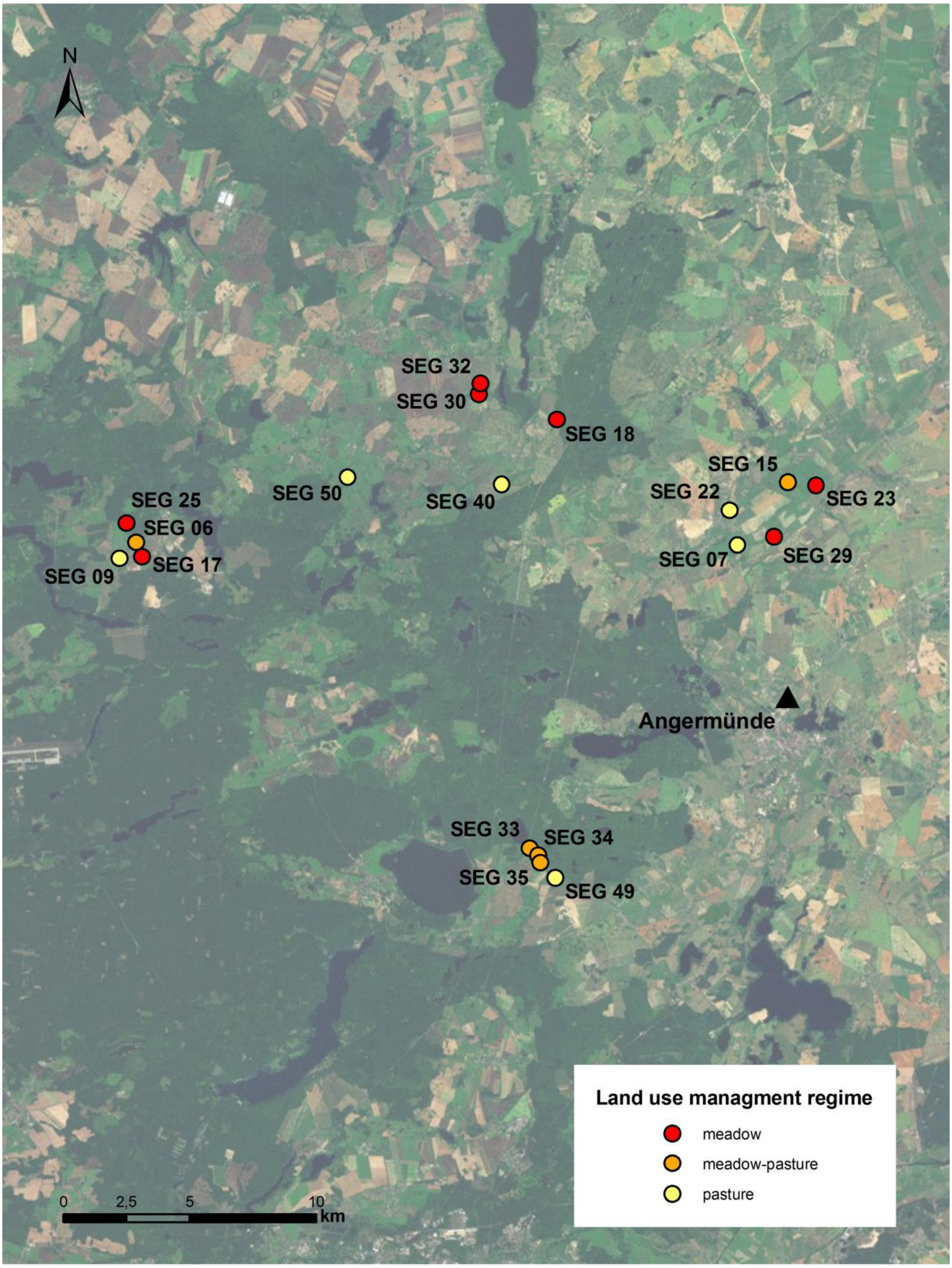

Figure 1.5 The distribution of 18 plots in the study region Schorfheide near Angermünde (Brandenburg). Meadows are shown in red, meadow-pastures in orange and pastures in yellow. This figure is also given on the attached CD in the Supporting Information of chapter 2.

1.4 References

Adler, P., Raff, D., & Lauenroth, W. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479.

Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N., Böhm, S., Grassein, F., Hölzel, N., Klaus, V.H., Kleinebecker, T., Morris, E.K., Oelmann, Y., Prati, D., Renner, S.C., Rillig, M.C., Schaefer, M., Schloter, M., Schmitt, B., Schöning, I., Schrumpf, M., Solly, E., Sorkau, E., Steckel, J., Steffen-Dewenter, I., Stempfhuber, B., Tschapka, M., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., & Fischer, M. 2015. Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecology Letters* 18: 834–843.

Anthoni, P.M., Knohl, A., Rebmann, C., Freibauer, A., Mund, M., Ziegler, W., Kolle, O., & Schulze, E.-D. 2004. Forest and agricultural land-use-dependent CO2 exchange in Thuringia, Germany. *Global Change Biology* 10: 2005–2019.

Austrheim, G., Gunilla, E., Olsson, A., & Grøntvedt, E. 1999. Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, central Norway. *Biological Conservation* 87: 369–379.

Beals, E.W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14: 55.

Bennett, J.A., & Pärtel, M. 2017. Predicting species establishment using absent species and functional neighborhoods. *Ecology and Evolution* 7: 2223–2237.

Berendse, F. 1979. Competition between plant populations with different rooting depths. *Oecologia* 43: 19–26.

Bieling, C., Plieninger, T., & Schaich, H. 2013. Patterns and causes of land change: Empirical results and conceptual considerations derived from a case study in the Swabian Alb, Germany. *Land Use Policy* 35: 192–203.

Blom, C.W.P.M., & Voesenek, L.A.C.J. 1996. Flooding: the survival strategies of plants. *Trends in Ecology & Evolution* 11: 290–295.

Blüthgen, N., Dormann, C.F., Prati, D., Klaus, V.H., Kleinebecker, T., Hölzel, N., Alt, F., Boch, S., Gockel, S., Hemp, A., Müller, J., Nieschulze, J., Renner, S.C., Schöning, I., Schumacher, U., Socher, S.A., Wells, K., Birkhofer, K., Buscot, F., Oelmann, Y., Rothenwöhrer, C., Scherber, C., Tscharntke, T., Weiner, C.N., Fischer, M., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., & Weisser, W.W. 2012. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology* 13: 207–220.

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* 16: 533–540.

Briske, D.D. 1996. Strategies of plant survival in grazed systems: a functional interpretation. *The ecology and management of grazing systems*

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124: 255–279.

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S.M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V.D., Schrodt, F., Mahecha, M.D., Peet, R.K., Sandel, B., van Bodegom, P., Altman, J., Alvarez Davila, E., Arfin Khan, M.A.S., Attorre, F., Aubin, I., Baraloto, C., Barroso, J.G., Bauters, M., Bergmeier, E., Biurrun, I., Bjorkman, A.D., Blonder, B., Čarni, A., Cayuela, L., Černý, T., Cornelissen, J.H.C., Craven, D., Dainese, M., Derroire, G., De Sanctis, M., Díaz, S., Doležal, J., Farfan-Rios, W., Feldpausch, T.R., Fenton, N.J., Garnier, E., Guerin, G.R., Gutiérrez, A.G., Haider, S., Hattab, T., Henry, G., Hérault, B., Higuchi, P., Hölzel, N., Homeier, J., Jentsch, A., Jürgens, N., Kącki, Z., Karger, D.N., Kessler, M., Kleyer, M., Knollová, I., Korolyuk, A.Y., Kühn, I., Laughlin, D.C., Lens, F., Loos, J., Louault, F., Lyubenova, M.I., Malhi, Y., Marcenò, C., Mencuccini, M., Müller, J.V., Munzinger, J., Myers-Smith, I.H., Neill, D.A., Niinemets, Ü., Orwin, K.H., Ozinga, W.A., Penuelas, J., Pérez-Haase, A., Petřík, P., Phillips, O.L., Pärtel, M., Reich, P.B., Römermann, C., Rodrigues, A.V., Sabatini, F.M., Sardans, J., Schmidt, M., Seidler, G., Espejo, J.E.S., Silveira, M., Smyth, A., Sporbert, M., Svenning, J.-C., Tang, Z., Thomas, R., Tsiripidis, I., Vassilev, K., Violle, C., Virtanen, R., Weiher, E., Welk, E., Wesche, K., Winter, M., Wirth, C., & Jandt, U. 2018. Global trait–environment relationships of plant communities. *Nature Ecology and Evolution (in the press)*

Buckland, S.M., Thompson, K., Hodgson, J.G., & Grime, J.P. 2001. Grassland invasions: effects of manipulations of climate and management. *Journal of Applied Ecology* 38: 301–309.

Burke, M.J.W., & Grime, J.P. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776–790.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., & Weis, J.J. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences* 104: 18123–18128.

Casper, B.B., & Jackson, R.B. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* 28: 545–570.

Catorci, A., Ottaviani, G., Ballelli, S., & Cesaretti, S. 2011. Functional differentiation of central apennine grasslands under mowing and grazing disturbance regimes. *Polish Journal of Ecology* 59: 115–128.

Chambers, J.C., & MacMahon, J.A. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual review of ecology and systematics* 25: 263–292.

Chapin, F.S., Bloom, A.J., Field, C.B., & Waring, R.H. 1987. Plant responses to multiple environmental factors. *BioScience* 37: 49–57.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.

Chisté, M.N., Mody, K., Kunz, G., Gunczy, J., & Blüthgen, N. 2018. Intensive land use drives small-scale homogenization of plant- and leafhopper communities and promotes generalists. *Oecologia* 186: 529–540.

Christenhusz, M.J.M., & Byng, J.W. 2016. The number of known plants species in the world and its annual increase. *Phytotaxa* 261: 201–217.

Clark, C.J., Poulsen, J.R., Levey, D.J., & Osenberg, C.W. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Naturalist* 170: 128–142.

Colwell, R.K., & Fuentes, E.R. 1975. Experimental studies of the niche. *Annual Review of Ecology and systematics* 6: 281–310.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.

Cornwell, W.K., & Ackerly, D.D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.

Cornwell, W.K., Schwilk, D.W., & Ackerly, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* 87: 1465–1471.

Costanza, R., d'Arge, R., Groot, R. de, Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., & Belt, M. van den. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.

Díaz, S., Cabido, M., & Casanoves, F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122.

Díaz, S., Cabido, M., Zak, M., Martínez Carretero, E., & Araníbar, J. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science* 10: 651–660.

Díaz, S., Lavorel, S., McINTYRE, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., & Campbell, B.D. 2007. Plant trait responses to grazing – a global synthesis. *Global Change Biology* 13: 313–341.

DWD. 2018. Klimadaten Deutschland – Mittelwerte. Deutscher Wetterdienst – Bundesministeriums für Verkehr und digitale Infrastruktur. *https://www.dwd.de/DE/leistungen/klimadatendeutschland/vielj_mittelwerte.html?nn=16102&lsbId=343278.*

Dwyer, J.M., & Laughlin, D.C. 2017. Selection on trait combinations along environmental gradients. *Journal of Vegetation Science* 28: 672–673.

Ehrlen, J., & Eriksson, O. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81: 1667–1674.

Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E., & Bernasconi, G. 2007. Time after time: flowering phenology and biotic interactions. *Trends in Ecology & Evolution* 22: 432–439.

Fargione, J., & Tilman, D. 2005. Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia* 143: 598–606.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., & Weisser, W.W. 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology* 11: 473–485.

Fischer, M., & Wipf, S. 2002. Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. *Biological Conservation* 104: 1–11.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., & DeClerck, F. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12: 22–33.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., & Snyder, P.K. 2005. Global consequences of land use. *Science* 309: 570–574.

Foster, B.L., & Tilman, D. 2003. Seed limitation and the regulation of community structure in oak savanna grassland. *Journal of Ecology* 91: 999–1007.

Fraser, L.H., Garris, H.W., & Carlyle, C.N. 2016. Predicting plant trait similarity along environmental gradients. *Plant Ecology* 217: 1297–1306.

Gaston, K.J., & Chown, S.L. 2005. Neutrality and the niche. *Functional Ecology* 19: 1–6.

Gause, G.F. 1934. *The Struggle for Existence*. Williams & Wilkins Company, Baltimore.

Gerhold, P., Price, J.N., Püssa, K., Kalamees, R., Aher, K., Kaasik, A., & Pärtel, M. 2013. Functional and phylogenetic community assembly linked to changes in species diversity in a long-term resource manipulation experiment. *Journal of Vegetation Science* 24: 843–852.

Gossner, M.M., Lewinsohn, T.M., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S.C., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., Diekötter, T., Jorge, L.R., Jung, K., Keyel, A.C., Klein, A.-M., Klemmer, S., Krauss, J., Lange, M., Müller, J., Overmann, J., Pašalić, E., Penone, C., Perović, D.J., Purschke, O., Schall, P., Socher, S.A., Sonnemann, I., Tschapka, M., Tscharntke, T., Türke, M., Venter, P.C., Weiner, C.N., Werner, M., Wolters, V., Wurst, S., Westphal, C., Fischer, M., Weisser, W.W., & Allan, E. 2016. Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* 540: 266–269.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.

Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science* 17: 255–260.

Gross, N., Börger, L., Soriano-Morales, S.I., Le Bagousse-Pinguet, Y., Quero, J.L., García-Gómez, M., Valencia-Gómez, E., & Maestre, F.T. 2013. Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. *Journal of Ecology* 101: 637–649.

Grubb, P.J. 1998. A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 3–31.

Hansson, M., & Fogelfors, H. 2000. Management of a semi-natural grassland; results from a 15-year-old experiment in southern Sweden. *Journal of Vegetation Science* 11: 31–38.

Hardin, G. 1960. The competitive exclusion principle. *Science* 131: 1292–1297.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., & Lawton, # J. H. 1999. Plant diversity and productivity experiments in european grasslands. *Science* 286: 1123–1127.

Hejcman, M., Szaková, J., Schellberg, J., & Tlustoš, P. 2010. The Rengen Grassland Experiment: relationship between soil and biomass chemical properties, amount of elements applied, and their uptake. *Plant and Soil* 333: 163–179.

Holt, R.D. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106: 19659–19665.

Hubbell, S.P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19: 166–172.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, USA.

Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81–101.

Hutchinson, G.E. 1957. Concluding remarks. *Cold spring harbor symposium on quantitative biology* 22: 415–427.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* 93: 145–159.

IUSS Working Group, W.R.B. 2006. World reference base for soil resources. *World Soil Resources Report* 103:.

Jandt, U., & Bruelheide, H. 2012. German Vegetation Reference Database (GVRD). *Biodiversity & Ecology* 4: 355–355.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.

Kempel, A., Razanajatovo, M., Stein, C., Unsicker, S.B., Auge, H., Weisser, W.W., Fischer, M., & Prati, D. 2015. Herbivore preference drives plant community composition. *Ecology* 96: 2923–2934.

Klimešová, J., Latzel, V., de Bello, F., & van Groenendael, J.M. 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. *Preslia* 80: 245–253.

Klimešová, J., Martínková, J., & Herben, T. 2018. Horizontal growth: An overlooked dimension in plant trait space. *Perspectives in Plant Ecology, Evolution and Systematics* 32: 18–21.

Klimešová, J., Tackenberg, O., & Herben, T. 2016. Herbs are different: clonal and bud bank traits can matter more than leaf–height–seed traits. *New Phytologist* 210: 13–17.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A., & Mayfield, M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters* 13: 76–86.

Le Bagousse-Pinguet, Y., Gross, N., Maestre, F.T., Maire, V., de Bello, F., Fonseca, C.R., Kattge, J., Valencia, E., Leps, J., & Liancourt, P. 2017. Testing the environmental filtering concept in global drylands. *Journal of Ecology* 105: 1058–1069.

Liancourt, P., Corcket, E., Michalet, R., & Chiarucci, A. 2005. Stress tolerance abilities and competitive responses in a watering and fertilization field experiment. *Journal of Vegetation Science* 16: 713–722.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. *Ecology Letters* 3: 73–76.

Loreau, M., & Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.

Loughnan, D., & Gilbert, B. 2017. Trait-mediated community assembly: distinguishing the signatures of biotic and abiotic filters. *Oikos* 126: 1112–1122.

MacArthur, R.H. 1984. *Geographical ecology: Patterns in the distribution of species*. Princeton University Press.

MacArthur, R., & Levins, R. 1964. Competition, habitat selection and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences* 51: 1207–1210.

MacArthur, R., & Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101: 377–385.

Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. da S., Soussana, J.-F., & Louault, F. 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist* 196: 497–509.

Mason, N.W.H., & de Bello, F. 2013. Functional diversity: a tool for answering challenging ecological questions. *Journal of Vegetation Science* 24: 777–780.

Mayfield, M.M., & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.

McIntyre, S. 2008. The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. *Agriculture, Ecosystems & Environment* 128: 251–258.

Millet, J., Tran, N., Ngoc, N.V., Thi, T.T., & Prat, D. 2013. Enrichment planting of native species for biodiversity conservation in a logged tree plantation in Vietnam. *New Forests* 44: 369–383.

Mojzsis, S.J., Arrhenius, G., McKeegan, K.D., Harrison, T.M., Nutman, A.P., & Friend, C.R.L. 1996. Evidence for life on Earth before 3,800 million years ago. *Nature* 384: 55–59.

Mölder, A., Bernhardt-Römermann, M., & Schmidt, W. 2009. Vielfältige Baumschicht—reichhaltige Verjüngung? Zur Naturverjüngung von artenreichen Laubwäldern im Nationalpark Hainich. *Allg Forst Jagd* 180: 49–60.

Mueller, K.E., Tilman, D., Fornara, D.A., & Hobbie, S.E. 2013. Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. *Ecology* 94: 787–793.

Ordoñez, J.C., Van Bodegom, P.M., Witte, J.-P.M., Wright, I.J., Reich, P.B., & Aerts, R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography* 18: 137–149.

Osmond, C.B., Austin, M.P., Berry, J.A., Billings, W.D., Boyer, J.S., Dacey, J.W.H., Nobel, P.S., Smith, S.D., & Winner, W.E. 1987. Stress physiology and the distribution of plants. *BioScience* 37: 38–48.

Ozinga, W.A., Römermann, C., Bekker, R.M., Prinzing, A., Tamis, W.L.M., Schaminée, J.H.J., Hennekens, S.M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J.P., & Van Groenendael, J.M. 2009. Dispersal failure contributes to plant losses in NW Europe. *Ecology Letters* 12: 66–74.

Pacala, S.W., & Tilman, D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *The American Naturalist* 143: 222–257.

Pärtel, M. 2014. Community ecology of absent species: hidden and dark diversity. *Journal of Vegetation Science* 25: 1154–1159.

Pärtel, M., Szava-Kovats, R., & Zobel, M. 2011. Dark diversity: shedding light on absent species. *Trends in Ecology & Evolution* 26: 124–128.

Pavoine, S., Vallet, J., Dufour, A., Gachet, S., & Daniel, H. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118: 391–402.

Plantureux, S., Peeters, A., & McCracken, D. 2005. Biodiversity in intensive grasslands: Effect of management, improvement and challenges. *Agronomy Research* 3: 153–164.

Plieninger, T., Bieling, C., Ohnesorge, B., Schaich, H., Schleyer, C., & Wolff, F. 2013. Exploring futures of ecosystem services in cultural landscapes through participatory scenario development in the Swabian Alb, Germany. *Ecology and Society* 18:.

Poorter, H. 1989. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. *Causes and consequences of variation in growth rate and productivity of higher plants* 24: 45–68.

Rao, C.R. 1982. Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology* 21: 24–43.

Rathcke, B., & Lacey, E.P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16: 179–214.

Richardson, D.M., Allsopp, N., D'antonio, C.M., Milton, S.J., & Rejmánek, M. 2000. Plant invasions – the role of mutualisms. *Biological Reviews* 75: 65–93.

Ricotta, C., & Moretti, M. 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia* 167: 181–188.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G., & Mills, J. 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biological Conservation* 119: 137–150.

Rosindell, J., Hubbell, S.P., & Etienne, R.S. 2011. The Unified Neutral Theory of Biodiversity and Biogeography at age ten. *Trends in Ecology & Evolution* 26: 340–348.

Ryser, P., & Lambers, H. 1995. Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant and Soil* 170: 251–265.

Sala, O.E., Chapin, F.S., Iii, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Schulzke, D. 1995. Biosphärenreservat Schorfheide-Chorin. In *Biosphärenreservate in Deutschland*, pp. 159–185. Springer, Berlin, Heidelberg.

Schweizer, D., Gilbert, G.S., & Holl, K.D. 2013. Phylogenetic ecology applied to enrichment planting of tropical native tree species. *Forest Ecology and Management* 297: 57–66.

Socher, S.A., Prati, D., Boch, S., Müller, J., Baumbach, H., Gockel, S., Hemp, A., Schöning, I., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., Weisser, W.W., & Fischer, M. 2013. Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. *Basic and Applied Ecology* 14: 126–136.

Socher, S.A., Prati, D., Boch, S., Müller, J., Klaus, V.H., Hölzel, N., & Fischer, M. 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *Journal of Ecology* 100: 1391–1399.

Spasojevic, M.J., & Suding, K.N. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* 100: 652–661.

Stein, A., Gerstner, K., & Kreft, H. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17: 866–880.

Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C., & Kartesz, J. 2008. The myth of plant species saturation. *Ecology Letters* 11: 313–322.

Stohlgren, T.J., Barnett, D.T., & Kartesz, J.T. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* 1: 11–14.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81–92.

Van Wieren, S.E. 1995. The potential role of large herbivores in nature conservation and extensive land use in Europe. *Biological Journal of the Linnean Society* 56: 11–23.

Vesk, P.A., Warton, D.I., & Westoby, M. 2004. Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos* 107: 72–89.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

Volkov, I., Banavar, J.R., Hubbell, S.P., & Maritan, A. 2003. Neutral theory and relative species abundance in ecology. *Nature* 424: 1035–1037.

Weiher, E., Clarke, G.D.P., & Keddy, P.A. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81: 309–322.

Wellstein, C., & Kuss, P. 2010. Diversity and frequency of clonal traits along natural and land-use gradients in grasslands of the swiss alps. *Folia Geobotanica* 46: 255–270.

Whittaker, R.H. 1965. Dominance and diversity in land plant communities. *Science* 147: 250–260.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1–80.

Wilson, J.B. 2011. The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *Journal of Vegetation Science* 22: 184–195.

Wilson, J.B. 2007. Trait-divergence assembly rules have been demonstrated: Limiting similarity lives! A reply to Grime. *Journal of Vegetation Science* 18: 451–452.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., & Svenning, J.-C. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15–30.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Zobel, M., Otsus, M., Liira, J., Moora, M., & Möls, T. 2000. Is small-scale species richness limited by seed availability or microsite availability? *Ecology* 81: 3274–3282.

Chapter 2 – Do newcomers stick to the rules of the residents? Designing trait-based community assembly tests

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2.1 Abstract

Questions: How similar or dissimilar must a species be to the resident plant community in order to successfully colonize grassland communities that vary in land-use intensity? Is land-use intensity an environmental filter that affects the survival rate of newcomers? Do species that are more likely to co-occur with the resident species show higher survival rates than those that are more similar / dissimilar to the resident community or randomly chosen species?

Location: Schwäbische Alb, Hainich and Schorfheide, Germany.

Methods: We planted different species from the regional grassland species pool into extant grassland communities exposed to different levels of land-use intensity. Species composition was recorded across 54 sites comprising meadows, mown meadows and grazed grasslands located within the 'Biodiversity Exploratories' project areas in three different regions of Germany. New species were selected for enrichment planting in the plots according to four different scenarios: species with highly similar or dissimilar traits, species with the highest degree of co-occurrence (derived from vegetation records held in the German vegetation reference database) and randomly chosen species. The changes in community mean trait distances brought about by enrichment planting and the transplant survival were related to land-use intensity.

Results and Conclusion: Land use was found to be an important environmental filter, as mean trait distance consistently declined with increasing land-use intensity across all scenarios. The planted species with the highest probability of co-occurrence with the resident species did not change the mean pair-wise trait distances across all plots, which indicates that they reflected the same degree of environmental filtering as the resident species. Accordingly, the species that commonly co-occur with the resident species survived best. These findings open a new avenue for using vegetation databases to assess the relative importance of environmental filtering.

Keywords: Beals index; Community assembly rules; Dissimilarity; Environmental filtering; Plant functional traits; Transplant experiment; Vegetation databases

2.2 Introduction

Recent years have witnessed significant progress in the understanding of community assembly rules (Weiher et al. 2011; Götzenberger et al. 2012). One central idea of assembly rules is that species in a community have to be similar enough to pass environmental filters prevailing at a given site (Díaz et al. 1998; Wilson 2007). Species that survive the filter can be expected to have similar functional trait values (Ordoñez et al. 2009). In contrast, the theory of limiting similarity predicts that species have to be dissimilar, at least to some degree, in trait values to resident species to avoid competition (MacArthur & Levins 1967; Pacala & Tilman 1994). In principle, environmental filtering and niche differentiation are opposing processes that simultaneously and jointly structure plant communities (Maire et al. 2012; Spasojevic & Suding 2012; Gross et al. 2013). Communities subjected to more severe environmental conditions are expected to be composed of species with similar trait values. In contrast, the role of competition is equivocal: on the one hand, in communities with strong competition, species should diverge in their trait values to avoid competition through niche differentiation, while on the other hand, equalizing mechanisms allow species with very similar trait values to escape competitive exclusion if fitness differences among them are minimized (Chesson 2000). Furthermore, species with excessively diverging trait values might also be eliminated from the community as a result of competitive exclusion (Mayfield & Levine 2010; Gerhold et al. 2013). Neither of these processes operates exclusively in a given community, and the balance of the outcome of all these processes should be evident in the species composition, which should demonstrate phenotypic clustering or over-dispersion, i.e. amore similar or dissimilar trait value composition (Cavender-Bares et al. 2004). As it is not possible to isolate the different processes in a field study, for the present study we followed the suggestion of Mayfield & Levine (2010), whereby the definition of environmental filtering is broadened by incorporating competitive exclusion, which occurs as a result of competitive ability differences among species, and further biotic factors such as presence or absence of symbionts, pollinators, hosts, herbivores or pathogens. In this way, species that are excluded from a community can be viewed as competitively or mutualistically inferior under the environmental conditions of the focal site, or, alternatively, species that are excluded might not match the environment given the biotic interactions present at the site. Assessing the strength of environmental filtering in field studies is not straightforward, as extant communities are not only the result of deterministic processes but are also formed by dispersal, disturbance and stochasticity (Cavender-Bares et al. 2009). This is particularly the case for German agricultural grasslands that have been exposed to high land-use pressures in recent decades, accompanied by dispersal limitation and species loss (Ozinga et al. 2009). Thus, many more species have the potential to grow in the same local community but are absent for stochastic or historic reasons – a phenomenon referred to as 'dark diversity' (Pärtel et al. 2011). To overcome such stochastic limitations, we designed a field experiment in which new species were added as transplants to resident grassland communities (hereafter referred to as enrichment planting) with mesic grassland species (order Arrhenatheretalia, (Dierschke 1997). The resident grasslands were selected across a long gradient of land-use intensity, ranging from annual mowing or grazing with low stocking densities in combination with minimal fertilization, to frequently mown grasslands with high levels of fertilization and intensive grazing in the late season (Fischer et al. 2010; Blüthgen et al. 2012).

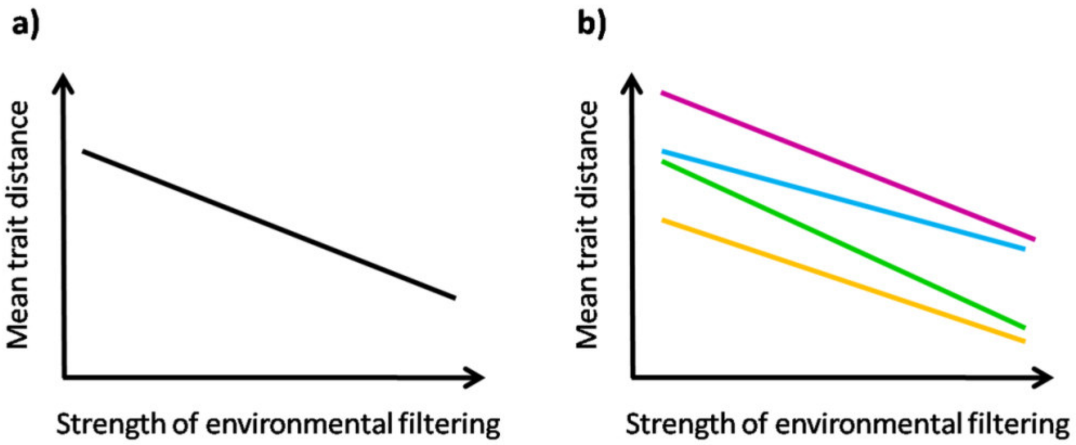

Figure 2.1 Scheme of the response of mean pair-wise trait distance to environmental filtering. (a) If environmental filtering occurs in a community, species with specific trait values will be favoured, rendering the species in the resident community to be more similar to each other with increasing strength of environmental filtering. (b) If additional species are introduced to the community, they change the mean trait distance to a larger or smaller extent, depending on whether they are more dissimilar (magenta) or similar (orange) to the resident community. With increasing strength of environmental filtering, additional species that most likely do co-occur with the resident species (green) should become more similar to the resident community, which would be seen in the mean trait distances that approach those of the most similar additional species. Correspondingly, randomly chosen additional species (blue) should become more dissimilar to the resident community, which would be seen in mean trait distances that approach those of the most dissimilar additional species.

In such grasslands, land use is a strong environmental filter, and the resident species are expected to be more similar in trait values with increasing land-use intensity (Fig. 2.1a). To test which species are favoured or suppressed at different levels of land-use intensity, we devised four different scenarios of enrichment planting. Two of the four scenarios were trait-based approaches where we added species that were the most similar or dissimilar to the resident species in the community in terms of trait values, hereafter referred to as Sim and Dissim scenarios, respectively. We expected that adding the most similar species would decrease the pair-wise trait distance of the community, irrespective of land-use intensity (Fig. 2.1b). Conversely, adding the most dissimilar species should increase the pair-wise trait distances. Two further scenarios of enrichment planting were implemented that were not based on traits. In the so-called Beals scenario, we made use of the co-occurrence information available from large vegetation plot databases (Schaminée et al. 2009). This empirical approach is based on the consideration that the species that fit best in a community will be those that co-occur with the resident species in a multitude of other places. We therefore derived the degree of match of a newcomer to the resident community from the probability of co-occurrence recorded in large vegetation databases. For the fourth scenario, we added species randomly and expected their pair-wise trait distances to fall between the Sim and Dissim scenario.

Under the assumption that land-use regimes affect environmental filtering, the relative position of pair-wise trait distances among the four scenarios is expected to change. In particular, with increasing land-use intensity, the Beals scenario should approach the Sim scenario (Fig. 2.1b), because species that frequently co-occur with species in communities subjected to strong environmental filtering should be more similar to the resident species. In contrast, the scenario with randomly added species should converge with the Dissim scenario, because with increasing land-use intensity, the probability that the random trait values of added species do not match the trait values of species of the resident species should increase (Fig. 2.1b).

Our study incorporated a transplant observation period of 2 yrs, with the expectation that survival rates would differ among the four scenarios. In particular, we expected the survival rate of the species added in the Beals scenario to be significantly higher than that of the species with the most similar or dissimilar traits or the randomly added species, because the species with the highest empirical probability of co-occurrence with the resident species should directly reflect the optimal trait combination for a given degree of environmental filtering, including the intensity of land-use, the degree of competitive exclusion and other biotic interactions. Species with similar and dissimilar trait values to the residents were expected to only survive better at very high and very low land-use intensities, respectively.

Our study had two objectives: (i) to study the change in trait distances brought about by the four scenarios of enrichment planting, and (ii) to follow the fate of the transplants over two vegetation periods. With respect to the first objective, we tested the hypotheses that (i) mean trait distances among added species are lowest in the Sim and highest in the Dissim scenario. This would be expected because additional species that are most similar or dissimilar to the resident species would likewise be most similar or dissimilar to one another. Furthermore, we hypothesized that (ii) mean trait distances of the resident community decrease with increasing land-use intensity. Such a result would provide evidence for our basic assumption that land-use intensity is an important environmental filter, Also, we tested the hypothesis that (iii) those additional species that most likely co-occur with the resident species show trait distances between the most similar and dissimilar species; with trait distances being closer to the scenario with the most similar species, the more the community is dominated by environmental filtering. Furthermore, with respect to survival rates, we tested the hypotheses that (iv) survival rates decrease with increasing land-use intensity, and that (v) the additional species that most likely co-occur with the resident species show higher survival rates than the additional species that are most similar or dissimilar to those in the resident community or randomly chosen species. To our knowledge, this is the first study that empirically derives the relative strength of environmental filtering and niche differentiation in natural plant communities.

2.3 Methods

Experimental plots and design

The study plots formed part of the experimental plot network of the German Biodiversity Exploratories (Fischer et al. 2010) in the three study regions of Schwäbische Alb (south Germany), Hainich (central Germany) and Schorfheide (northeast Germany). In each of the three regions 18 grassland sites were selected, of which each six sites represented the three main land-use types (meadow, pasture, mown pasture) and different land-use intensities (Fig. S2.1 – S2.4). One plot (9 x 5 m) was established at each of the sites, consisting of eight subplots of 1 x 1 m (Fig. S2.5). Each subplot received six plant individuals of six different species, selected from the 130 species raised in the greenhouse according to the scenarios described below. The plants were arranged within two 50-cm long parallel rows (three plants per row) with spacing of 25 cm between species and from the edges of the subplot (Fig. S2.5). The six individuals were randomly allocated to the six planting positions within each subplot.

Vegetation records

The species composition of each subplot was recorded in summer 2011 by estimating the visual plant cover of every species as a percentage of the subplot area (1 m^2), yielding a total of 432 subplots with 197 vascular plant species. We constructed the species composition of each whole plot by combining the species lists of all eight subplots. This allowed us to carry out all calculations on the different species selections for the scenarios at the plot level, which was also the level at which the grasslands differed environmentally, with particular regard to land-use intensity.

Seed collection and raising seedlings

Seeds from grassland species of the three Exploratories were collected in 2011. During the winter of 2011/12, these seeds were sown and seedlings raised in 5 × 5-cm pots in climate chambers in the experimental greenhouse at the Institute of Biology/Geobotany, Martin-Luther-University, Halle-Wittenberg. In total, 18 223 individuals of 150 species were raised, of which 2592 individuals of 130 species were finally used in this project. In addition, a further 368 individuals were used for replanting.

Trait measurements

Trait distance calculations were based on ten different traits (Table 2.1). As we used young plants in the experiment, and thus deliberately excluded the germination stage, we focused on persistence traits and disregarded seed and reproduction traits. Therefore, traits were chosen that reflected competitive ability through affecting growth rates, such as specific leaf area (SLA), leaf dry matter content (LDMC), height, leaf anatomy, leaf persistence and leaf distribution (Cornelissen et al. 2003; Kleyer et al. 2008). Furthermore, we included traits that increased persistence after disturbance by providing the ability to colonize or re-colonize habitats through means of vegetative reproduction, clonal growth organs or lateral spread. We also included the trait of ‘physical defence mechanisms’, because it directly relates to land-use. Plants that have physical defence traits such as thorns or hooks are less likely to be grazed. SLA and LDMC were measured on leaf samples collected in the experimental plots and their surroundings from 166 of the 197 species, with three individuals being sampled per species and Exploratory site. Shoot height of the sampled species was measured in the field. In the trait analysis, we only used species mean trait values, as we expected interspecific variability to be higher than intraspecific variability (Kröber et al. 2012; Kazakou et al. 2013). In particular, SLA and LDMC were found to display lower intraspecific variation than other traits, e.g. chemical leaf traits. The three replicates per species approach was employed to ensure no unrealistic trait measurements were taken.

Table 2.1 Traits used for trait distance calculations. The full trait matrix comprised 223 species. Scale Q: quantitative (i.e. ratio scale), N: nominal (coded as binary variables), B: binary (i.e. variables with only two alternative states). The following databases were used: Biopop (Poschlod et al. 2003), Biolflor (Klotz et al. 2002), LEDA (Kleyer et al. 2008), Rothmaler (Jäger& Werner 2001).

Trait	Abbreviation	Unit	Explanation	Scale	Data origin
Specific Leaf Area	SLA	$m^2\ kg^{-1}$	Leaf area per dry mass	Q	For 189 species own measured values, further values obtained from regression with values from Biopop and LEDA
Leaf Dry Matter Content	LDMC	$mg^{-1}\ g$	Leaf dry mass per leaf fresh mass	Q	For 189 species own measured values, further values obtained from regression with values from LEDA
Height	Height	m	Shortest distance from ground to highest leaf	Q	For 198 species values from Rothmaler, further values obtained from regression with values from LEDA and regressions to own measured values
Leaf Anatomy	Anat		Succulent, scleromorphic, mesomorphic, hygromorphic, helomorphic, hydromorphic	N	Biolflor
Leaf Persistence	Persist-		Spring green, summer green, overwintering green, persistent green	N	Biolflor
Leaf Distribution	Distr-		Evenly spread leaves, rosettes, semi-rosettes	N	Biopop, with additional values from own observations
Vegetative Reproduction	VegReproduction		Absent or present (then as stolons, stolon-rhizomes, bulbs, bulbils, fragmentation, gemmae, buds with storage roots, buds with root tubers, phyllogenous shoots, rhizomes, shoot tubers, turios, adventitious shoots, onions)	B	Biolflor
Clonal Growth Organs	CGO		Absent or present (then as bulbs, epigeogenous below-ground stems, lateral roots, tillers or tussocks)	B	Biopop
Lateral Spread	Lateral Spread		Absent or lateral growth larger than 0 cm per year	B	Biopop
Physical Defence	Physical Defence		Absent or present (then as hooks, prickles, spines, stinging hairs, thorns)	B	Biopop

Traits of a further 23 species were measured on leaf samples of plants raised from seed in the greenhouse. Fresh leaf samples were weighed and scanned. The leaf scans were analysed with the computer program WinFOLIA v Pro 2004a to obtain leaf area (Regent Software, Quebec City, Canada). Dry mass was determined after the leaf samples had been dried for 3 d at 60 °C. Mean values of the respective traits (SLA, LDMC and height) per species were compiled. As our goal was to obtain a full data matrix without missing values for all species, further trait values were complemented from trait databases and literature: Biolflor (Klotz et al. 2002), LEDA (Kleyer et al. 2008), Biopop (Poschlod et al. 2003), Rothmaler (Jäger & Werner 2001). We established linear regressions between the different trait databases based on the species that were both present in the database and measured by us and applied them to 52 species, for which we did not measure SLA and LDMC values in our study. This avoided the introduction of bias, from systematic differences in trait measurements, which were significant for some traits such as plant height, where we used trait values established by regression for 44 species. The trait databases were also used to obtain data on further plant traits (leaf anatomy, leaf persistence, leaf distribution, vegetative reproduction, clonal growth organs, lateral spread and physical defence). Finally, we generated a full trait matrix for 223 of a total of 251 species, which occurred either in the plots or were raised from seed to serve as transplants. Omitted species were either woody recruits, which we did not include in the analysis because these species strongly deviated in their trait values, or seedlings or rosettes of species that could not be identified to the species level. All omitted species occurred only with one or two individuals in the plots.

Trait distance calculations

A trait distance matrix including all resident and raised species was calculated with the dist.ktab function of the R ade4 package (Pavoine et al. 2009; R Foundation for Statistical Computing, Vienna, AT). This function uses Gower's distances, which allow for the simultaneous use of variables of different scale, which in our case were either quantitative variables measured on a ratio scale or nominal traits coded as binary variables (Pavoine et al. 2009). The ten traits listed in Table 2.1 were used for calculating pair-wise trait distances according to equation (1).

$$(1)\ D_{ij} = \sqrt{\frac{1}{n}\sum_{k=1}^{n}\left(z_{ik} - z_{jk}\right)^2}$$

Gower's distance D_{ij} between species i and j is the mean Euclidean distance between n traits, using the scaled trait distances z. Scaling was conducted per trait k by dividing every trait value x through the range of that trait R_k according to equation (2).

$$(2)\ z_{ik} = \left|\frac{x_{ik}}{R_k}\right|$$

Nominal variables can have non-exclusive states (i.e. they are multi-choice variables), in which case they are expressed as proportions of the different levels (Pavoine et al. 2009). We calculated D_{ij} both across all ten traits (in the following called multi-trait approach) and separately by trait. Figure S2.6 shows a principal coordinate analysis (PCoA) of all species based on Gower's distance D_{ij}. The first axis of the PCoA shows that the main gradient in traits was formed by species with means of vegetative reproduction and presence of clonal growth organs (CGO) vs those that persist over winter, while the second axis reflects evergreen (i.e. persistently green) vs summer-persistent species. The PCoA also demonstrates that the traits chosen were not redundant.

After calculating trait pair-wise distances between all species, a distance matrix d_{ij} was produced for each of the vegetation records of the 54 plots, including only the species that occurred in that plot. Mean pair-wise trait distance $\bar{d}$ between the N species present in a particular plot was calculated according to equation (3).

$$(3)\ \bar{d} = \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} dij}{N \cdot N}$$

It should be noted that the arithmetic average also included the zeros in the diagonal of the distance matrix. However, calculating the mean by excluding the diagonal is linearly related to $\bar{d}$ and obtained by multiplying $\bar{d}$ with $N/(N-1)$ (Böhnke et al. 2014). As mean trait distance is not weighted by species abundance, $\bar{d}$ is linearly related to functional attribute diversity (FAD) according to Walker et al. (1999), to functional diversity (FD) according to Petchey & Gaston (2002) and to modified functional attribute diversity (MFAD) according to Schmera et al. (2009).

Species addition scenarios

The six species planted in every subplot were selected specifically for each plot and for each of the four different scenarios described in the following.

The Sim and Dissim scenarios were based on the pair-wise trait distances $\bar{d}$ from the multi-trait approach. Mean pair-wise trait distances were calculated across all resident species in a plot and to all the other species that had been raised in the greenhouse and were present in the regional species pool but were not present in that particular plot. For the Sim scenario, species that resulted in lowest mean trait distance were planted, i.e. those additional six species that were most similar to the resident community. Correspondingly, the species chosen for the Dissim scenario were most dissimilar to the resident community.

In the Beals scenario, we planted those species that had the highest likelihood to co-occur with the resident species. We identified these species using the German Vegetation Reference

Database (GVRD; Jandt & Bruelheide 2012) and by calculating Beals index of sociological favourability (Beals 1984; equation 4).

$$(4)\ p_{pi} = \frac{1}{N_p} \sum_{j}^{N_p} \frac{M_{ij}}{M_j}$$

The probability *ppi* for species *i* to occur in a vegetation record of plot *p* is calculated from joint occurrences *Mij* to all species *j* of the total number of species in that plot *Np*, divided by the number of plots *Mj* in which the species *j* is present. Species with the highest probability of co-occurrence *ppi* with the resident species of a particular plot *p* were selected for enrichment planting in this scenario. Although originally developed to identify missing species in floristic inventories, the index has successfully been used to predict and evaluate habitat suitability, e.g. for grassland species (Münzbergová & Herben 2004). As this approach does not make a priori use of the species traits, the degree of similarity or dissimilarity in trait values of species selected in the Beals scenario to the resident species (i.e. the closeness of this scenario to the Sim scenario) can be used to draw conclusions on the relative importance of environmental filtering.

The Random scenario tested the possibility that random immigration occurs irrespective of the newcomers' traits. Thus, the newcomers might have similar or dissimilar traits compared to the resident species. For the Random scenario, six species were selected randomly for each plot. As in the Beals scenario, the traits of the species were irrelevant for species selection. Thus, we could test whether the mean trait distances of randomly added species converged with the Dissim scenario.

In addition to the selection criteria mentioned above, all species selected for enrichment planting had to be new to their target community. Therefore, we excluded species found in the vegetation records made in 2011. We also excluded species that had been encountered in the vegetation records independently made by B. Schmitt in 2010 and 2011 on the same sites adjacent to our subplots. Furthermore, species eligible for the enrichment scenarios had to be present in the regional species pool, which we constructed from regionally aggregated vegetation records of the GVRD (Jandt & Bruelheide 2012). Exceptions in the selection of the species for each scenario were made where there was a lack of transplants of the desired species. In such cases, the species with the next highest rank were used. The four different scenarios were assigned randomly to the eight subplots. The exact species composition of each of the four plot-specific scenarios was replicated once per plot, which allowed us to separate effects of the specific species composition from random plot effects.

Planting and monitoring

The 2592 plants were planted in the subplots in April 2012 (Fig. S2.7). One month later, we replaced individuals that had died. In 2012, all transplants were monitored four times for survival and growth and three times in 2013. Here, we report only the survival of the plants under the different land-use intensities for two vegetation periods: from May 2012 to May 2013 and from May 2012 to July 2013 in the field. We considered this duration sufficient to allow the impact of land-use intensity on the different scenarios to become apparent.

Land-use intensity

Land-use intensity was quantified using the land-use index (LUI) developed by Blüthgen et al. (2012) according to equation (5).

$$(5)\ LUI_p = \sqrt{\frac{G_p}{G} + \frac{F_p}{F} + \frac{M_p}{M}}$$

The land-use index for site *p* (*Lp*) is calculated from the sum of grazing intensity *Gp*, assessed as the density of livestock (number ha^{-1}) and duration of pasture (days yr^{-1}), amount of fertilizer application *Fp* (kg N yr^{-1} ha^{-1}) and mowing intensity *Mp*, defined as the number of cuttings per year. Every category *Gp*, *Fp* and *Mp* is scaled by the mean of this variable over all sites of the Biodiversity Exploratories ($\bar{G}$, $\bar{F}$ and $\bar{M}$, respectively). We used the mean of the LUI for the years 2006–2010, i.e. those preceding our experiment. The LUI values of our plots ranged from 0.58 to 3.12, reflecting low to high land-use intensity, respectively. Within the three different categories of land-use management regime (meadow, mown pasture and pasture), our plots covered a wide range of the land-use intensity index values, thereby including, for example, both high and low intensively used meadows.

Data analysis

While the species selection was carried out based on the vegetation record of the plot, we evaluated the outcome of this experiment at the subplot level. This was necessary because species composition differed slightly between the eight subplots. Thus, the similarity calculations were based on the immediate neighbourhood rather than on the wider plot surroundings. In addition, the subplot-level calculations served to confirm the correctness of the selection procedure in the Sim and Dissim scenario, thus providing the upper and lower boundaries in the community's mean trait distances that could potentially be changed by adding additional new species. First, we calculated $\bar{d}$ for the six selected species for the four different scenarios (Beals, Dissim, Random and Sim) per plot. As the same species were added in the two replicates per scenario per plot, the mean trait distances did not vary between the two replicates. Second, we calculated $\bar{d}$ for all resident species before enrichment planting and for all resident species including the six selected species after enrichment planting. The subplot-level evaluation had the effect that adding the same six species to the subplots of the two replicates of a particular scenario resulted in differences in the mean trait distances between the two replicates. Next, for every subplot, the change brought about by enrichment planting was calculated as the absolute difference between mean trait distances before and after additional species were planted. The calculations were made using $\bar{d}$ across all ten traits in the multi-trait approach, and by using $\bar{d}$ derived from the ten traits separately. These comparisons showed which single traits followed the multi-trait approach or displayed similar diverging patterns in the different scenarios. Survival rates were calculated as the mean of the six species planted into one subplot.

Differences between the four scenarios in mean trait distances as well as survival rates were calculated with mixed linear models in R (lme, package nlme) (Pinheiro et al. 2013), using Exploratory (Schwäbische Alb, Hainich or Schorfheide) and plot nested in Exploratory as random factors and scenario, LUI and the interaction between scenario and LUI as fixed factors. To derive estimates for the scenarios across all plots, we centred LUI to its mean value. Testing the significance of the interaction between LUI and scenario showed whether, with increasing land-use intensity, the Beals and Random scenario approached the Sim and Dissim scenario, respectively. Mean values across all plot mean trait distances were obtained from the estimated parameters of these models. Differences between scenarios were tested with Tukey post-hoc tests using the glht command from the multcomp package (Hothorn et al. 2008). Differences in slopes were obtained from the P-values of the summary output using the scenarios Beals, Dissim and Random on Intercept position to obtain results for all six possible categorical comparisons.

2.4 Results

Among the four scenarios, the mean trait distances across all ten traits of the six added species were lowest in the Sim scenario (Fig. 2.2). This confirmed the expectation that the additional species that were most similar to the resident species were also most similar to one another. In contrast, the highest mean trait distances were not encountered in the Dissim but in the Random scenario. The six species in the Beals scenario as well as the species of the Dissim scenario showed intermediate mean trait distances among each other (Fig. 2.2).

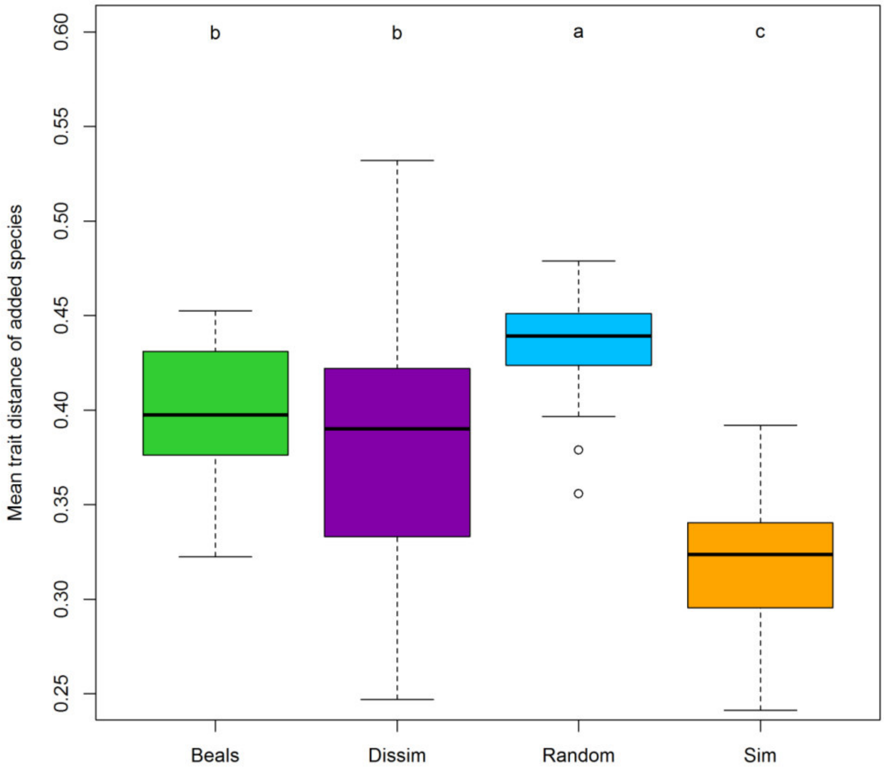

Figure 2.2 Mean pair-wise trait distances among the six species added in the four scenarios (Beals, Dissim, Random and Sim). Values are multi-trait distances and based on ten traits. Boxes show quartiles and medians across all 54 plots and two subplots per plot (n = 108 per scenario). Whiskers show 1.5 times the interquartile ranges. Small letters indicate statistically significant differences among the scenarios according to a Tukey post-hoc test.

Before enrichment planting, there was no difference in the mean trait distances among the four scenarios (Fig. 2.3a, Tables 2.2 and 2.3), demonstrating that no initial differences existed between subplots. Plot accounted for 58% of the random variation, followed by variation among subplots within plots (40%) and by Exploratory (2%, i.e. Schorfheide, Hainich or Schwäbische Alb; for absolute values of random variation see Table S2.2).

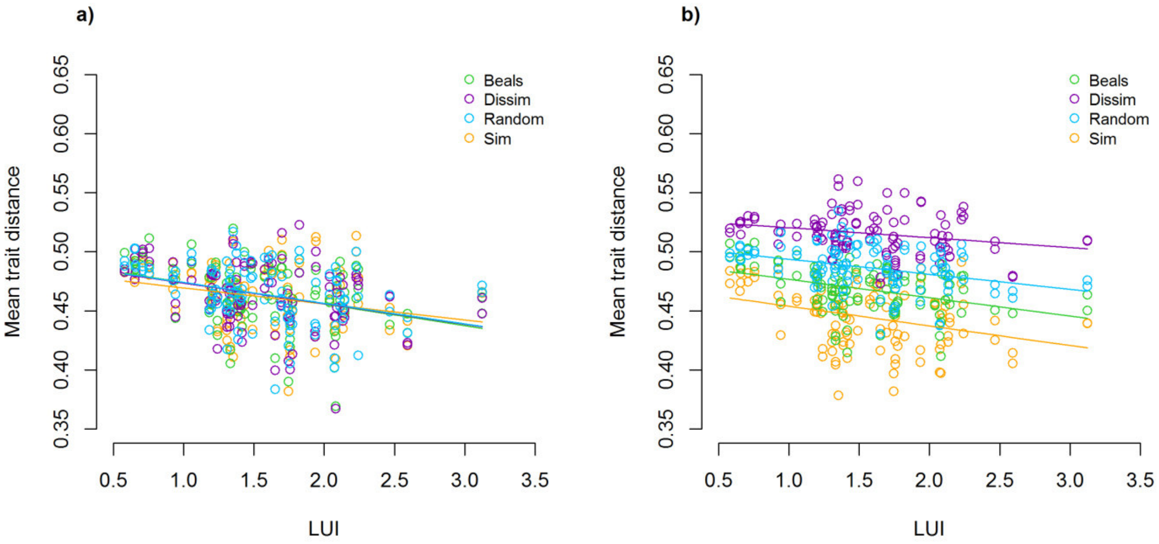

Figure 2.3 Mean pair-wise trait distances as a function of land-use intensity (LUI) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting. Regression lines were obtained from a mixed model with random factors plot nested in Exploratory (see Table 2.3). Significant differences are indicated in Table 2.2.

Table 2.2 Results of the mixed linear models for the response of mean pair-wise trait distances and survival rates to the four different scenarios (Beals, Dissim, Random and Sim) and land-use intensity, expressed as LUI for the years 2006 to 2010. Survival rates for the first and second year refer to the period May 2012 to May 2013 and May 2012 to July 2013, respectively. Estimates are predicted values for the scenarios at overall LUI mean (intercepts) and slopes of LUI. Significant differences between scenarios and slopes are derived from Tukey posthoc tests and shown as different letters. df = 372 for all terms involving scenarios and df = 50 for LUI. For variance of random factors see Table S2.2.

	Trait distances before enrichment planting		Trait distances after enrichment planting		Change in trait distances		Survival rates one year after planting		Survival rates in the second year	
	Estimates	Tukey	Estimates	Tukey	Estimates	Tukey	Estimates	Tukey	Estimates	Tukey
Intercepts										
Scenario Beals	0.464	a	0.468	c	0.004	c	0.769	a	0.712	a
Scenario Dissim	0.464	a	0.516	a	0.052	a	0.550	c	0.417	c
Scenario Random	0.464	a	0.487	b	0.022	b	0.561	c	0.455	c
Scenario Sim	0.462	a	0.445	d	-0.017	d	0.637	b	0.571	b
Slopes of LUI										
Scenario Beals	-0.018	a	-0.016	a	0.003	ab	-0.086	a	-0.062	a
Scenario Dissim	-0.017	a	-0.008	a	0.009	a	-0.113	a	-0.163	a
Scenario Random	-0.018	a	-0.013	a	0.005	a	-0.116	a	-0.089	a
Scenario Sim	-0.014	a	-0.017	a	-0.003	b	-0.070	a	-0.060	a

Table 2.3 ANOVA results of the mixed linear models for the response in mean pair-wise trait distances and survival rates to the four different scenarios (Beals, Dissim, Random and Sim) and land-use intensity, expressed as LUI for the years 2006–2010 before, after and the level of change through enrichment planting.

	Trait distances before enrichment planting				Trait distances after enrichment planting				Change in trait distances				Survival rates one year after planting				Survival rates in the second year			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F-value	p-value	nDF	dDF	F-value	p-value
Scenario	3	372	0.473	0.701	3	372	458.154	<0.001	3	372	774.657	<0.001	3	372	25.812	<0.001	3	372	45.700	<0.001
LUI	1	50	9.770	0.003	1	50	13.875	<0.001	1	50	1.953	0.168	1	50	4.744	0.034	1	50	3.811	0.057
Senario x LUI	3	372	0.513	0.674	3	372	1.809	0.145	3	372	6.031	0.001	3	372	0.320	0.811	3	372	1.569	0.196

After enrichment planting, significant differences in mean trait distances emerged between all four scenarios (Table 2.2). As expected, the species planted into the Dissim subplots resulted in an increase of mean trait distances by 0.052 compared to the pre-planting state (Table 2.2, Fig. 2.3b). In contrast, the species planted in the Sim subplots resulted in a decrease of mean trait distance after enrichment planting by 0.017 (Table 2.2, Fig. 2.3b). After enrichment planting, the Beals and Random scenarios ranked between the Dissim and Sim scenarios, with mean trait distances of 0.468 and 0.487, respectively. In the Random scenario the increase in mean trait distances brought about by enrichment planting was 0.022 (Table 2.2). In contrast, the species selected by the Beals scenario only marginally changed mean trait distances after enrichment planting, with a change in the overall mean of 0.004 (Table 2.2), which, according to the model estimates, was not significantly different from 0.

Before and after enrichment planting, mean pair-wise trait distances significantly decreased with land-use intensity ($P = 0.003$ and $P < 0.001$, respectively, Table 2.3). The regression lines did not differ in slope from one another (Table 2.2), showing that the relationship between mean trait distances and LUI did not differ between the scenarios. In particular, the regression line of the Random scenario did not approach that of the Dissim scenario, nor did the regression line of the Beals scenario approach that of the Sim scenario (Fig. 2.3b). Taking the difference in mean trait distances between the Sim and Dissim as a reference, the Beals scenario ranked closer to the Sim scenario (at 32%) and the Random scenario ranked closer to the Dissim scenario (at 59%). These differences were only slightly modified by land-use intensity (Fig. 2.3b).

Compared to the multi-trait approach, the single trait approaches (see Figs S2.8–S2.17 and Tables S2.1–S2.2) for LDMC (Fig. S2.9) and leaf distribution (Fig. S2.13) showed the same pattern as the multi-trait approach, with significant decreases with LUI in mean trait distances before and after enrichment planting. In addition, trait distances of leaf anatomy (Fig. S2.11) and physical defence (Fig. S2.17) decreased significantly with LUI before enrichment planting. After enrichment planting, trait distances for these two traits decreased with LUI for all scenarios except for the Dissim scenario. In contrast, SLA (Fig. S2.8), height (Fig. S2.10), leaf persistence (Fig. S2.12), vegetative reproduction (Fig. S2.14) and clonal growth organs (Fig. S2.15) were not related to LUI, either before or after enrichment planting. An exceptional pattern was encountered for lateral spread (Fig. S2.16), which was only positively related to LUI before enrichment planting. Random variance components of the single traits showed a similar pattern as in the multi-trait approach, with Exploratory accounting for the lowest amount of random variation, both before and after enrichment planting (Table S2.2).

Survival rates after 1 yr (Fig. S2.18) differed between the scenarios (Table 2.2). While the unbiased estimate for the survival rate in May 2013 in the Beals scenario was 77%, survival rates were only 55%, 56%and 64%in the Dissim, Random and Sim scenario, respectively. According to a Tukey post-hoc test, the Dissim and Random scenarios were not significantly different from one another, but all differed from the Beals and Sim scenarios (Table 2.2). Survival rates after 1 yr decreased with increasing LUI (P = 0.0341) according to an ANOVA on the mixed model across all scenarios (Table 2.3), while there were no differences in the relationship between survival rates and LUI between the scenarios (Table 2.3). Survival rates after a second vegetation period in July 2013 (Fig. 2.4) were 71%, 42%, 46% and 57% for the Beals, Dissim, Random and Sim scenarios, respectively, with the same Tukey post-hoc differences as in May 2013 (Table 2.2). Survival rates in July 2013 only marginally significantly decreased with increasing LUI (P = 0.0565), according to an ANOVA on the mixed model across all scenarios (Table 2.3).

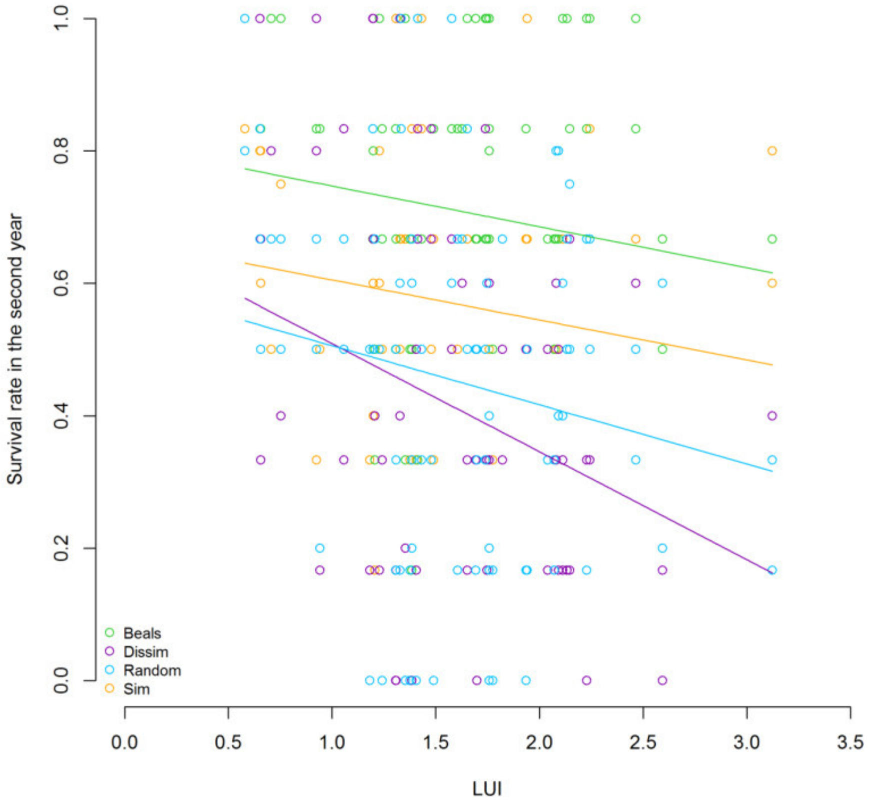

Figure 2.4 Survival rates of transplanted individuals in the second vegetation period from May 2012 to July 2013 as a function of land-use intensity (LUI) of the four scenarios (Beals, Dissim, Random, Sim). Regression lines were obtained from a mixed model with random factors plot nested in Exploratory (see Table 2.3).

2.5 Discussion

Our approach of enrichment planting clearly demonstrated that the success of a species to become established in a community could be predicted from trait space. Land use was found to be an environmental filter that significantly decreased survival rates of newcomers with increasing land-use intensity. A key result was that species with a high probability of co-occurrence with the resident species show higher survival rates than those that are most similar or dissimilar to the resident community or randomly chosen species. These results were already clearly visible 1 yr after enrichment planting, and remained consistent after a second vegetation period.

The four different scenarios devised at the plot level changed the mean trait distances at the subplot level as expected, with a decrease and increase in mean pair-wise distances in the Sim and Dissim scenarios respectively, while changes in the Beals and Random scenarios ranked between those in the Sim and Dissim scenarios. However, we could not confirm our first hypothesis that the mean trait distances of the six added species were lowest in the Sim and highest in the Dissim scenario. Mean trait distances of the added species were lower in the Dissim than in the Random scenario, which showed that the species that were most dissimilar to the resident species shared certain characteristics, making them more similar to each other than to randomly chosen species.

One striking result of our study was that the Beals scenario did not result in a change in mean pair-wise trait distances across all plots. The most probable species that were added to the community almost had the same distances in trait values to the resident species as the resident species had among themselves. This means that traits of the newcomer species in the Beals scenario reflected the same degree of environmental filtering as those of the resident species. It seems that the species in the Beals scenario were 'pre-filtered'. In other words, the newcomers stuck to the assembly rules of the resident species. In contrast to the Beals scenario, there was a higher change in mean trait distances in the Random scenario. This shows that the regional species pool contains more dissimilar than similar species with respect to the communities investigated. This confirms the observation of Zobel (1997) that the results of richness manipulation experiments strongly depend on the specific pool from which the species are chosen. Although we put great care in constructing a habitat-specific regional species pool based on the GVRD (Jandt & Bruelheide 2012), the higher mean trait distances of species in the Random scenario indicate that the habitat definition of the regional species pool might have been somewhat broader than the combined local pools investigated by us. This clearly highlights the difficulties in establishing a regional species pool, even where intimate knowledge of the species' habitat preferences is available (see Pärtel et al. 2011) and then used to establish null models (de Bello et al. 2012). However, our finding that adding randomly chosen species increased mean trait distances in the resident community confirms the results of Cornwell et al. (2006), who showed that observed plant communities occupy less trait space than expected from a random assembly.

Our second hypothesis of decreasing trait distances with increasing land-use intensity was fully supported, confirming the role of land-use as a key environmental filter that drives species composition in Central European grasslands (Fischer et al. 2010). However, this does not exclude the possibility that there are other selective forces that shape the trait space of the community. In addition to the current land-use addressed in our study, nutrient supply, pH or water regimes may represent additional environmental filters that affect community species composition (Karlík & Poschlod 2009).

We have to reject our third hypothesis that the mean trait distances in the Beals scenario converge to the Sim scenario with increasing land-use intensity. Likewise, the Random scenario did not approach the Dissim scenario with increasing LUI, as hypothesized in Fig. 2.1b. The finding that the Beals scenario was located at about one-third between the mean pair-wise trait distances between the Sim and Dissim scenarios and that this position was not affected by land-use intensity suggests a universal principle. Given our findings that the species in the Beals scenario were 'pre-filtered', and therefore exactly reflected the mean trait distances of the resident communities, and that the absolute trait distances decreased with increasing environmental filtering, the relative position on the scale of minimum to maximum trait distances remained constant. This means that the local community was uniformly assembled with similar and dissimilar species from the regional species pool, with a balance in favour of the more similar species. It seems that the species in the community maintained a certain relative degree of dissimilarity to each other, irrespective of the strength of environmental filtering. Should this finding be confirmed for different types of vegetation, it would show that limiting similarity is equally relevant under weak and strong filtering regimes and that limiting similarity is consequently not an opposing force of environmental filtering, as was previously suggested (Mayfield & Levine 2010). A constant preponderance of more similar species in a community would also explain why, in the majority of cases, null models of community assembly support the environmental filtering hypothesis (e.g. Gerhold et al. 2013; Sommer et al. 2014). In any case, these considerations give us further support to consider biotic processes as an inherent component of environmental filtering.

Our single trait analysis allowed us to determine which traits responded most to land-use intensity. Mean pairwise trait distances of LDMC, leaf anatomy, leaf distribution and physical defence showed significant decreases with LUI, those of other traits, such as SLA, height, leaf persistence, vegetative reproduction or clonal growth organs were unaffected by LUI, while lateral spread even increased with LUI. Similarly diverging results for different traits have been reported by Carboni et al. (2014), who studied trait divergence and convergence along a productivity gradient in wet meadows and found that some of the traits became more similar among the resident species along the gradient, while others became more divergent. However, in our study, combining different traits with varying responses to LUI in one multi-trait distance resulted in a significant slope to LUI. This shows that although a single trait might not be responsive to environmental filtering, several traits in combination might be, which is a strong argument supporting the use of multiple trait dimensions. In accordance with our findings, Koyanagi et al. (2013) also found that for identifying indicator species that respond to grassland management such as grazing or mowing, only the multi-trait approaches produce clearer clustering of vegetation plots compared to the single-trait approaches, where inappropriate indicator species were selected.

The LDMC as the leaf trait with the strongest response to LUI has also been identified as a key trait for land-use intensity in other studies (Duru et al. 2008). For example, in a set of 178 French grassland sites, Michaud et al. (2012) found LDMC to be the trait most closely linked to livestock density and soil fertility, with a negative effect size as in our study. The unresponsiveness of SLA is surprising, considering that effects on land-use have previously been reported for LDMC as being essentially reciprocal to those for SLA (Quétier et al. 2007; McIntyre 2008; Laliberté et al. 2012). The single-trait analyses also showed that our trait selection might not have been optimal with respect to land-use intensity. Furthermore, there may be other dimensions of environmental filtering beyond that of land-use intensity. For example, species responses may also be affected by drought or low nutrient supply in the soil (Fonseca et al. 2000; Al Haj Khaled et al. 2005). Moreover, different biological responses might be affected differently by different traits. As such, focusing on fewer traits may preclude later options of relating observed responses to particular traits.

Following the fate of transplants for two vegetation periods, we found that survival decreased with LUI, thus confirming our fourth hypothesis that land-use intensity is an important environmental filter. We also confirmed our fifth and final hypothesis that the species that survive best show the highest degree of co-occurrence with the resident species of that community. This is the second key result of our study. Given the other important finding that the Beals scenario did not result in a change in mean pair-wise trait distances across all plots, the higher survival rates in the Beals scenario also mean that the chances for a species to survive are higher if it has exactly the same degree of trait similarity or dissimilarity to the resident community. As outlined in the Introduction, the reasons for the lower survival rate of transplants in the Sim and Dissim scenarios cannot be exclusively attributed to abiotic filtering or exclusion of competitively or mutualistically inferior species. It may well be that the relative importance of these processes differs along the LUI gradient; however, our experiment was not designed to answer such a question. Nevertheless, the Beals scenario clearly captured the right degree of similarity that did not result in abiotic filtering or competitive exclusion. The species in the Beals scenario also had significantly higher survival rates than randomly chosen species, probably because the mean pair-wise trait distances deviated to a similar magnitude from those in the Beals scenario, as the distances in the Sim scenario differed from those in the Beals scenario. Our finding provides an explanation as to why studies on the role of limiting similarity for colonization success have been equivocal in the past. This can be exemplified for invasive plant species, which in some cases show reduced invasion risk with increasing functional similarity between invaders and residents, but not in others (Price & Pärtel 2012). The idea that species have to be more similar than dissimilar to achieve maximum coexistence would also explain why competitive exclusion has not been found to result in saturated communities, neither in the case of biological invasions (Stohlgren et al. 2008), nor in natural succession series (Bruelheide et al. 2011).

When discussing the impact of a certain degree of similarity or dissimilarity on colonization, we have to consider that our experiment only lasted for 1.5 yrs. The decreasing survival rates between the May and July monitoring dates demonstrate that environmental filtering is ongoing. However, the survival rates at the two monitoring dates did not differ with respect to scenarios and LUI, indicating that the direction of environmental filtering remained unchanged. It should also be noted that exclusively monitoring the presence and growth of initial transplants becomes less informative with time, because single plants have limited life spans and the ultimate success of colonization can only be seen in the demography of every species (Ebenhard 1991).

In conclusion, our finding that empirically best-fitting species survived best while showing a distinct degree of similarity and dissimilarity to the resident community adds to our understanding of assembly rules in plant ecology. We clearly demonstrated the validity of using vegetation databases to assess the relative importance of environmental filtering. It will now have to be tested as to whether this rule of most likely co-occurring species performing best also applies to other vegetation types.

2.6 Acknowledgements

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2.7 References

Al Haj Khaled, R., Duru, M., Theau, J.P., Plantureux, S., & Cruz, P. 2005. Variation in leaf traits through seasons and N-availability levels and its consequences for ranking grassland species. *Journal of Vegetation Science* 16: 391–398.

Beals, E.W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14: 55.

de Bello, F., Price, J.N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W., Gerhold, P., Götzenberger, L., Lavergne, S., Lepš, J., Zobel, K., & Pärtel, M. 2012. Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93: 2263–2273.

Blüthgen, N., Dormann, C.F., Prati, D., Klaus, V.H., Kleinebecker, T., Hölzel, N., Alt, F., Boch, S., Gockel, S., Hemp, A., Müller, J., Nieschulze, J., Renner, S.C., Schöning, I., Schumacher, U., Socher, S.A., Wells, K., Birkhofer, K., Buscot, F., Oelmann, Y., Rothenwöhrer, C., Scherber, C., Tscharntke, T., Weiner, C.N., Fischer, M., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., & Weisser, W.W. 2012. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology* 13: 207–220.

Böhnke, M., Kröber, W., Welk, E., Wirth, C., & Bruelheide, H. 2014. Maintenance of constant functional diversity during secondary succession of a subtropical forest in China. *Journal of Vegetation Science* 25: 897–911.

Bruelheide, H., Böhnke, M., Both, S., Fang, T., Assmann, T., Baruffol, M., Bauhus, J., Buscot, F., Chen, X.-Y., Ding, B.-Y., Durka, W., Erfmeier, A., Fischer, M., Geißler, C., Guo, D., Guo, L.-D., Härdtle, W., He, J.-S., Hector, A., Kröber, W., Kühn, P., Lang, A.C., Nadrowski, K., Pei, K., Scherer-Lorenzen, M., Shi, X., Scholten, T., Schuldt, A., Trogisch, S., von Oheimb, G., Welk, E., Wirth, C., Wu, Y.-T., Yang, X., Zeng, X., Zhang, S., Zhou, H., Ma, K., & Schmid, B. 2011. Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs* 81: 25–41.

Carboni, M., de Bello, F., Janeček, Š., Doležal, J., Horník, J., Lepš, J., Reitalu, T., & Klimešová, J. 2014. Changes in trait divergence and convergence along a productivity gradient in wet meadows. *Agriculture, Ecosystems & Environment* 182: 96–105.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A., & Bazzaz, F.A. 2004. Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist* 163: 823–843.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., & Kembel, S.W. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H. ter, Morgan, H.D., Heijden, M.G.A. van der, Pausas, J.G., & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Cornwell, W.K., Schwilk, D.W., & Ackerly, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* 87: 1465–1471.

Díaz, S., Cabido, M., & Casanoves, F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122.

Dierschke, H. 1997. Synopsis der Pflanzengesellschaften Deutschlands. Molinio-Arrhenatheretea (E1). Teil 1: Arrhenatheretalia. *Floristisch-soziologische Arbeitsgemeinschaft e.V. Göttingen*

Duru, M., Cruz P, P., Raouda, A.H.K., Ducourtieux, C., & Theau, J.P. 2008. Relevance of plant functional types based on leaf dry matter content for assessing digestibility of native grass species and species-rich grassland communities in spring. *Agronomy Journal* 100: 1622.

Ebenhard, T. 1991. Colonization in metapopulations: a review of theory and observations. *Biological Journal of the Linnean Society* 42: 105–121.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., & Weisser, W.W. 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology* 11: 473–485.

Fonseca, C.R., Overton, J.M., Collins, B., & Westoby, M. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* 88: 964–977.

Gerhold, P., Price, J.N., Püssa, K., Kalamees, R., Aher, K., Kaasik, A., & Pärtel, M. 2013. Functional and phylogenetic community assembly linked to changes in species diversity in a long-term resource manipulation experiment. *Journal of Vegetation Science* 24: 843–852.

Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., & Zobel, M. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews* 87: 111–127.

Gross, N., Börger, L., Soriano-Morales, S.I., Le Bagousse-Pinguet, Y., Quero, J.L., García-Gómez, M., Valencia-Gómez, E., & Maestre, F.T. 2013. Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. *Journal of Ecology* 101: 637–649.

Hothorn, T., Bretz, F., & Westfall, P. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50: 346–363.

Jäger, E., & Werner, K. 2001. *Exkursionsflora von Deutschland, Bd.4, Gefäßpflanzen, Kritischer Band*. Spektrum Akademischer Verlag.

Jandt, U., & Bruelheide, H. 2012. German Vegetation Reference Database (GVRD). *Biodiversity & Ecology* 4: 355–355.

Karlík, P., & Poschlod, P. 2009. History or abiotic filter: which is more important in determining the species composition of calcareous grasslands? *Preslia* 81: 321–340.

Kazakou, E., Violle, C., Roumet, C., Navas, M.-L., Vile, D., Kattge, J., & Garnier, E. 2014. Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science* 25: 235–247.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. m., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. g., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W. a., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. j., Tackenberg, O., Wilmann, B., Cornelissen, J. h. c., Eriksson, O., Garnier, E., & Peco, B. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.

Klotz, S., Kühn, I., & Durka, W. 2002. *Biolflor: eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland*. Bundesamt für Naturschutz, Bonn.

Koyanagi, T., Kusumoto, Y., Hiradate, S., Morita, S., Yokogawa, M., Takahashi, Y., & Sato, C. 2013. New method for extracting plant indicators based on their adaptive responses to management practices: application to semi-natural and artificial grassland data. *Applied Vegetation Science* 16: 95–109.

Kröber, W., Böhnke, M., Welk, E., Wirth, C., & Bruelheide, H. 2012. Leaf trait-environment relationships in a subtropical broadleaved forest in South-East China. *PLoS ONE* 7: e35742.

Laliberté, E., Shipley, B., Norton, D.A., & Scott, D. 2012. Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology* 100: 662–677.

MacArthur, R., & Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101: 377–385.

Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. da S., Soussana, J.-F., & Louault, F. 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist* 196: 497–509.

Mayfield, M.M., & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.

McIntyre, S. 2008. The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. *Agriculture, Ecosystems & Environment* 128: 251–258.

Michaud, A., Plantureux, S., Amiaud, B., Carrère, P., Cruz, P., Duru, M., Dury, B., Farruggia, A., Fiorelli, J.L., Kerneis, E., & Baumont, R. 2012. Identification of the environmental factors which drive the botanical and functional composition of permanent grasslands. *The Journal of Agricultural Science* 150: 219–236.

Münzbergová, Z., & Herben, T. 2004. Identification of suitable unoccupied habitats in metapopulation studies using co-occurrence of species. *Oikos* 105: 408–414.

Ordoñez, J.C., Van Bodegom, P.M., Witte, J.-P.M., Wright, I.J., Reich, P.B., & Aerts, R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography* 18: 137–149.

Ozinga, W.A., Römermann, C., Bekker, R.M., Prinzing, A., Tamis, W.L.M., Schaminée, J.H.J., Hennekens, S.M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J.P., & Van Groenendael, J.M. 2009. Dispersal failure contributes to plant losses in NW Europe. *Ecology Letters* 12: 66–74.

Pacala, S.W., & Tilman, D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *The American Naturalist* 143: 222–257.

Pärtel, M., Szava-Kovats, R., & Zobel, M. 2011. Dark diversity: shedding light on absent species. *Trends in Ecology & Evolution* 26: 124–128.

Pavoine, S., Vallet, J., Dufour, A., Gachet, S., & Daniel, H. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118: 391–402.

Petchey, O.L., & Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5: 402–411.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Development Core Team. 2013. nlme: linear and nonlinear mixed effects models. R package version 3.1-109. *R Foundation for Statistical Computing, Vienna*

Poschlod, P., Kleyer, M., Jackel, A.-K., Dannemann, A., & Tackenberg, O. 2003. BIOPOP — A database of plant traits and internet application for nature conservation. *Folia Geobotanica* 38: 263–271.

Price, J.N., & Pärtel, M. 2013. Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. *Oikos* 122: 649–656.

Quétier, F., Thébault, A., & Lavorel, S. 2007. Plant traits in a state and transition framework as markers of ecosystem response to land-use-change. *Ecological Monographs* 77: 33–52.

Schaminée, J.H.J., Hennekens, S.M., Chytrý, M., & Rodwell, J.S. 2009. Vegetation-plot data and databases in Europe: an overview. *Preslia* 81: 173–185.

Schmera, D., Podani, J., & Erős, T. 2009. Measuring the contribution of community members to functional diversity. *Oikos* 118: 961–971.

Sommer, B., Harrison, P.L., Beger, M., & Pandolfi, J.M. 2014. Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology* 95: 1000–1009.

Spasojevic, M.J., & Suding, K.N. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* 100: 652–661.

Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C., & Kartesz, J. 2008. The myth of plant species saturation. *Ecology Letters* 11: 313–322.

Walker, B., Kinzig, A., & Langridge, J. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems* 2: 95–113.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2403–2413.

Wilson, J.B. 2007. Trait-divergence assembly rules have been demonstrated: Limiting similarity lives! A reply to Grime. *Journal of Vegetation Science* 18: 451–452.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution* 12: 266–269.

2.8 Supporting Information

Additional Supporting Information of this chapter may be found on the attached CD:

Table S2.1: ANOVA tables of linear mixed models (analyses ofmean trait distances of all ten single traits separately).

Table S2.2: Tables of variance of random factors of all linear mixed models (analyses of survival rates, multi-trait approaches and single trait approaches).

Figure S2.1: Map of geographic location of the three study regions Schorfheide, Hainich and Schwäbische Alb in Germany.

Figure S2.2: Map of the geographic distribution of 18 plots in the study region Schorfheide.

Figure S2.3: Map of the geographic distribution of 18 plots in the study region Hainich.

Figure S2.4: Map of the geographic distribution of 18 plots in the study region Schwäbische Alb.

Figure S2.5: Schema of plot design with position of subplots and transplants within one plot.

Figure S2.6: Graph of principal coordinate analysis (PCoA) on multi-trait distances based on all ten traits.

Figure S2.7: Photograph showing the planting procedure in spring 2012 in the study region Schorfheide on plot SEG50.

Figure S2.8: Graph of SLA single trait approach (a) before and (b) after enrichment planting.

Figure S2.9: Graph of LDMC single trait approach (a) before and (b) after enrichment planting.

Figure S2.10: Graph of height single trait approach (a) before and (b) after enrichment planting.

Figure S2.11: Graph of leaf anatomy single trait approach (a) before and (b) after enrichment planting.

Figure S2.12: Graph of leaf persistence single trait approach (a) before and (b) after enrichment planting.

Figure S2.13: Graph of leaf distribution single trait approach (a) before and (b) after enrichment planting.

Figure S2.14: Graph of vegetative reproduction single trait approach (a) before and (b) after enrichment planting.

Figure S2.15: Graph of clonal growth organs single trait approach (a) before and (b) after enrichment planting.

Figure S2.16: Graph of lateral spread single trait approach (a) before and (b) after enrichment planting.

Figure S2.17: Graph of physical defence single trait approach (a) before and (b) after enrichment planting.

Figure S2.18: Graph of survival rates of transplanted individuals after 1 yr.

Chapter 3 – Using co-occurrence information and trait composition to understand individual plant performance in grassland communities

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3.1 Abstract

Depending on the strength of environmental filtering and competitive exclusion, successful colonizers of plant communities show varying degrees of similarity to resident species with respect to functional traits. For the present study, colonizer's performance was assessed in relation to the degree of fit with the resident community, and in addition, in relation to the community's trait profile and the environmental factors at the study locations.

The two-year field experiment investigated the relative growth rates of 130 species that had been transplanted into German grassland communities varying in intensities of land-use. The transplanted species were selected in accordance with the following scenarios: species with highly similar or dissimilar traits to residents, species with highest degree of co-occurrence with resident species and species chosen randomly from the local species pool.

The performance of transplanted phytometers depended on the scenario according to which the species were selected, on community trait diversity, and in addition, often on the interaction of both and on land use intensity. The total amount of explained variance in performance was low, but increased considerably when species identity was taken into account. In general, individuals in the co-occurrence scenario performed better than those selected based on trait information or those selected randomly. Different predictors were important in different seasons, demonstrating a limited temporal validity of performance models.

3.2 Introduction

The assessment of trait dispersion patterns of species within communities is commonly used as a tool to understand community assembly mechanisms (Weiher & Keddy 1995), with trait requisites being determined by a set of filters constraining colonization, establishment and persistence in a given habitat (Weiher et al. 2011). While filters are assumed to be mechanistically linked to performance of the individual in the community (Webb et al. 2010), few studies have measured the performance of individual plants of a larger number of species along environmental gradients. However, there is also strong evidence that traits affect growth directly and indirectly through biotic interactions. For example, in a transplant experiment conducted in subalpine grasslands hosting five grass species, Gross et al. found individual growth to be strongly driven by specific leaf area (SLA) (Gross et al. 2009). Similarly, the relative growth rates of 20 common grassland species transplanted into the German biodiversity Exploratory grasslands were best described by the traits of the phytometers (Herz et al. 2017b).

In grassland communities the strongest filter is often land-use (Sala et al. 2000; Laliberté et al. 2010). High-intensity land-use in grasslands seeks to increase productivity, involving the extensive application of fertilizer (Socher et al. 2012). As a consequence, competition intensity increases with increasing land-use intensity (Blüthgen et al. 2012), resulting in a decline in the growth rates of competitively inferior species and increased competitive exclusion (MacArthur & Levins 1967). However, such intensive land-use also involves more frequent biomass extraction, either by more frequent mowing or increased stocking densities (Turner et al. 1993; Weigelt et al. 2009). In consequence, species that are able to regrow after disturbance may be favored (Vesk et al. 2004), because competition intensity is alleviated (Wilson & Tilman 1991; Blüthgen et al. 2012). Such opposing effects of more intensive land-use make it difficult to predict how any specific plant species responds to simultaneously increased levels of disturbance and nutrient supply. In addition to land-use, species growth strongly depends on climatic conditions. For example, biomass production has been shown to be limited by cold temperatures in spring and high temperatures in combination with low water availability in summer (Chollet et al. 2014).

Under strong abiotic filtering conditions, species that co-occur in a community are expected to show a high degree of similarity in their functional trait values (Ordoñez et al. 2009). In contrast, under competition conditions, those species with less similar traits are more likely to avoid competitive exclusion (MacArthur & Levins 1967). In principle, this rule of limiting similarity ensures trait divergence in communities (Thompson et al. 2010). There is also growing evidence that negative interactions brought about by competition can turn into positive interactions, i.e. facilitation, if the species display trait dissimilarity in certain shared traits. For example, in an experiment on Tibetan grasslands pairwise species interactions became increasingly positive with increasing dissimilarity in maximum height (Lyu et al. 2017). Similarly, in dry alkali grasslands in Hungary, dissimilarity in canopy height of subordinate species was positively related to the biomass of the dominant species (Kelemen et al. 2015). There are however also limits to trait divergence, as species with extremely diverging trait values might also be excluded as a consequence of strong competition (Mayfield & Levine 2010; Gerhold et al. 2013), resulting in trait convergence (Grime 2006). Furthermore, Gross et al. demonstrated that in the same community some traits can show convergence while others exhibit divergence (Gross et al. 2013). In consequence, it is not clear whether species that are more similar to a resident community perform better than dissimilar species, or vice versa. In grasslands, this question also depends on land-use intensity. Under heavy land-use intensity, and the associated strong abiotic filtering regime combined with higher competition intensity, newcomers with a higher trait similarity to the extant community should perform better and species with more divergent trait values should perform worse. Recently, we suggested that the optimal degree of trait similarity a new species should have to enter a community can be derived empirically from the probability of co-occurrence with the resident species (Breitschwerdt et al. 2015). These probabilities can be extracted from large vegetation databases (such as the German Vegetation Reference Database, GVRD) (Jandt & Bruelheide 2012) without making any assumptions on trait similarities or dissimilarities between a new species and the receiving community. In our previous paper we found that species that commonly co-occur with the resident species in a community survived best (Breitschwerdt et al. 2015), and accordingly, we also expected them to also perform best.

Finally, under a given level of land-use intensity and filtering conditions, a community itself might determine plant growth. It has convincingly been demonstrated that productivity in grassland communities is positively affected by producer diversity (Tilman et al. 2014). In particular, biomass production was shown to be higher in communities with higher functional diversity (FD) (Cardinale et al. 2011; Allan et al. 2011; Schittko et al. 2014). Such relationships have mostly been based on community responses and rarely tested for individual plant species (Diemer & Schmid 2001; Scherber et al. 2006; Fornara & Tilman 2008; Maire et al. 2012). As the community response is the sum of all individual plant responses, one would expect that, on average, individual plant performance might increase with community FD. In addition to FD, the potential to integrate new species into a community might also depend on the abundance-weighted mean values of certain traits (Shipley et al. 2006), expressed as community-weighted means (CWM) (Garnier et al. 2004) . For example, a community with taller plants on average might also force new species to grow taller to access enough light. Similarly, plants in a community with low leaf dry matter content (LDMC) tended to show higher growth rates than in those with high LDMC (Gross et al. 2007). Such functional attributes of the community are not independent of each other, as FD and CWM can also be the result of external environmental filtering processes, such as land-use intensity and, in turn, may indirectly contribute to environmental filtering themselves. For example, CWMs of SLA have been found to increase with increasing fertilization or disturbance intensity (Knops & Reinhart 2000; McIntyre 2008; Lienin & Kleyer 2012), which should result in a high photosynthetic capacity and overall improved growth conditions, thereby intensifying the competition intensity for light.

For the present study, we set out to disentangle the impact of land-use and community trait composition in a large transplant experiment in mesic grasslands differing in land-use intensity and community trait composition. We used extant grassland communities and made use of the given land-use but manipulated the degree of how well a species new to the community might fit into that community. This putative fit was varied by selecting species according to four different scenarios (Breitschwerdt et al. 2015). Two of the scenarios were trait-based, selecting the species most similar and dissimilar to the resident species ("Sim" and "Dissim"). In the third scenario, species were introduced to the community that had the highest degree of co-occurrence with the resident species ("Beals"), while in the fourth scenario species were chosen randomly ("Random"). The objective of our study was to identify the predictors (land-use intensity, CWM or FD of key traits) that determined growth rates and biomass production as well as the actual traits of the colonizing species within the respective grassland communities. We monitored transplants over two years and tested whether the species' performance differed between seasons. In particular, we hypothesized, (i) that the species with highest probability of occurring in the resident community (i.e. those in the Beals scenario) perform better than those of the other scenarios with respect to growth rates and biomass production under all conditions of land-use intensity and community trait composition. (ii) Furthermore, we expected species similar to the resident species to perform better with increasing land-use intensity. (iii) Moreover, of all drivers of plant performance investigated we hypothesized land-use intensity to have a higher explanatory power on species growth and biomass production than FDs and CWMs. (iv) Finally, we tested whether in addition to the selection scenario, land-use intensity and community trait composition, climate (including air and soil temperature, relative air humidity and soil moisture) had additional impact on the phytometers' responses.

3.3 Results

Before the six phytometer species were planted into the plots, mean multi-trait distance did not differ among the resident species that grew in the respective subplots, which had been randomly assigned to the four different scenarios (Fig. 3.1). While the colonizer species in the Sim scenario displayed exactly the same trait dissimilarity to residents as the residents did among themselves, (with a multi-trait dissimilarity of 0.45), the species in all other scenarios were more dissimilar to the resident species in the respective subplots, with 0.47, 0.54 and 0.64 in the Beals, Random and Dissim scenarios, respectively.

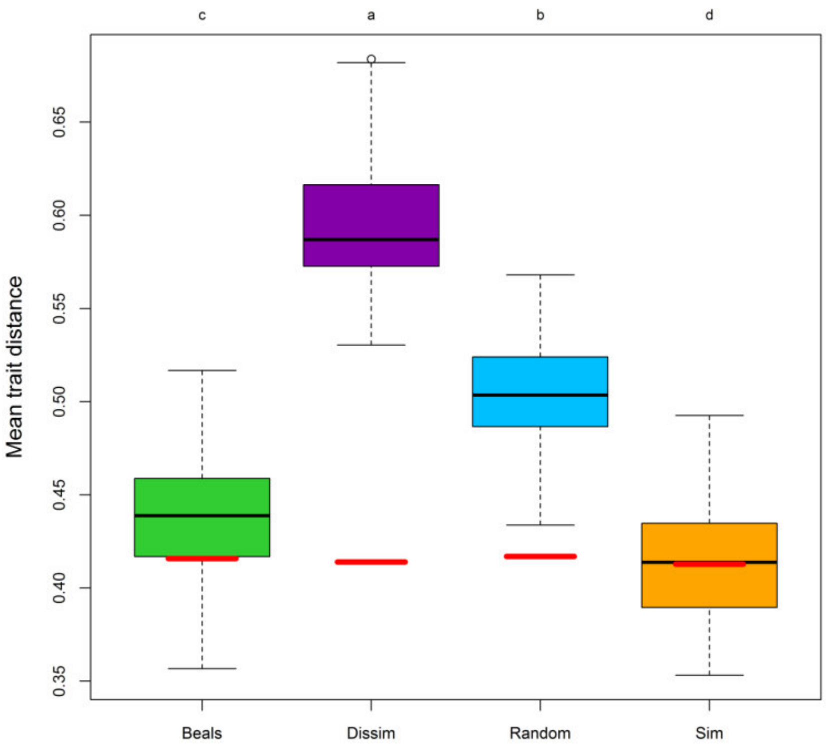

Figure 3.1 Mean pairwise trait distances between the six introduced species in the four scenarios (Beals, Dissim, Random and Sim) and all resident species. Values are multi-trait distances and based on eight traits. Boxes show quartiles and medians across all 54 plots and two subplots per plot (n = 108 per scenario). Whiskers show 1.5 times the interquartile ranges. Small letters indicate statistically significant differences among the scenarios according to a Tukey post-hoc test. As a reference, the red lines show the mean pairwise trait distances among the resident species before six phytometer species were planted into every subplot.

The design variables in our study – i.e. the identity of the species planted into the plots, the identity of the plot and the scenario of how the species were selected – explained a varying overall amount of variation in the responses (Table 3.1). Variation explained by plot ranged from 4% for RGR of leaf number in the first monitoring interval to 39% for RGR height in the 3rd interval, between 0% and 0.4% explained by scenario (for RGR leaf length 1st interval) and between 9% (for RGR leaf length 3rd interval) and 38% (for RGR height 1st interval) explained by species identity.

Table 3.1 Proportional variance of RGR of all variables at all observation intervals (1 – 4 = vegetation period 2012; 4 – 5 = winter 2012/2013; and 5 – 7 = vegetation period 2013) and aboveground biomass, LDMC and SLA at the final harvest in September 2013), exclusively explained by plot, scenario and species, jointly by two of these factors or all of them as well as residual variance. All components add up to 1. p. proj. area = plant projection area.

	Exclusively explained by			Jointly explained by				
Response variable	**Plot**	**Scenario**	**Species**	**Plot & Scenario**	**Scenario & Species**	**Plot & Species**	**Species, Plot & Scenario**	**Residual Variance**
RGR height 1 - 4	0.127	0	0.376	0	0.05	0	0.002	0.452
RGR p. proj. area 1 - 4	0.121	0	0.203	0	0	0.006	0	0.67
RGR leaf length 1 - 4	0.127	0.003	0.206	0	0.004	0.002	0.002	0.658
RGR leaf number 1 - 4	0.043	0.002	0.202	0	0.009	0.014	0	0.731
RGR height 4 - 5	0.356	0.001	0.146	0.001	0.033	0	0	0.478
RGR p. proj. area 4 - 5	0.204	0	0.134	0	0.049	0.012	0	0.611
RGR leaf length 4 - 5	0.275	0	0.106	0	0.025	0.037	0	0.565
RGR leaf number 4 - 5	0.092	0	0.202	0.001	0.019	0.053	0	0.642
RGR height 5 - 7	0.391	0.002	0.16	0.004	0.016	0.015	0	0.422
RGR p. proj. area 5 - 7	0.188	0	0.159	0.001	0.002	0	0	0.657
RGR leaf length 5 - 7	0.312	0	0.097	0	0.002	0.051	0.002	0.537
RGR leaf number 5 - 7	0.083	0	0.193	0	0.007	0.012	0	0.71
Biomass	0.121	0	0.222	0.001	0.001	0.061	0.001	0.594
LDMC	0.134	0.002	0.299	0	0.014	0.043	0.017	0.492
SLA	0.191	0	0.224	0	0.024	0.015	0.026	0.522

As an example, Fig. 3.2 shows the variances in RGR of height of the first monitoring interval exclusively and jointly explained by plot, scenario, species and trait variable (SLA FD). In the variance partitioning analysis, community traits explained maximally 6.5% (CWM of SLA for aboveground biomass at harvest, SI Table S3.4). Whenever trait variables explained variance, this fraction was also jointly explained by plot and species but not by scenario (column n in SI Table S3.4 compared to columns i, k, o, m, see also Fig. 3.2), which indicate that community trait variables did not vary much with environmental differences among subplots.

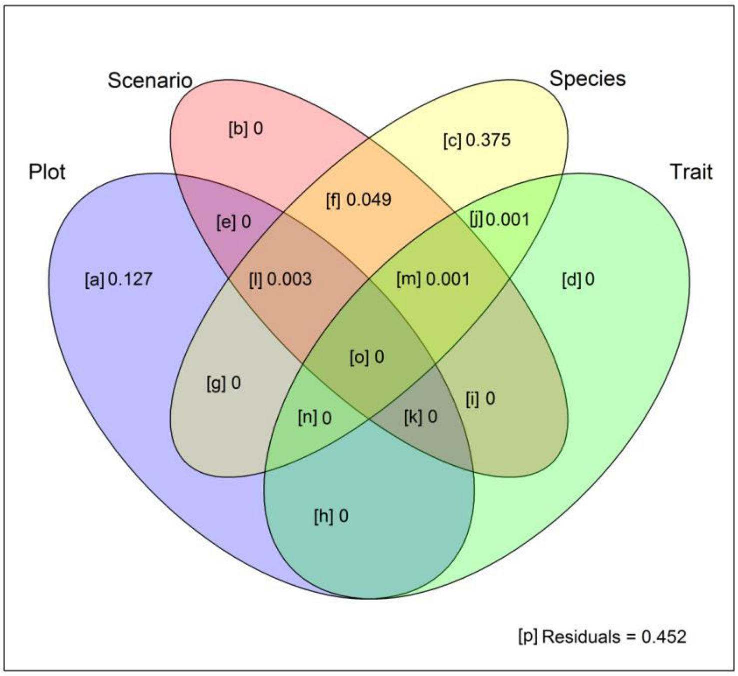

Figure 3.2 Variance partitioning for RGR height of the first vegetation period 2012 (interval 1 – 4) correlated with FD of SLA. Results for all other response variables are given in SI Table S3.4. Variance components < 0.001 not shown.

The different responses of RGR in the different monitoring periods as well as aboveground biomass, SLA and LDMC at the final harvest were explained to varying degrees by the final mixed linear regression models (Table 3.2). The conditional R^2 captured by these models explained between 33% and 68% variation, while the models' marginal R^2 accounted for only 0.4% to 7% variation (Table 3.2). The difference between conditional and marginal R^2 showed that random factors significantly contributed to explaining variance, with species identity explaining most (between 9% and 38%), followed by Exploratory (0% to 38%), plot (5% to 17%), and subplot (0% to 4%, SI Table S3.5).

The best single-predictor mixed models revealed different predictors for the different observation intervals, with LUI occurring in most of the best models, and with positive and negative estimates on growth variables in the winter and second summer intervals, respectively (Fig. 3.3). CWMs of SLA and height affected RGRs only in the second summer intervals, while FD measures were only the best predictors in the first vegetation period, with FD of SLA, FD of height and multi-trait FD positively affecting RGR in height, leaf length and plant projection area, respectively (Fig. 3.3).

Table 3.2 Results of the minimum linear mixed effects models for the transplant's relative growth rates in height, plant projection area, leaf length and number of leaves for the three monitoring periods in 2012 and 2013 and for aboveground biomass, specific leaf area (SLA) and leaf dry matter content (LDMC) at the final harvest in September 2013. All models were simplified starting with the same suite of predictors: land-use intensity (LUI), community weighted means (CWM), functional diversity (FD), scenario (Beals, Dissim, Random, Sim, see text for explanation) and all interactions of scenario with LUI, CWM, and FD. CWM and FD were based on the single traits SLA, LDMC and height, while multi-trait FD was based on all eight traits (see Methods). All variables were scaled by mean and standard deviation, thus the estimates show the direction and magnitude of impact on the plant responses. Marginal R^2 refers to the variance explained by fixed factors and conditional R^2 to the variance explained by both fixed and random factors. Random factors in the model included Exploratory (Schwäbische Alb, Hainich and Schorfheide), plot (n = 54) nested in Exploratory, subplot (n = 432) nested in plot and species identity (n = 130). For variance of random factors see SI Table S3.5.

Responses	Predictors	Estimate	p-value	Marginal R^2	Conditional R^2
Veg. period 2012					
RGR height	Intercept	0.150	0.424	0.004	0.536
	Multi-trait FD	0.058	0.038		
RGR p. proj. area	Intercept	-0.018	0.865	0.008	0.419
	Multi-trait FD	0.097	0.004		
RGR leaf length	Intercept (Scen Beals)	0.085	0.551	0.011	0.384
	Height FD	0.068	0.024		
	Scen Dissim	-0.094	0.411		
	Scen Random	-0.225	0.005		
	Scen Sim	-0.028	0.704		
RGR leaf number	Intercept (Scen Beals)	0.129	0.216	0.013	0.328
	SLA FD (Scen Beals)	0.097	0.050		
	Scen Dissim	-0.154	0.202		
	Scen Random	-0.262	0.002		
	Scen Sim	-0.154	0.052		
	SLA FD:Scen Dissim	-0.102	0.126		
	SLA FD:Scen Random	-0.236	0.002		
	SLA FD:Scen Sim	-0.069	0.318		
Winter 2012/2013					
RGR height	Intercept (Scen Beals)	-0.039	0.918	0.069	0.634
	LUI	0.250	0.000		
	Height FD (Scen Beals)	0.137	0.006		
	Height CWM (Scen Beals)	-0.142	0.025		
	Scen Dissim	-0.163	0.107		
	Scen Random	-0.194	0.009		
	Scen Sim	0.065	0.340		
	Height FD:Scen Dissim	-0.178	0.013		
	Height FD:Scen Random	-0.070	0.345		
	Height FD:Scen Sim	-0.199	0.007		
	Height CWM:Scen Dissim	0.171	0.020		
	Height CWM:Scen Random	0.024	0.726		
	Height CWM:Scen Sim	0.173	0.020		
RGR p. proj. area	Intercept (Scen Beals)	0.014	0.957	0.061	0.492
	LUI	0.215	0.001		
	Height FD (Scen Beals)	0.183	0.000		
	SLA CWM	0.130	0.006		
	LDMC CWM	0.092	0.035		
	Height CWM	-0.100	0.035		
	Scen Dissim	-0.194	0.095		
	Scen Random	-0.185	0.025		
	Scen Sim	-0.054	0.468		

Continued

Responses	Predictors	Estimate	p-value	Marginal R²	Conditional R²
	Height FD:Scen Dissim	-0.146	0.027		
	Height FD:Scen Random	-0.173	0.013		
	Height FD:Scen Sim	-0.153	0.026		
RGR leaf length	Intercept (Scen Beals)	0.060	0.863	0.051	0.544
	LUI	0.210	0.001		
	Height FD (Scen Beals)	0.129	0.016		
	Height CWM (Scen Beals)	-0.119	0.077		
	Scen Dissim	-0.218	0.039		
	Scen Random	-0.091	0.249		
	Scen Sim	0.001	0.984		
	Height FD:Scen Dissim	-0.156	0.045		
	Height FD:Scen Random	-0.079	0.326		
	Height FD:Scen Sim	-0.213	0.008		
	Height CWM:Scen Dissim	0.133	0.094		
	Height CWM:Scen Random	0.041	0.586		
	Height CWM:Scen Sim	0.210	0.009		
RGR leaf number	Intercept (Scen Beals)	-0.168	0.297	0.013	0.440
	LUI	0.086	0.086		
	Height FD	0.057	0.075		
	SLA CWM (Scen Beals)	0.024	0.659		
	Scen Dissim	0.016	0.904		
	Scen Random	0.008	0.927		
	Scen Sim	0.045	0.554		
	SLA CWM:Scen Dissim	-0.093	0.155		
	SLA CWM:Scen Random	-0.068	0.308		
	SLA CWM:Scen Sim	0.066	0.269		
Veg. period 2013					
RGR height	Intercept	0.079	0.864	0.012	0.682
	LUI	-0.126	0.046		
RGR p. proj. area	Intercept	0.029	0.910	0.005	0.398
	SLA FD	0.086	0.020		
RGR leaf length	Intercept	0.017	0.967	0.026	0.568
	SLA FD	0.124	0.000		
	Height CWM	-0.138	0.001		
RGR leaf number	Intercept	0.040	0.729	0.014	0.357
	Multi-trait FD	-0.090	0.017		
	SLA FD	0.114	0.005		
Harvest 2013					
Biomass	Intercept (Scen Beals)	-0.016	0.865	0.064	0.423
	LUI	0.170	0.002		
	Multi-trait FD (Scen Beals)	0.003	0.960		
	LDMC FD (Scen Beals)	-0.116	0.076		
	SLA CWM (Scen Beals)	-0.094	0.107		
	Scen Dissim	-0.116	0.382		
	Scen Random	-0.066	0.476		
	Scen Sim	-0.048	0.535		
	Multi-trait FD:Scen Dissim	0.217	0.029		
	Multi-trait FD:Scen Random	0.064	0.514		
	Multi-trait FD:Scen Sim	-0.080	0.333		
	LDMC FD:Scen Dissim	0.052	0.581		

Continued

	LDMC FD:Scen Random	0.018	0.854		
	LDMC FD:Scen Sim	0.226	0.008		
	SLA CWM:Scen Dissim	0.292	0.000		
	SLA CWM:Scen Random	0.228	0.007		
	SLA CWM:Scen Sim	0.185	0.016		
SLA	Intercept (Scen Beals)	0.095	0.683	0.044	0.509
	Height CWM	0.140	0.001		
	LDMC CWM (Scen Beals)	-0.118	0.024		
	Scen Dissim	-0.347	0.005		
	Scen Random	-0.040	0.644		
	Scen Sim	0.041	0.574		
	LDMC CWM:Scen Dissim	0.196	0.003		
	LDMC CWM:Scen Random	0.212	0.003		
	LDMC CWM:Scen Sim	-0.013	0.825		
LDMC	Intercept (Scen Beals)	0.062	0.557	0.036	0.556
	SLA FD	-0.080	0.030		
	LDMC FD	0.077	0.042		
	SLA CWM (Scen Beals)	-0.020	0.757		
	LDMC CWM (Scen Beals)	0.065	0.300		
	Scen Dissim	0.275	0.041		
	Scen Random	0.037	0.682		
	Scen Sim	0.046	0.531		
	SLA CWM:Scen Dissim	-0.005	0.952		
	SLA CWM:Scen Random	-0.076	0.362		
	SLA CWM:Scen Sim	0.164	0.027		
	LDMC CWM:Scen Dissim	-0.041	0.611		
	LDMC CWM:Scen Random	-0.268	0.001		
	LDMC CWM:Scen Sim	0.104	0.157		

In many cases, the optimized multi-predictor models identified the same predictors as shown in the single predictor models of Fig. 3.3. For example, in the vegetation period in 2012 multi-trait FD was the sole predictor for RGR in plant projection area and FD of height predicted RGR of leaf length (Table 3.2). Similarly, the best models for RGR in height in winter and early spring (2012/2013) contained LUI as a predictor (Table 3.2). In the same monitoring intervals, the different growth variables were best explained by different predictors. For example, the best predictors for RGR in height and projection area in the first monitoring interval were multi-trait FD (Fig. 3.4, Table 3.2), while leaf length and leaf number were best predicted by FD of height or SLA in combination with scenario (Table 3.2). In the winter monitoring interval, plant performance depended strongly on FD (Fig. 3.5). In the same period, LUI was a predictor in all significant models (Table 3.2) and remained important the following summer and at the final harvest (Table 3.2, Fig. 3.6). In general, growth rates increased with LUI in winter, but decreased with LUI in the subsequent summer (Figs. 3.3, 3.6, Table 3.2). At the final harvest, aboveground biomass was again positively related to LUI (Table 3.2).

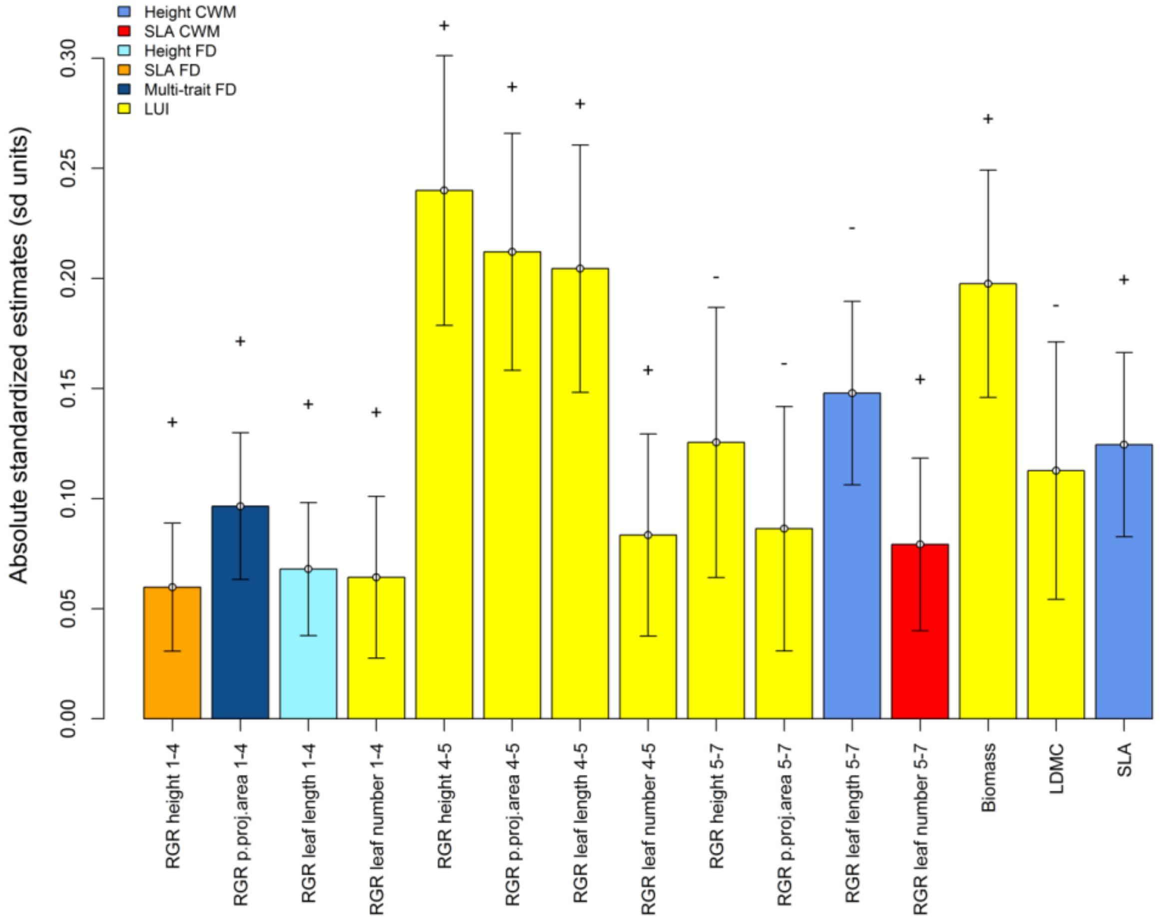

Figure 3.3 Absolute standardized model estimates of the best single-predictor models with their corresponding standard errors for the different growth rates (RGR of height, plant projection area, leaf length and leaf number) in the three time intervals (1 – 4, 4 – 5 and 5 – 7), and aboveground biomass, LDMC and SLA at the time of the final harvest. Only the predictors (see different color legend) are shown that had the highest explanatory power on the responses. Multi-trait FD refers to FD based on eight traits (SLA, LDMC, height, leaf anatomy, leaf persistence, leaf distribution, physical defense and vegetative reproduction). Plus and minus signs above bars indicate positive or negative effects.

Across all models, scenario was a more frequent predictor than LUI and occurred in nine of the 15 models. Seven of these nine models predicted performance, of which five models displayed highest growth rates of phytometers in the Beals scenario, followed by Sim, while Dissim and Random ranked lowest (Table 3.2). Plants in the Beals scenario also performed better in combination with trait measures, such as with FD of height (Fig. 3.5, increasing RGR of plant projection area in the Beals scenario in winter). Growth of plants in the Beals scenario also depended differently on traits. At the final harvest, in contrast to the other three scenarios aboveground biomass decreased with increasing CWM of SLA (Fig. 3.7). Similarly, interactions with scenario were encountered in the explaining of SLA (Fig. 3.8) and LDMC (Table 3.2) at the final harvest. In general, the responses of transplants in the Beals scenario often differed from those in the other scenarios, particularly when compared to those in the

Random and Dissim scenarios (Figs. 3.5, 3.7 and 3.8). In contrast, the patterns in the Sim scenario were sometimes closer to the Beals scenario (Fig. 3.8) or the Random and Dissim scenarios (Figs. 3.7 and 3.5). Among the remaining predictors, FD explained growth in more of the models than CWM. FD was retained in 13 of the 15 models across all monitoring intervals, while CWM was only retained in eight of them (Table 3.2). Among all FD measures, multi-trait FD, on which the species selection for the scenarios was based, FD of SLA and FD of height were the most frequent predictors for plant performance and were included in four, five and five models, respectively (Table 3.2). In contrast, CWM was more important in explaining the community mean SLA (Fig. 3.8) and LDMC (Table 3.2) at the time of harvest.

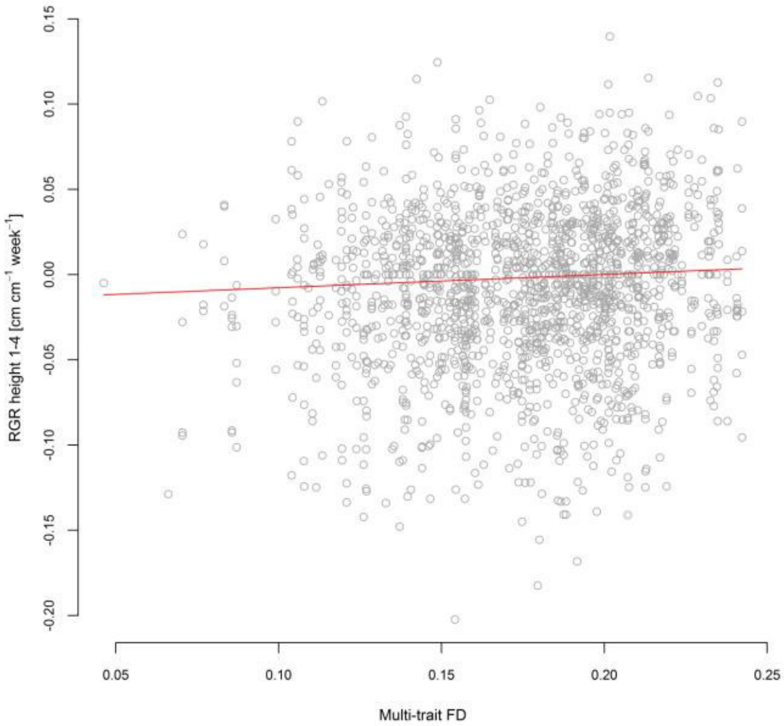

Figure 3.4 RGR height in the first vegetation period (1 – 4) as a function of Multi-trait FD. For parameter estimates and p-values see Table 3.2; for variance of random factors see SI Table S3.5.

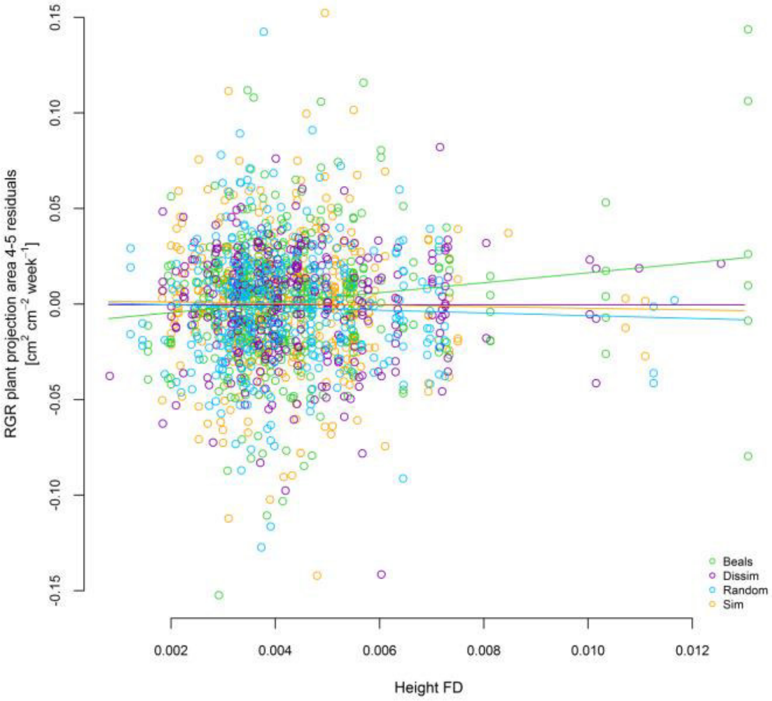

Figure 3.5 RGR plant projection area residuals in winter (4 – 5) as a function of height FD and scenario. For parameter estimates and p-values see Table 3.2; for variance of random factors see SI Table S3.5.

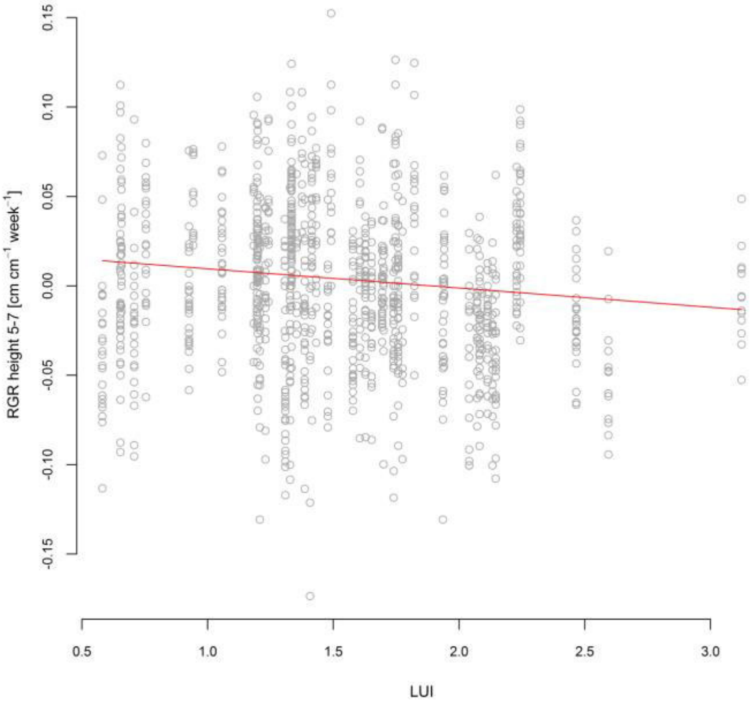

Figure 3.6 RGR height in the second vegetation period (5 – 7) as a function of LUI. For parameter estimates and p-values see Table 3.2; for variance of random factors see SI Table S3.5.

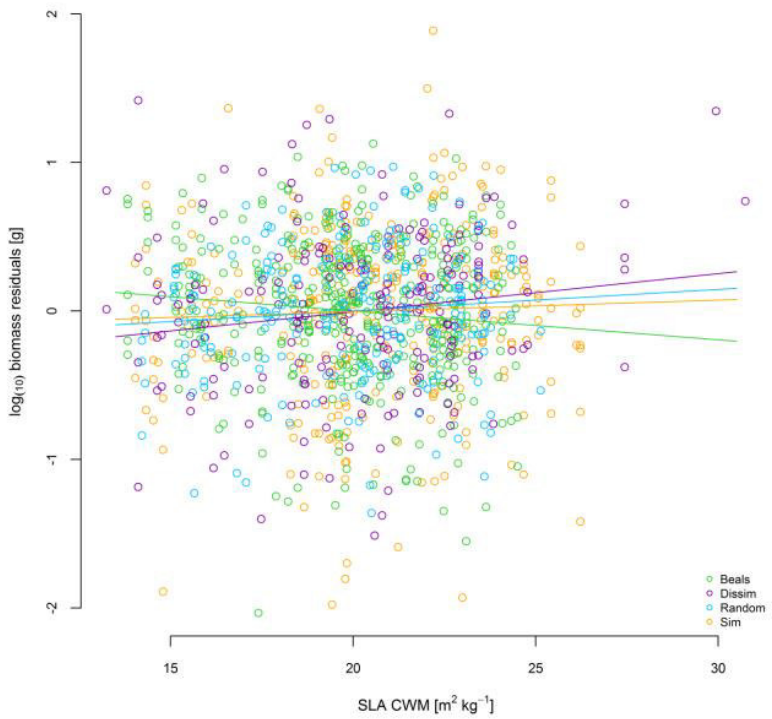

Figure 3.7 Aboveground biomass residuals (log scale) at time of harvest (end of second vegetation period) as a function of SLA CWM and scenario. For parameter estimates and p-values see Table 3.2; for variance of random factors see SI Table S3.5.

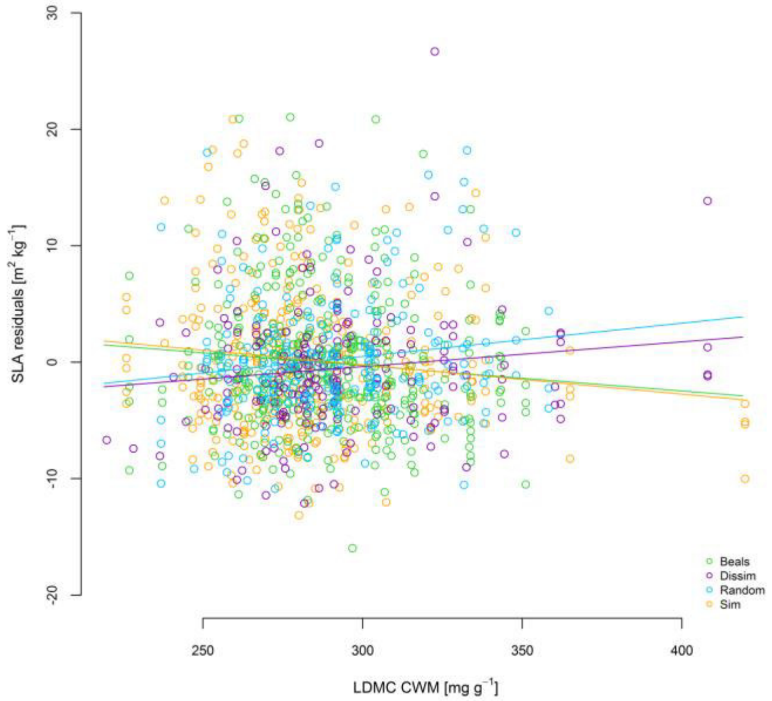

Figure 3.8 SLA residuals at time of harvest (end of second vegetation period) as a function of LDMC CWM and scenario. For parameter estimates and p-values see Table 3.2; for variance of random factors see SI Table S3.5.

The climatic conditions differed significantly between the two summer periods and the winter with respect to relative air humidity and soil moisture (SI Fig. S3.2). The second vegetation period in 2013 was also warmer, as demonstrated by higher air and soil temperatures. Adding each one of these four climate variables to the final models did not result in model improvement, with the exception of soil moisture (SI Table S3.6). In winter, soil moisture had significantly negative impacts on growth variables, while in summer the effects were positive, e.g. on RGR plant projection area (Fig. 3.9, SI Table S3.6). In addition, soil moisture had also positive effects on RGR of height and leaf length in the vegetation period 2013 and on SLA and LDMC at the time of harvest (SI Table S3.6). In all cases, where models were improved by including climate variables, the other predictors remained significant after the climate variable had been added.

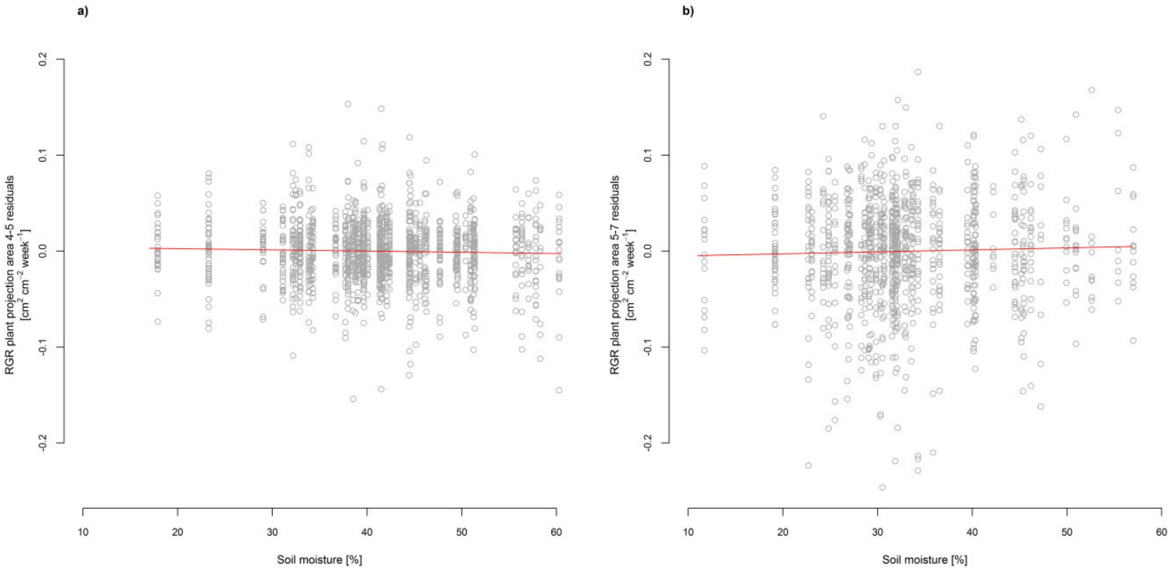

Figure 3.9 RGR plant projection area residuals (a) in winter 2012/2013 (4 – 5) and (b) in the following vegetation period 2013 (5 – 7) as a function of soil moisture. For parameter estimates and p-values see SI Table S3.6.

3.4 Discussion

We showed that the performance of newly colonizing species strongly depended on the trait composition of the resident community and land-use intensity. In addition, the scenario according to which the phytometer species were selected had a strong influence on how well the phytometer performed.

In many of the monitoring intervals and for many growth variables, phytometer species selected by the scenario based on co-occurrence probability of added and resident species derived from a vegetation database (Beals) performed better than those selected by trait information (Sim, Dissim) or random selection (Random). These results support our first hypothesis and also confirm the observed higher survival rates in the Beals scenario (Breitschwerdt et al. 2015). More generally, this finding demonstrates the huge potential of co-occurrence-based approaches in growth models (Mildén et al. 2006; Breitschwerdt et al. 2015). Although no traits were used in the Beals selection process of species, and the species selected were not as similar as they possibly could have been, a surprising feature of this scenario was that the added species did not result in a change in mean pair-wise trait distances across all plots (Breitschwerdt et al. 2015). Assuming the species in the resident community had a trait composition filtered by land-use and other factors at that site, and that this trait composition facilitated the survival of the resident species, the traits of the newcomer species in the Beals scenario had exactly the same degree of similarity or dissimilarity to the resident species, which increased their survival and, at the same time, their performance compared to species in the other scenarios. This also implies that rather than the most similar or dissimilar species, it were those with trait values at intermediate distances to the resident species that performed best. The Beals scenario was found to rank closer to the Sim than to Dissim scenario (at 32% of the distance between Sim and Dissim) (Breitschwerdt et al. 2015). This also explains why species in the Sim scenario often ranked second in growth after those in the Beals scenario but were superior to the Dissim and Random scenarios. It is however noted that the phytometer species of the Beals scenario did not always show the highest growth rates in all intervals or the highest aboveground biomass production. Slow growth, shade tolerance, higher investment into roots compared to leaves or other strategies alternative to fast growth (Westoby et al. 2002) might also apply to the higher survival success of species of the Beals scenario (Breitschwerdt et al. 2015). Similarly, our second hypothesis has to be rejected that species of the Sim scenario performed better with increasing land-use intensity because none of the best models included the interaction between land-use and scenario.

As stated in our third hypothesis, land-use intensity was one of the strongest drivers of phytometer performance. In our study, LUI often had an additive effect together with scenario, FD and CWM on the growth of plant individuals, particularly in the winter and early spring interval. In this period, fewer disturbances occurred and the plants had the chance to grow without being eaten, cut or trampled on. As a high LUI is often combined with high levels of fertilization, early spring was probably the season when plants benefitted most from a higher nutrient supply. In contrast, LUI had a negative effect on height growth in the subsequent summer interval, probably because the plants remained smaller due to more frequent mowing or grazing events.

In addition to the strong effect of scenario and land-use intensity, and often interacting with these predictors, FD also played a role in the performance of the added species, which confirms other approaches of predicting biomass from traits (Duru et al. 2009). With the exception of trait responses (SLA and LDMC at the time of harvest), the estimates for FD measures on growth were always positive, showing that the added species benefitted from a functionally more diverse community. In particular, FD in SLA was found to be a consistent positive predictor. Given that SLA reflects the main axis in the leaf economics spectrum (Wright et al. 2004), the importance of FD of SLA points to a pattern of niche partitioning in resource use. For example, it has been described that grassland species in diverse mixtures absorb up to 20% more light than those in monocultures as a result of a greater three-dimensional use of space, brought about by more overlapping plant architecture, and in consequence, a higher biomass density (Spehn et al. 2000). Consistent with our results, the authors also encountered an increase in canopy height (Spehn et al. 2000). Similarly, a positive correlation between individual plant height and functional richness (Schmidtke et al. 2010) and an increased aboveground use of space with increasing functional richness (Lorentzen et al. 2008) is in accordance with our results. Some FD predictors only had effects in certain scenarios, such as FD of height, which increased the growth rates in plant area in the Beals scenario only. Thus, it might well be that FD effects can only play out if the species added to the community have already been environmentally filtered. Then, the finding that multi-trait FD, which was based on the traits chosen by us for devising the scenarios, was also a frequent predictor is an indication that the traits chosen for this index are ecologically meaningful for growth and persistence.

Finally, there were also a few but notable effects of CWM trait values on plant performance. For example, CWM of SLA had a positive impact on aboveground biomass at the end of the experiment in the Sim, Dissim and Random scenario in the second year, which might reflect better overall resource supply. However, the significant interaction with scenario and the negative response of species in the Beals scenario shows that different species respond differently to a community's trait composition, and the conditions that are favorable for one group might be disadvantageous for another. For example, a high CWM of SLA also indicates stronger competition for light (Violle et al. 2009), making it more difficult for less tall species to persist in the shady undergrowth (Schwinning & Weiner 1998). However, the increased resource partitioning of light through the addition of smaller species to a community, can result in only very slight increases in community biomass production (Daßler et al. 2008). Another explanation for a negative response to CWM of SLA might be that the FD of a trait is not independent from the CWM of the same trait, since trait variation is constrained by the mean (Dias et al. 2013). Thus, extreme values of CWM values result in low values of FD and conversely, a negative relationship to CWM of a trait might only indicate a positive relationship to FD of the same trait. Finally, responses to CWM also depended on the different scenarios. Accordingly, the expected negative relationship of the target plant's SLA with the CWM of LDMC (Cornelissen et al. 2003) was only encountered in the Sim and Beals scenarios, where species had been selected with the highest similarity (Sim) or at least with some similarity (Beals) to the resident community. The finding that the target plant's SLA increased with the CWM of LDMC in the Random and Dissim scenarios shows that they became more divergent to the residents, which simply reflects the selection procedure.

Despite the clear patterns found in our study, a lot of variation in growth remained unaccounted for. The high importance of random factors such as "Exploratory" and "plot" results from the realistic field conditions under which the experiment has been carried out. The vast range of soil, climate and management conditions across all plots were only partially captured by the few environmental variables used as fixed predictors in our study. Similarly, the high variation brought about by species identity is explained by the large pool of species (130) from which we drew the phytometer species for the different scenarios. We also may have missed an important compartment of the plants. As we only focused on aboveground biomass we do not know whether allocation patterns between leaves and roots differed among scenarios. For example, in another study on the same grasslands, root volume was found to increase with land-use intensity and root-to-shoot ratio to depend both on the local neighbourhood and the level of land-use intensity (Herz et al. 2017a). However, they found root biomass to be only poorly predicted by traits and environmental factors (Herz et al. 2017b). In contrast to our study, where the phytometer traits were captured in the scenarios, Herz et al. used single traits measured on the phytometers to predict performance. In their models, root traits such as root calcium and root carbon content considerably improved the model quality for aboveground biomass. Root carbon concentration indicates the prevalence of more reduced and polymerized structural carbohydrates, which was negatively related to above- and belowground growth (Herz et al. 2017b). However, accounting for root traits in our study would have required to include them in the different scenarios from the beginning, which was not feasible given the large size of the species pool from which the scenarios were constructed. Elsewhere, in the high semi-arid Andes, it has been observed that with increasing grazing pressure, more biomass is allocated to roots (Patty et al. 2010). Similarly, we do not know the proportion of aboveground biomass extracted by land-use. However, biomass measurements in the Exploratory grassland plots have shown that productivity increased with higher levels of fertilization (Socher et al. 2012) and fertilization is a component of the LUI (Blüthgen et al. 2012). We therefore have to acknowledge that monitoring growth rates with simultaneous biomass extraction does not allow for simple explanations. Many plant individuals had more or less the same aboveground size at the end of our experiment as at the beginning. As grazing occurred at different times in different plots, and compensatory growth after grazing also varies with time of recovery (Oesterheld & McNaughton 1991), the fixed monitoring dates might not have always captured plant growth in the most accurate way. However, given the logistic effort already involved, plot-wise adaptation of monitoring dates would not have been feasible. Such varying dates would also have precluded relationships to weather conditions, which varied over time and space. In addition, incorporating climate variables into our models supported our fourth hypothesis that they explained additional variance. In particular, soil moisture had a positive effect on plant growth and SLA in summer 2013, when temperatures were higher than in summer 2012. This is in accordance with findings of increased biomass production and growth at increased soil moisture under warm conditions (Veihmeyer & Hendrickson 1950; Flanagan & Johnson 2005; Thorne & Frank 2009). In contrast, under low temperatures in winter soil moisture had a negative effect on plant growth, which might be explained by water logging which negatively affects N mineralization (Laanbroek 1990). Accordingly, seasonal variation in RGR, biomass production and SLA has also been reported in numerous other studies (e.g. Al Haj Khaled et al. (2005), Ma et al. (2011), Dwyer et al. (2013)).

In summary, our finding that co-occurrence information allows conclusions to be drawn on plant growth bodes well for the capability to predict individual as well as community performance from vegetation databases, which has, as yet, not been attempted before. This potential predictive power became particularly evident when we combined co-occurrence data with functional traits. The fact that plant responses to community trait composition differed among scenarios, might point to a hierarchical cascade of community assembly. Thus, species might only respond to community FD or CWM after they have passed other environmental filters. We also confirmed the key role of land-use intensity for plant performance (Lienin & Kleyer 2011). However, the finding that land-use intensity played different roles at different times of the year demonstrates that temporal resolution is required when assessing land-use impacts on plant performance at larger spatial scales (Allan et al. 2014; Rota et al. 2017).

3.5 Materials and Methods

Study Sites and Experimental Design

We planted different vascular plant species into 54 grasslands communities, making use of the network of experimental plots in the German Biodiversity Exploratories (Fischer et al. 2010). In each of the three study regions (Schwäbische Alb, South Germany; Hainich, Central Germany and Schorfheide, Northeast Germany), 18 grassland plots were selected that represent the three main land-use types (i.e. each six plots of meadows, pastures and mown pastures). The plots differed in land-use intensity, which was assessed by an index (LUI) that combines mowing and grazing frequencies, number of grazers per hectare and fertilization levels (Blüthgen et al. 2012) according to formula (1).

$$(1)\ LUI_p = \sqrt{\frac{G_p}{\bar{G}} + \frac{F_p}{\bar{F}} + \frac{M_p}{\bar{M}}}$$

The land-use index for a site p (LUI_p) was calculated from the sum of grazing intensity G_p, assessed as the density of livestock (number per ha) and duration of pasture (days per year), amount of fertilizer application F_p (kg nitrogen per year and ha) and mowing intensity M_p, defined as the number of cutting events per year. Each category G_p, F_p and M_p was scaled by the mean of this variable over all sites from each of the three regions of the Biodiversity Exploratories ($\overline{G}$, $\overline{F}$ and $\overline{M}$, respectively). We used the mean of the LUI for the years 2006 to 2010, i.e. those preceding our experiment. There were eight subplots per plot, each measuring 1 × 1 m, which were planted with six phytometers of six different species, selected from a total pool of 130 species according to the four transplant addition scenarios, namely Sim, Dissim, Beals and Random. The six species planted in each subplot were specifically selected based on each plot's species composition, and they therefore differed among plots. Species in the Sim and Dissim scenarios were selected that they would have respectively have the lowest and highest mean pairwise trait distance $\bar{d}$ to the extant species in each plot, with the selection based on eight functional traits (SLA, LDMC, height, leaf anatomy, leaf persistence, leaf distribution, vegetative reproduction, physical defense; see SI Table S3.1). These traits closely reflect the trait constellation of all resident and phytometer species in the study (SI Fig. S3.1). As we used only young plants in the experiment, and deliberately excluded plants at the germination stage, we focused on persistence traits and disregarded seed and reproduction traits. As such, traits were chosen that reflect competitive ability through their capacity to affect growth rates such as specific leaf area (SLA), leaf dry matter content (LDMC), height, leaf anatomy, leaf persistence and leaf distribution (Cornelissen et al. 2003; Kleyer et al. 2008). SLA and LDMC were somewhat correlated ($r^2 = 0.23$) across all phytometer and resident species in the community, while both were uncorrelated with height (SI Fig. S3.1). Furthermore, we included traits that increased persistence after disturbance by providing the ability to colonize or re-colonize habitats through means of vegetative reproduction. We also included the trait of "physical defense mechanisms", because it directly relates to land-use. Plants that have physical defense traits such as thorns or hooks are less likely to be grazed. Thus, the traits used represented independent axes of specialization. Trait distance calculations were based on all these eight traits using Gower's distance. In the Beals scenario, species used had the highest probability of co-occurrence with the resident species in the German Vegetation Reference Database (GVRD) (Jandt & Bruelheide 2012), while in the Random scenario, the species were randomly selected from the species pool. We calculated both the mean pairwise trait distances among all resident species before the phytometer species were planted and between the six introduced species in the four scenarios (Beals, Dissim, Random and Sim) and all resident species.

In total, we planted 2592 individuals (3 Exploratories, 18 plots per Exploratory, 8 subplots per plot, 6 plant individuals per subplot). Detailed information of the experimental design and the scenarios is reported in a previous paper (Breitschwerdt et al. 2015). SI Table S3.1 shows the mean trait values of the phytometers planted under the four different scenarios. With the exception of SLA, all scenarios differed in their trait values. On average, of all species selected for the different scenarios, species in the Beals scenario had leaves that were to a higher degree hygromorphic and arranged in rosettes and reproduced more frequently vegetatively. In contrast, Sim species ranked highest in mesomorphic and evergreen leaf types and regular leaf distribution. Dissim species were tallest, more scleromorphic and they often had semi-rosettes. Finally, species chosen for the Random scenario had leaves with the highest LDMC, which were more summer-green (Table S3.1).

After planting in April 2012, the phytometers were monitored regularly for growth and survival in April, May, July, August and October 2012 and in May, June/July and September 2013. These eight monitoring events were numbered from zero to seven. At each date, we recorded height, aboveground plant projection area (calculated from two diameters using the ellipse formula), leaf length and number of leaves. At the last monitoring date in September 2013, aboveground biomass of all surviving plants was harvested, dried and weighed. Regressions of height and projection area on aboveground biomass at the time of harvest showed a high positive correlation of r = 0.47 and 0.78, respectively, indicating that our non-destructive variables were good proxies for aboveground biomass. Photographs were taken of fresh leaf samples for every individual and then analyzed using Image J (version 1.48e, Rasband (2008), National Institutes of Health) to assess leaf area. Fresh leaf samples and aboveground biomass were dried for three days at 60 °C. Dry leaves and dry aboveground biomass were weighed and summed to calculate total aboveground biomass. SLA was calculated by dividing leaf area (m²) by dry leaf mass (kg). LDMC was calculated by dividing dry leaf mass (mg) by fresh leaf mass (g) (Cornelissen et al. 2003). As most species did not produce flowers or fruits in the presence of grazing and cutting, we could not analyze individual fitness but instead focused on relative growth rates (RGR) as a measure of performance. RGR was calculated according to formula (2) (Hunt & Cornelissen 1997), where M is any growth variable and t is the time span in weeks between the two monitoring dates 1 and 2.

$$(2)\ RGR_i = \frac{\ln(M_2)-\ln(M_1)}{t_2-t_1}$$

We calculated RGR for three intervals, May to October 2012 (1 – 4), October 2012 to May 2013 (4 – 5), and May to September 2013 (5 – 7).

CWM calculation

The community-weighted mean value (CWM) of SLA, LDMC and height was calculated according to formula (3):

$$(3)\ \mathrm{CWM} = \sum_{i=1}^{s} p_i * x_i$$

where p_i is the relative cover of species i (i = 1, 2, ..., s) obtained from vegetation records on all subplots made in 2011, when the visual plant cover of every species was estimated as a percentage of the subplot area (1 m^2). Total plant cover included the cover of transplants, obtained from the aboveground plant projection area calculated from two diameters using the ellipse formula and then transferred to percentage. As the six transplanted individuals contributed to the CWM trait value of the subplot, only the surviving transplants were included in the calculation. In addition, as the transplants were of different size on the various monitoring dates, CWMs differed among dates. The trait value (x_i) of species i (i = 1, 2, ..., s) refer to species mean trait values measured in 2011, complemented from the databases LEDA (Kleyer et al. 2008), BIOPOP (Poschlod et al. 2003), BIOLFLOR (Klotz et al. 2002) and Rothmaler (Jäger & Werner 2001). Species with missing trait values were excluded from CWM calculation.

FD calculation

FD was calculated according to Rao´s defined quadratic entropy (Rao 1982) according to formula (4):

$$(4)\ FD_Q = \sum_{i=1}^{s} \sum_{j=i+1}^{s-1} D_{ij} * p_i * p_j$$

where p_i and p_j are relative cover and D_{ij} the trait distances between all species i and j in one subplot. The calculation employed the same traits as in CWM (SLA, LDMC and height) and the same multi-trait distance D_{ij} that was used for selecting the species for the Sim and Dissim scenario (see above). As in CWM, FD included the sizes of all survivors at the end of the three time intervals.

Climate Data

Air temperature and relative air humidity were measured at 2 m above the ground, while soil temperature and moisture were measured at 10 cm below the ground. All climate data were collected at 10 minutes intervals using data loggers installed in the same plots and aggregated to monthly mean values (see Acknowledgements). The monthly means were averaged for the three time intervals in our study (vegetation period 2012, winter 2012/2013 and vegetation period 2013).

Data Analysis

In a first step, to analyse the total amount of variation explained by our study design, we subjected all 15 response variables to a variance partitioning analysis (i.e. height, aboveground plant projection area, leaf length and number of leaves, for each of the three monitoring intervals as well as aboveground biomass, SLA and LDMC at the time of harvest). The exclusive and jointly explained variances by plot (nested in Exploratory: Schwäbische Alb, Hainich and Schorfheide), scenario and species identity were assessed using the varpart command in the vegan package in R (Oksanen et al. 2015). We repeated the analysis including additional subplot-based trait measures to serve as a fourth predictor category (both CWM and FD of height, SLA and LDMC as well as FD of all traits).

Thereafter, regressions were calculated using mixed linear models in R (lmer, package lmerTest (Kuznetsova et al. 2013)) using “Exploratory”, “plot” nested in “Exploratory”, “subplot” nested in “plot” and “species identity” as random factors. This random structure was used in all subsequent models.

In the second step, we calculated single fixed-predictor linear mixed effects models that related RGR of the 15 different response variables (height, plant projection area, leaf length, number of leaves, for each of the three monitoring intervals, and the variables at the time of harvest, i.e. aboveground biomass, SLA and LDMC) to eight predictor variables (CWM and FD of height, SLA and LDMC as well as to FD of all traits used in the scenario definition (multi-trait FD) and land-use intensity (LUI)). We identified the models with the highest absolute standardized estimates of the predictor and plotted standardized estimates for all 15 response variables.

In the third step, we constructed full multiple-predictor linear mixed effects models that related the RGR of the different response variables to land-use intensity (LUI), scenario (Beals, Dissim, Sim, Random), CWM (separately for SLA, LDMC and height) and FD (of the single traits SLA, LDMC and height and the multi-trait FD). Logger failure resulted in plots with missing values for one of the four climate variables (see SI Table S3.3), which precluded the inclusion of climate variables in the full models for all 54 plots. As we were particularly interested in how the different scenarios modified the phytometer responses, we also included all two-fold interactions with scenario. Aboveground biomass was log transformed to achieve normal distribution. The models were then improved by backward selection of predictor variables using the step command of R package lmerTest to eliminate insignificant effects (Kuznetsova et al. 2013). The final models were then compared with models to which one of the four climate variables (air temperature, relative air humidity, soil temperature and soil moisture) was added as an additional predictor, using AIC. This required recalculating the models both with and without climate variables for the subsets for which climate data were available (SI Table S3.3). Models with climate variables were considered better than those without if ΔAIC was >1.

We used the method described by Nakagawa & Schielzeth to calculate the amount of variance explained by the mixed models (Nakagawa & Schielzeth 2013), both as marginal R^2 (i.e. the variance explained by fixed factors), and as conditional R^2 (i.e. the variance explained by both fixed and random factors). While all graphs were produced using unscaled variables, all predictor variables in the multiple regression models and those reported in the tables were scaled by mean and standard deviation, which allowed for the direct comparison of parameter estimates of effect sizes. All estimates refer to the Beals scenario (when scenario as a categorical predictor was included in the model Beals was coded as intercept in the model's design matrix) and to the mean of all continuous variables in the final model. The parameter estimates of these final models were then used to calculate regression lines. Partial regressions were produced by calculating a linear mixed effects model without the target variable and then relating the residuals of that model to the target variable in an ordinary linear model. For all statistical analyses, we used the software R version 3.4.3 (R Core Team 2013).

The datasets analysed during the current study are available from the corresponding author upon request; for trait values also see supporting information Table S3.2.

3.6 References

Al Haj Khaled, R., Duru, M., Theau, J.P., Plantureux, S., & Cruz, P. 2005. Variation in leaf traits through seasons and N-availability levels and its consequences for ranking grassland species. *Journal of Vegetation Science* 16: 391–398.

Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tscharntke, T., Blüthgen, N., Bellach, M., Birkhofer, K., Boch, S., Böhm, S., Börschig, C., Chatzinotas, A., Christ, S., Daniel, R., Diekötter, T., Fischer, C., Friedl, T., Glaser, K., Hallmann, C., Hodac, L., Hölzel, N., Jung, K., Klein, A.M., Klaus, V.H., Kleinebecker, T., Krauss, J., Lange, M., Morris, E.K., Müller, J., Nacke, H., Pašalić, E., Rillig, M.C., Rothenwöhrer, C., Schall, P., Scherber, C., Schulze, W., Socher, S.A., Steckel, J., Steffan-Dewenter, I., Türke, M., Weiner, C.N., Werner, M., Westphal, C., Wolters, V., Wubet, T., Gockel, S., Gorke, M., Hemp, A., Renner, S.C., Schöning, I., Pfeiffer, S., König-Ries, B., Buscot, F., Linsenmair, K.E., Schulze, E.-D., Weisser, W.W., & Fischer, M. 2014. Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the National Academy of Sciences* 111: 308–313.

Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., & Hillebrand, H. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences* 108: 17034–17039.

Blüthgen, N., Dormann, C.F., Prati, D., Klaus, V.H., Kleinebecker, T., Hölzel, N., Alt, F., Boch, S., Gockel, S., Hemp, A., Müller, J., Nieschulze, J., Renner, S.C., Schöning, I., Schumacher, U., Socher, S.A., Wells, K., Birkhofer, K., Buscot, F., Oelmann, Y., Rothenwöhrer, C., Scherber, C., Tscharntke, T., Weiner, C.N., Fischer, M., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., & Weisser, W.W. 2012. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology* 13: 207–220.

Breitschwerdt, E., Jandt, U., & Bruelheide, H. 2015. Do newcomers stick to the rules of the residents? Designing trait-based community assembly tests. *Journal of Vegetation Science* 26: 219–232.

Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I., & Gonzalez, A. 2011. The functional role of producer diversity in ecosystems. *American Journal of Botany* 98: 572–592.

Chollet, S., Rambal, S., Fayolle, A., Hubert, D., Foulquié, D., & Garnier, E. 2014. Combined effects of climate, resource availability, and plant traits on biomass produced in a Mediterranean rangeland. *Ecology* 95: 737–748.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H. ter, Morgan, H.D., Heijden, M.G.A. van der, Pausas, J.G., & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Daßler, A., Roscher, C., Temperton, V.M., Schumacher, J., & Schulze, E.-D. 2008. Adaptive survival mechanisms and growth limitations of small-stature herb species across a plant diversity gradient. *Plant Biology* 10: 573–587.

Dias, A.T.C., Berg, M.P., de Bello, F., Van Oosten, A.R., Bílá, K., & Moretti, M. 2013. An experimental framework to identify community functional components driving ecosystem processes and services delivery. *Journal of Ecology* 101: 29–37.

Diemer, M., & Schmid, B. 2001. Effects of biodiversity loss and disturbance on the survival and performance of two Ranunculus species with differing clonal architectures. *Ecography* 24: 59–67.

Duru, M., Adam, M., Cruz, P., Martin, G., Ansquer, P., Ducourtieux, C., Jouany, C., Theau, J.P., & Viegas, J. 2009. Modelling above-ground herbage mass for a wide range of grassland community types. *Ecological Modelling* 220: 209–225.

Dwyer, J.M., Hobbs, R.J., & Mayfield, M.M. 2013. Specific leaf area responses to environmental gradients through space and time. *Ecology* 95: 399–410.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., & Weisser, W.W.

2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology* 11: 473–485.

Flanagan, L.B., & Johnson, B.G. 2005. Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology* 130: 237–253.

Fornara, D.A., & Tilman, D. 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. *Journal of Ecology* 96: 314–322.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.

Gerhold, P., Price, J.N., Püssa, K., Kalamees, R., Aher, K., Kaasik, A., & Pärtel, M. 2013. Functional and phylogenetic community assembly linked to changes in species diversity in a long-term resource manipulation experiment. *Journal of Vegetation Science* 24: 843–852.

Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science* 17: 255–260.

Gross, N., Börger, L., Soriano-Morales, S.I., Le Bagousse-Pinguet, Y., Quero, J.L., García-Gómez, M., Valencia-Gómez, E., & Maestre, F.T. 2013. Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. *Journal of Ecology* 101: 637–649.

Gross, N., Kunstler, G., Liancourt, P., De Bello, F., Suding, K.N., & Lavorel, S. 2009. Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology* 23: 1167–1178.

Gross, N., Suding, K.N., & Lavorel, S. 2007. Leaf dry matter content and lateral spread predict response to land use change for six subalpine grassland species. *Journal of Vegetation Science* 18: 289–300.

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., & Bruelheide, H. 2017a. Drivers of intraspecific trait variation of grass and forb species in German meadows and pastures. *Journal of Vegetation Science* 28: 705–716.

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., & Bruelheide, H. 2017b. Predicting individual plant performance in grasslands. *Ecology and Evolution* 7: 8958–8965.

Hunt, R., & Cornelissen, J.H.C. 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist* 135: 395–417.

Jäger, E., & Werner, K. 2001. *Exkursionsflora von Deutschland, Bd.4, Gefäßpflanzen, Kritischer Band*. Spektrum Akademischer Verlag.

Jandt, U., & Bruelheide, H. 2012. German Vegetation Reference Database (GVRD). *Biodiversity & Ecology* 4: 355–355.

Kelemen, A., Török, P., Valkó, O., Deák, B., Tóth, K., & Tóthmérész, B. 2015. Both facilitation and limiting similarity shape the species coexistence in dry alkali grasslands. *Ecological Complexity* 21: 34–38.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. m., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. g., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W. a., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. j., Tackenberg, O., Wilmann, B., Cornelissen, J. h. c., Eriksson, O., Garnier, E., & Peco, B. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.

Klotz, S., Kühn, I., & Durka, W. 2002. *Biolflor: eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland*. Bundesamt für Naturschutz, Bonn.

Knops, J.M., & Reinhart, K. 2000. Specific leaf area along a nitrogen fertilization gradient. *The American Midland Naturalist* 144: 265–272.

Kuznetsova, A., Brockhoff, P.B., & Christensen, R.H.B. 2013. Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-0.

Laanbroek, H.J. 1990. Bacterial cycling of minerals that affect plant growth in waterlogged soils: a review. *Aquatic Botany* 38: 109–125.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A., & Mayfield, M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters* 13: 76–86.

Lienin, P., & Kleyer, M. 2011. Plant leaf economics and reproductive investment are responsive to gradients of land use intensity. *Agriculture, Ecosystems & Environment* 145: 67–76.

Lienin, P., & Kleyer, M. 2012. Plant trait responses to the environment and effects on ecosystem properties. *Basic and Applied Ecology* 13: 301–311.

Lorentzen, S., Roscher, C., Schumacher, J., Schulze, E.-D., & Schmid, B. 2008. Species richness and identity affect the use of aboveground space in experimental grasslands. *Perspectives in Plant Ecology, Evolution and Systematics* 10: 73–87.

Lyu, S., Liu, X., Venail, P., & Zhou, S. 2017. Functional dissimilarity, not phylogenetic relatedness, determines interspecific interactions among plants in the Tibetan alpine meadows. *Oikos* 126: 381–388.

Ma, S., Baldocchi, D.D., Mambelli, S., & Dawson, T.E. 2011. Are temporal variations of leaf traits responsible for seasonal and inter-annual variability in ecosystem CO2 exchange? *Functional Ecology* 25: 258–270.

MacArthur, R., & Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101: 377–385.

Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. da S., Soussana, J.-F., & Louault, F. 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist* 196: 497–509.

Mayfield, M.M., & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.

McIntyre, S. 2008. The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. *Agriculture, Ecosystems & Environment* 128: 251–258.

Mildén, M., Münzbergová, Z., Herben, T., & Ehrlén, J. 2006. Metapopulation dynamics of a perennial plant, Succisa pratensis, in an agricultural landscape. *Ecological Modelling* 199: 464–475.

Nakagawa, S., & Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.

Oesterheld, M., & McNaughton, S.J. 1991. Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* 85: 305–313.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. 2015. *vegan: Community Ecology Package*.

Ordoñez, J.C., Van Bodegom, P.M., Witte, J.-P.M., Wright, I.J., Reich, P.B., & Aerts, R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography* 18: 137–149.

Patty, L., Halloy, S.R.P., Hiltbrunner, E., & Körner, C. 2010. Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes. *Flora - Morphology, Distribution, Functional Ecology of Plants* 205: 695–703.

Poschlod, P., Kleyer, M., Jackel, A.-K., Dannemann, A., & Tackenberg, O. 2003. BIOPOP — A database of plant traits and internet application for nature conservation. *Folia Geobotanica* 38: 263–271.

R Core Team. 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rao, C.R. 1982. Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology* 21: 24–43.

Rasband, W.S. 2008. ImageJ. *http://rsbweb.nih.gov/ij/*

Rota, C., Manzano, P., Carmona, C.P., Malo, J.E., & Peco, B. 2017. Plant community assembly in Mediterranean grasslands: understanding the interplay between grazing and spatio-temporal water availability. *Journal of Vegetation Science* 28: 149–159.

Sala, O.E., Chapin, F.S., Iii, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Scherber, C., Milcu, A., Partsch, S., Scheu, S., & Weisser, W.W. 2006. The effects of plant diversity and insect herbivory on performance of individual plant species in experimental grassland. *Journal of Ecology* 94: 922–931.

Schittko, C., Hawa, M., & Wurst, S. 2014. Using a multi-trait approach to manipulate plant functional diversity in a biodiversity-ecosystem function experiment. *PLoS ONE* 9: e99065.

Schmidtke, A., Rottstock, T., Gaedke, U., & Fischer, M. 2010. Plant community diversity and composition affect individual plant performance. *Oecologia* 164: 665–677.

Schwinning, S., & Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113: 447–455.

Shipley, B., Vile, D., & Garnier, É. 2006. From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science* 314: 812–814.

Socher, S.A., Prati, D., Boch, S., Müller, J., Klaus, V.H., Hölzel, N., & Fischer, M. 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *Journal of Ecology* 100: 1391–1399.

Spehn, E.M., Joshi, J., Schmid, B., Diemer, M., & Körner, C. 2000. Above-ground resource use increases with plant species richness in experimental grassland ecosystems. *Functional Ecology* 14: 326–337.

Thompson, K., Petchey, O.L., Askew, A.P., Dunnett, N.P., Beckerman, A.P., & Willis, A.J. 2010. Little evidence for limiting similarity in a long-term study of a roadside plant community. *Journal of Ecology* 98: 480–487.

Thorne, M.A., & Frank, D.A. 2009. The effects of clipping and soil moisture on leaf and root morphology and root respiration in two temperate and two tropical grasses. *Plant Ecology* 200: 205–215.

Tilman, D., Isbell, F., & Cowles, J.M. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* 45: 471–493.

Turner, C.L., Seastedt, T.R., & Dyer, M.I. 1993. Maximization of aboveground grassland production: The role of defoliation frequency, intensity, and history. *Ecological Applications* 3: 175–186.

Veihmeyer, F.J., & Hendrickson, A.H. 1950. Soil moisture in relation to plant growth. *Annual Review of Plant Physiology* 1: 285–304.

Vesk, P.A., Warton, D.I., & Westoby, M. 2004. Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos* 107: 72–89.

Violle, C., Garnier, E., Lecoeur, J., Roumet, C., Podeur, C., Blanchard, A., & Navas, M.-L. 2009. Competition, traits and resource depletion in plant communities. *Oecologia* 160: 747–755.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., & LeRoy Poff, N. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* 13: 267–283.

Weigelt, A., Weisser, W.W., Buchmann, N., & Scherer-Lorenzen, M. 2009. Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. *Biogeosciences* 6: 1695–1706.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2403–2413.

Weiher, E., & Keddy, P.A. 1995. Assembly rules, null models, and trait dispersion: New questions from old patterns. *Oikos* 74: 159.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., & Wright, I.J. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

Wilson, S.D., & Tilman, D. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia* 88: 61–71.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

3.7 Acknowledgements

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3.8 Supplementary Information

Additional Supplementary Information of this chapter may be found on the attached CD:

Table S3.1: Differences in trait values between the different scenarios.

Table S3.2: Trait values (SLA, LDMC, height, leaf anatomy, leaf persistence, leaf distribution, physical defense and vegetative reproduction), scenario information, survival rate and RGR height 4 – 5 of the 130 transplant species.

Table S3.3: Number of included plots for calculating the mean of climatic variables.

Table S3.4: Results of extended variance partitioning analyses.

Table S3.5: Final models and their relative proportion of variances explained by the random factors.

Table S3.6: Final models that were improved with respect to AIC by adding climate variables.

Figure S3.1: Principal coordinate analysis (PCoA) on multi-trait distances based on 11 traits.

Figure S3.2: Mean climate data during the time of our experiment.

Chapter 4 – Trait-performance relationships of grassland plant species differ between common garden and field conditions

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4.1 Abstract

The way functional traits affect growth of plant species may be highly context-specific. We asked which combinations of trait values are advantageous under field conditions in managed grasslands as compared to conditions without competition and land use. In a two-year field experiment, we recorded the performance of 93 species transplanted into German grassland communities differing in land-use intensity and into a common garden, where species grew unaffected by land-use under favorable conditions regarding soil, water and space. The plants' performance was characterized by two independent dimensions (relative growth rates (RGR) of height and leaf length versus aboveground biomass and survival) that were differently related to the eight focal key traits in our study (leaf dry matter content (LDMC), specific leaf area (SLA), height, leaf anatomy, leaf persistence, leaf distribution, vegetative reproduction and physical defense). We applied multivariate procrustes analyses to test for the correspondence of the optimal trait-performance relationship between field and common garden conditions. RGRs were species-specific and species ranks of RGRs in the field and the common garden were significantly correlated. Different traits explained the performance in the field and the common garden; for example, leaf anatomy traits explained species performance only in the field, whereas plant height was found to be only important in the common garden. The ability to reproduce vegetatively, having leaves that are summer-persistent and with high leaf dry matter content (LDMC) were traits of major importance under both settings, albeit the magnitude of their influence differed slightly between the field and the common garden experiment. All optimal models included interactions between traits, pointing out the necessity to analyze traits in combination. The differences between field and common garden clearly demonstrate context dependency of trait-based growth models, which results in limited transferability of favorable trait combinations between different environmental settings.

Key-words: Common garden experiment, land use, managed grassland, plant functional traits, plant performance, relative growth rates

4.2 Introduction

Plant functional traits are connected with species differences in productivity and performance (Poorter & Bongers 2006; Enquist et al. 2007; Comas et al. 2013). Moreover, it has been shown that traits strongly depend on the environment (Díaz et al. 1998; Bruelheide et al. 2018). Therefore, different combinations of traits may be advantageous under different environmental conditions. For example, under field conditions in managed grasslands other traits may be important as compared to conditions without land use and competition. However, it is still poorly understood how trait-performance relationships of different plant species vary under different environmental settings.

Differences in relative growth rates (RGRs) reflect species-specific adaptations to abiotic factors such as climate, water-, nutrient and light availability as well as biotic factors such as competition, pathogens or herbivory (Poorter 1989; Bultynck et al. 1999). Stress-tolerant species are considered to have low potential RGRs suitable for environments with low nutrient supply, whereas species with high potential RGRs are superior in highly productive habitats (Grime & Hunt 1975; Lambers & Poorter 1992). However, RGR of the same species varies with environment.

Under common garden conditions, species can be grown under favorable conditions regarding soil and water and growth is unaffected by mowing, grazing or negative species interactions such as competition. RGRs under these conditions can be expected to be higher and approach the species' potential growth rates, compared to natural field conditions.

Under controlled conditions, species RGRs are expected to be mainly correlated with leaf traits (Grime et al. 1997). High leaf dry matter content (LDMC) of plant species indicates low productive species, whereas high specific leaf area (SLA) is considered characteristic of competitive species (Suter & Edwards 2013). For example, in a greenhouse experiment high potential growth rates were found to be correlated with high SLA (Poorter & Remkes 1990; Hunt & Cornelissen 1997), which however is not universally true, as was demonstrated for woody species (Böhnke & Bruelheide 2013; Paine et al. 2015). This contrast between high LDMC and high SLA that distinguishes slow from fast growing species is known as the leaf economics spectrum (Wright et al. 2004).

In contrast, under realistic field conditions in managed grasslands abiotic and biotic factors can be expected to reduce species' growth rates. Disturbances caused by land-use have strong influences on species growth (Deng et al. 2014; Herz et al. 2017). Furthermore, resources have to be shared with other species or defended against herbivores, which both can limit growth rates (Lind et al. 2013). However, plants were also found to increase growth rates to compensate for biomass loss from grazing (Zheng et al. 2014). Under realistic field conditions other traits may be advantageous than in interaction-free environments. For example, under high grazing pressure plants may grow smaller (Lienin & Kleyer 2012), and/ or have chemical and physical defense traits to avoid or reduce herbivory (Hanley et al. 2007). Disturbances by trampling may benefit plants with clonal growth organs as they are able to invade much faster into disturbed areas (Bullock et al. 2001; Klimešová et al. 2008). Competition between plant species may also favor species with certain traits, for example it has been reported that under competition for nutrients plants grow longer roots or under competition for light plants grow taller (Craine & Dybzinski 2013). Roscher et al. (2011) found that a combination of monoculture biomass, plant growth rates and resource-use traits associated with nutrient and light acquisition best explained non-legume species performance in a grassland biodiversity experiment.

In order to analyze the effects of different environmental settings on trait-performance relationships we conducted two different experiments: A field experiment with impacts of land-use and biotic interactions within the community and a common garden experiment where individual plants grew without land-use and communities. For the field experiment we established a large transplant experiment in mesic grasslands differing in land-use intensity, management and species composition in the three regions Schorfheide, Hainich and Schwäbische Alb of Germany. 2592 individuals of 130 different grassland species new to the communities were planted into 54 grassland plots and monitored for growth over 2 years. Parallel to this field experiment, all 130 species were also grown in the common garden experiment at the Botanical Garden of the Martin-Luther-University of Halle-Wittenberg in Germany. In this study we focused on the performance (biomass, survival and RGR) of 93 species out of the 130 planted species, because of mortality of some species during the two-years observation time. To disentangle the correlations between performance and traits of plant species we compared the performance of individuals grown under natural conditions, with the performance of the same species grown under common garden conditions, where species grew under favorable conditions concerning soil, water and competition regimes. In this context we tested two main hypotheses:

1. We expected that growth rates are highly species-specific and that abiotic and biotic factors under field conditions reduce relative growth rates (RGRs), but result in similar overall patterns compared to RGRs in the common garden. In particular, we hypothesized that the species' RGRs observed in the field experiment correspond to the RGRs when grown under common garden conditions.

2. Secondly, we hypothesized that the magnitude of growth and performance are correlated with different plant traits in field and common garden. In particular, we expected strong correlations with traits of the leaf economics spectrum (LES) (Wright et al. 2004) in the common garden experiment, whereas the traits vegetative reproduction and physical defense should be more relevant in the field experiment.

4.3 Methods

Field experiment

Different grassland species were planted into managed grassland communities, making use of the network of experimental plots in the German Biodiversity Exploratories (Fischer et al. 2010). In each of the three study regions (Schwäbische Alb, South Germany; Hainich, Central Germany and Schorfheide, Northeast Germany) 18 grassland plots were selected, each six of them representing the three main land-use types (meadow, pasture, mown pasture). The plots differed in land-use intensity, species richness and functional diversity. Each plot was divided into eight subplots of 1 x 1 m which each were planted with six phytometers of six different species, selected from a total pool of 130 species. The six species planted in every subplot were selected specifically based on every plot's species composition, and thus differed among plots. Detailed information of the experimental design and the different planting scenarios is reported in Breitschwerdt et al. (2015). The experimental design resulted in different amounts of individuals per species across all plots. In total, we planted 2592 individuals (3 Exploratories (= regions), 18 plots per Exploratory, 8 subplots per plot, 6 plant individuals per subplot). After being planted in April 2012, the phytometers were monitored regularly for growth and survival in 2012 in April, May, July, August and October and in 2013 in May, June/July and September. At each date, we recorded height, aboveground plant projection area calculated from two diameters using the ellipse formula, length of leaves and number of leaves. At the last monitoring date in September 2013, aboveground biomass of all surviving plants was harvested, dried and weighed.

Common garden experiment

All 130 species used for transplantations in the field were also planted in a common garden experiment at the Botanical Garden of the Martin-Luther University Germany in a threefold repetition in April 2012. In each of three gardening patches, rows of 12 individuals each with 0.25 cm distance to each other were established with one individual per plant species. All species were assigned randomly to their planting positions. The experiment was regularly weeded and watered. Snails and slugs were removed from the patches. Furthermore, we installed mollusk barriers consisting of metal sheets, buried 0.1 m belowground and extending 0.2 m aboveground to exclude slugs and snails. In addition, the metal was bent outward and lubricated with lemon-based mollusk repellent (IRKA® "Schneckenabwehrpaste", Germany). In addition, we spread slug pellets (Neudorff Ferramol® Schneckenkorn, Germany). Despite these exclosures, mollusks still caused damage on some plants. All phytometers were monitored for growth and survival in 2012 in April, May, June and August and in 2013 in May and July/August. The same growth variables (height, aboveground plant projection area, leaf length and number of leaves) were recorded as in the field experiment. Aboveground biomass was harvested at the end of the vegetation period in 2013.

Data analysis

Relative growth rates (RGR) were calculated for every individual plant according to formula (1) (Hunt & Cornelissen 1997; Hoffmann & Poorter 2002), where M is any growth variable and t is the time span in weeks between the two monitoring dates 1 and 2.

$$(1) \qquad RGR_i = \frac{\ln(M_2) - \ln(M_1)}{t_2 - t_1}$$

We calculated RGR mean values for all variables (height, plant projection area, leaf length and number of leaves) per species. Therefore, we first aggregated the different time spans of the RGR of the both experiments per species and variable and then formed one RGR mean value per species and variable over all time spans (six time spans in the field and five in the common garden). Survival was calculated by taking the percentage of individuals per species that survived until the end of the experiments in relation to the amount of individuals per species planted at the start of the experiment. Total biomass at the end of the experiments in 2013 was aggregated to mean value per species and then log transformed to achieve normal distribution. As in both experiments (field and common garden) different species survived until the end, data on some of the 130 species had to be discarded, yielding to a total of 93 remaining species. The numbers of individuals that were included in the mean value calculations for each of the 93 species are shown in Supporting Information Table S4.2.

For the 93 species we compiled a full trait matrix of eight traits (SLA, LDMC, height, leaf anatomy (succulent, scleromorphic, mesomorphic, hygromorphic, helomorphic and hydromorphic), leaf persistence (in spring, summer or overwinter green or evergreen), leaf distribution (evenly spread leaves, rosettes or semi-rosettes), physical defense and vegetative reproduction). Trait values were measured in 2011 (Breitschwerdt et al. 2015) and complemented from the databases LEDA (Kleyer et al. 2008), BIOPOP (Poschlod et al. 2003), BIOLFLOR (Klotz et al. 2002) and Rothmaler (Jäger & Werner 2001). The species mean values of all traits are provided in Supporting Information Table S4.1. As none of the 93 species had hydromorphic leaves or leaves that are persistent over winter, these trait states were excluded from calculations. Furthermore, we excluded leaf persistence evergreen and leaf distribution evenly spread leaves from analyses to avoid redundant information.

PCA and Procrustes analyses

We performed principal component analyses (PCAs) with the vegan package of R (Oksanen et al. 2015). We based the calculations on all species-mean performance variables (mean RGR of height, plant projection area, leaf length and number of leaves, biomass and survival rates), and carried out PCAs separately for the field experiment and the common garden experiment. These performance PCAs of field and common garden observations were compared to a PCA based on all species traits, using procrustes rotation (procrustes function in vegan). Applied to the pair of performance and trait PCAs the procedure rotates and scales the PC scores of the second PCA to maximally fit those of the first target PCA, minimizing the sum of squared differences. To test whether different traits were relevant in the field and the common garden, we then searched for an optimized corresponding trait PCA that best explained performance, using a forward selection of traits, also including two-way interaction of traits. This optimization procedure was carried out separately for the field and common garden PCA. We developed a stepwise forward selection by adding that trait or trait interaction to the trait PCA that resulted in the best correlation in a symmetric procrustes rotation between the performance and trait matrix. The correlation coefficient was obtained by the protest command of the procrustes analyses in vegan package of R (Oksanen et al. 2015), using 9999 permutations. We run this forward selection until further addition of traits or trait interactions did no longer improve the procrustes correlation coefficient between each of the two performance PCAs and the corresponding trait PCA. We also considered forward selection of predictors using redundancy analyses (RDAs), but in comparison to the procrustes approach found RDA to be too greedy, resulting in much longer final trait lists. Furthermore, the automated forward procedure (ordistep or ordiR2step in vegan) could not be used, because the trait states of the same trait had to enter the model as a group (e.g. leaf anatomy, leaf persistence and leaf distribution), also interactions with the different trait states had be handled as group and once discarded traits had be considered in subsequent steps. Therefore, we considered procrustes analyses the most appropriate way to select the best combination of predictor traits.

Univariate analyses

In addition, we employed ordinary linear regression models, relating the final traits to all performance variables of the field and the common garden experiment. Furthermore, the species' ranks of each performance variable in both experiments (field and common garden) were compared using a Spearman correlation test.

4.4 Results

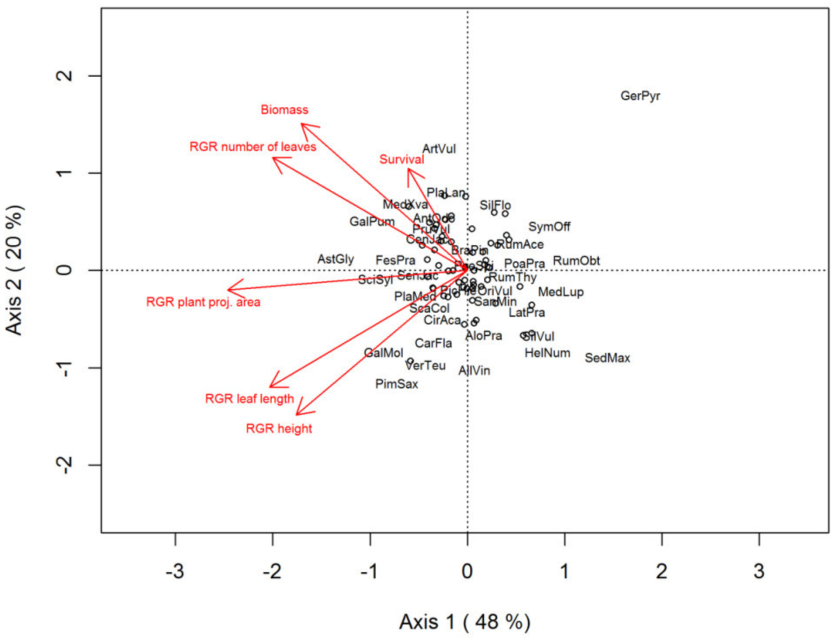
All performance variables except RGR plant projection area showed a strong correlation between the mean values of the 93 study species obtained in the field compared to the common garden experiment according to Spearman's rank correlation coefficient (see Supporting Information Table S4.4). The best match was encountered for biomass production (r_s = 0.42), followed by RGR leaf length and survival (each 0.32), RGR height (0.28) and RGR number of leaves (0.22).

Principal components analyses (PCA) of all species based on mean relative growth rates of height, plant projection area, leaf length, number of leaves, biomass and survival showed very similar relationships between performance variables in the field and in the common garden experiment (Fig. 4.1 a and b). While in both PCAs, the first axis reflected relative growth rates, in the field they were mostly related to projection area and in the common garden to leaf number as well as to biomass. The second PCA axis both in the field and common garden was characterized by positive loadings of survival, biomass and RGR of number of leaves and negative ones for increasing values of RGR of height, leaf length and plant projection area(Fig. 4.1 a and b).

Species with lowest scores on the first PCA axis, and thus, highest performance, were *Astragalus glycyphyllos* (AstGly), *Galium pumilum* (GalPum) and *Scirpus sylvaticus* (SciSyl) in the field and *Medicago x varia* (MedXva), *Galium pumilum* (GalPum) and *Galium mollugo* (GalMol) the common garden (Fig. 4.1a and b, for scores of all species see Supporting Information Table S4.3). Low scores on the second PCA axis, and thus high RGR in height, leaf number or projection area, were found for *Pimpinella saxifraga* (PimSax), *Allium vineale* (AllVin), *Veronica teucrium* (VerTeu) and *Galium mollugo* (GalMol) in the field and for

Pimpinella saxifraga (PimSax), *Rumex thyrsiflorus* (RumThy) and *Pastinaca sativa* (PasSat) in the common garden experiment (Fig. 4.1a and b).

a) Field experiment



b) Common garden experiment

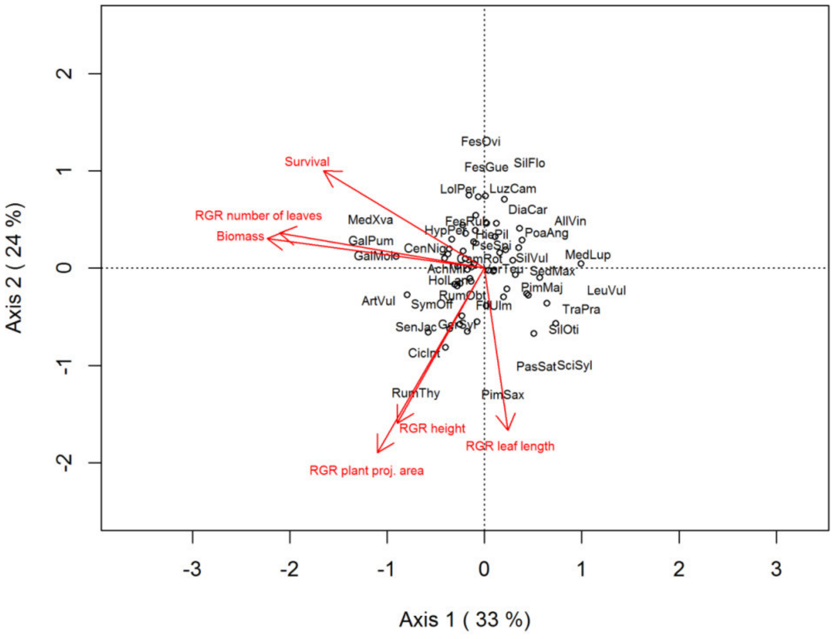


Figure 4.1 PCA of 93 species (abbreviations see attached CD Supporting information Table S4.1) based on mean relative growth rates (RGR) of height, plant projection area, leaf length, number of leaves, biomass and survival a) in the field experiment and b) in the common garden experiment. Explained variance of axes is given in percentage. Eigenvalues of the first two PCA axes in a) were 2.88 and 1.18 and in b) 1.99 and 1.42.

Comparing the performance PCAs of the field and the common garden experiment with procrustes analyses resulted in a correlation of 0.31 (p = 0.0003, Table 4.1). The PCA of all traits showed that the dimensions of 14 traits were not well captured by only one or two axes, which explained 17% and 13% of variation in trait values (Fig. S4.1). Thus, we used the whole ordination of traits as predictor for performance. In both PCAs of performance in the field and in the common garden the procrustes correlation with the PCA based on all traits was insignificant (Table 4.1), showing the necessity to eliminate uninformative traits.

Table 4.1 Results of Procrustes analyses based on the principal component analyses (PCAs) of all species´ performance variables (RGR of height, plant projection area, leaf length and number of leaves, biomass and survival) and traits. Traits in the field experiment were LDMC, leaf anatomy (succulent, scleromorphic, mesomorphic, hygromorphic, helomoprhic), leaf persistence (green in spring or summer), vegetative reproduction and the three interaction traits between LDMC with leaf anatomy succulent, leaf persistence green in summer and vegetative reproduction. Traits in the common garden experiment were LDMC, height, leaf persistence (green in spring green or in summer), vegetative reproduction and the interaction between LDMC and vegetative reproduction.

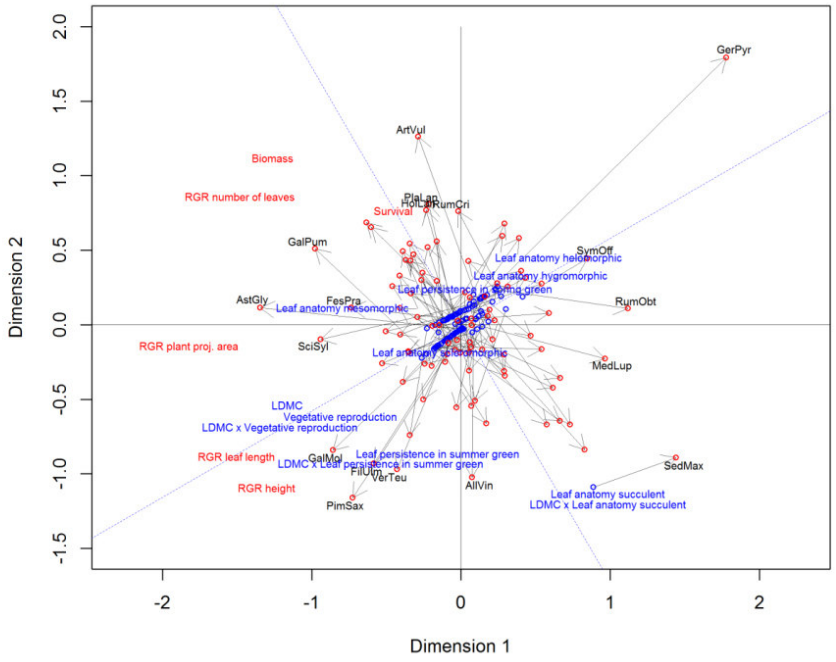
	Correlation in a symmetric procrustes rotation	Significance
PCA performance field vs. PCA performance CG	0.3134	0.0003
PCA performance field vs. PCA all traits	0.144	0.2717
PCA performance CG vs. PCA all traits	0.185	0.083
PCA performance field vs. PCA traits optimized for field	0.3106	0.0028
PCA performance CG vs. PCA traits optimized for CG	0.3673	0.0001
PCA performance field vs. PCA traits optimized for CG	0.139	0.3011
PCA performance CG vs. PCA traits optimized for field	0.1683	0.1438

The optimization process of the trait PCA to explain performance in the field experiment resulted in 12 traits (LDMC, leaf anatomy (5 categories), leaf persistence (2 categories), vegetative reproduction and the three interaction traits LDMC with anatomy succulent, persistence summer and vegetative reproduction, Fig. 4.2a). The optimized trait PCA explaining common garden performance contained six traits (LDMC, height, leaf persistence (2 categories), vegetative reproduction and the interaction of LDMC with vegetative reproduction (Fig. 4.2b). The procrustes correlation coefficients between the performance PCAs for field or common garden data and the corresponding trait PCA based on the optimized set of traits were 31% and 37%, respectively (p = 0.028 and 0.0001, Table 4.1). However, the reciprocal application of trait PCA optimized for the field performance PCA to the common garden performance PCA and vice versa resulted in insignificant correlations (Table 4.1).

The trait-wise analyses of all performance variables in separate linear regression models (Table 4.2) reflected the results of the procrustes rotations (Fig. 4.2). For example, relative growth rates of leaf length and height based on field observations were positively correlated with LDMC, vegetative reproduction and the interaction between the two (Fig. 4.2a). In accordance with the linear models, relative growth rate of height was also correlated with persistence in summer and its interaction with LDMC, relative growth rate of plant projection area with leaf anatomy mesomorphic (Fig. 4.2a). Differences among predictor traits between the procrustes analyses of the field and the common garden were LDMC, vegetative reproduction and their interaction which were positively correlated with relative growth rates of plant projection area, height and leaf length in the field (Fig. 4.2a), but negatively in the common garden (Fig. 4.2b). In addition, there were positive correlations of survival with LDMC and the interaction between LDMC and vegetative reproduction in the common garden (Fig. 4.2b) but not in the field (Fig. 4.2a).

The comparison of the traits identified by the final procrustes models (Table 4.1) and the significant univariate relationships with performance variables (Table 4.2) reveals that multivariate relationships are not equally captured by univariate statistics. In the field experiment, RGRs of leaf length (Fig. 4.3a) and plant projection area (Fig. 4.3b) and survival were positively correlated with vegetative reproduction (Table 4.2). Furthermore, RGRs of plant projection area and survival were positively correlated with mesomorphic anatomy. RGR of height was positively correlated both with leaf persistence in spring and the interaction between LDMC and leaf persistence in summer (Table 4.2), showing that summer-green species had overall higher mean RGRs of height with increasing LDMC in the field. Biomass and RGR number of leaves correlated negatively with succulent anatomy and the interaction of LDMC with succulent anatomy (Table 4.2). In the common garden experiment, the finally selected traits displayed significant linear relationships with almost all performance variables except for RGR plant projection area (Table 4.2). Highest correlations were found between biomass and the plant height, showing that under unconstrained conditions biomass increased with potential plant height (Fig. 4.3c). Similarly, RGR of leaf length was also positively correlated with plant height (Table 4.2). Negative correlations were found between RGR height and the interaction of LDMC and vegetative reproduction, showing that species with vegetative reproduction decreased in RGR height with increasing LDMC (Fig. 4.3d). The single predictors LDMC and vegetative reproduction both had a negative impact on RGR height, while survival and RGR number of leaves increased with increasing LDMC and for species with vegetative reproduction (Table 4.2).

a) Field experiment



b) Common garden experiment

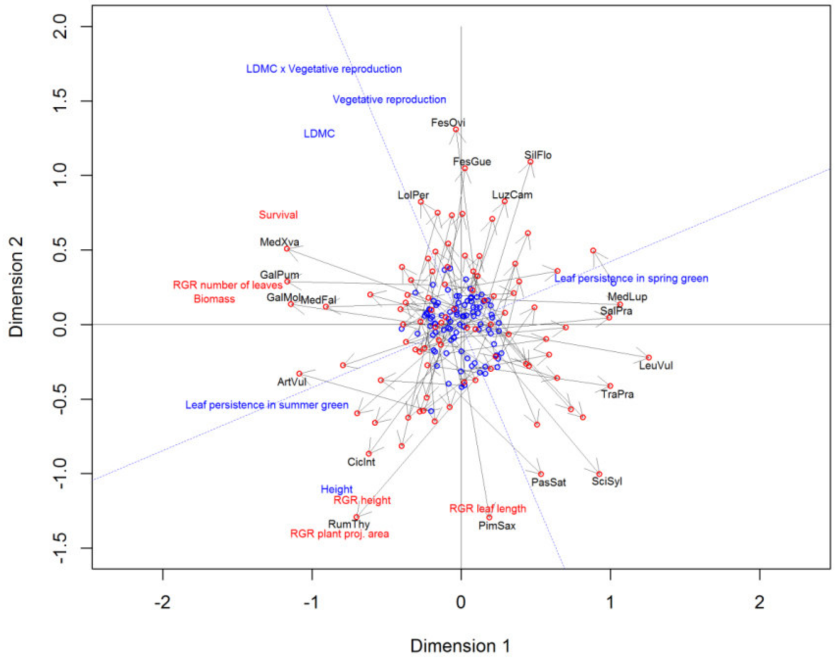


Figure 4.2 Procrustes analyses of PCAs: a) PCA of traits in the field rotated to match PCA of performance in the field; b) PCA traits in the common garden rotated to match PCA performance in the common garden. For the field experiment the optimized remaining traits were: LDMC, leaf anatomy (succulent, scleromorphic, mesomorphic, hygromorphic and helomorphic), leaf persistence (persistent in spring and persistent in summer), vegetative reproduction and the three interaction traits between LDMC with leaf anatomy succulent, persistence summer and vegetative reproduction. For the common garden experiment the optimized remaining traits were: LDMC, height, leaf persistence (persistent in spring and persistent in summer), vegetative reproduction and the interaction between LDMC and vegetative reproduction. Arrows show procrustes errors (longer arrows = higher errors) calculated by rotating species in 9999 permutations and comparing species positions of two PCA until finding positions with least differences. For abbreviations of species names see Supporting Information Table S4.1. Only species with highest scores on axes (above the 95th percentile or below the 5th percentile) are shown.

Table 4.2 Correlations between optimal traits found for each experiment (field and common garden) and the respective performance variables (biomass, survival, RGR of height, plant projection area, leaf length and number of leaves) of each experiment. Final traits were correlated in lm models in R with performance variables of field and common garden. Values are Pearson correlations coefficients. Significances are indicated with *. Significance levels are as following: from 0 to 0.001 = ***, from 0.001 to 0.01= **, from 0.01 to 0.05 = *. Grey marked correlations are shown in Fig. 4.3.

	Performance variables					
Traits field	**Biomass**	**Survival**	**RGR of height**	**RGR of plant projection area**	**RGR of leaf length**	**RGR of number of leaves**
LDMC	-0.099	0.048	0.097	0.119	0.143	0.152
Leaf anatomy succulent	-0.356 ***	-0.171	-0.198	-0.182	-0.112	-0.285 **
Leaf anatomy scleromorphic	-0.022	-0.100	0.112	-0.001	0.050	0.038
Leaf anatomy mesomorphic	0.170	0.206 *	0.021	0.210 *	0.086	0.173
Leaf anatomy hygromorphic	-0.136	0.205 *	-0.028	-0.174	-0.033	-0.145
Leaf anatomy helomorphic	0.144	-0.053	-0.061	0.016	-0.065	-0.018
Leaf persistence in spring green	-0.012	-0.162	0.262 *	-0.077	-0.020	-0.114
Leaf persistence in summer green	-0.095	-0.153	0.196	0.179	0.201	0.115
Vegetative reproduction	0.000	0.218 *	0.110	0.279 **	0.301 **	0.133
LDMC x Leaf anatomy succulent	-0.356 ***	-0.171	-0.198	-0.182	-0.112	-0.285 **
LDMC x Leaf persistence in summer green	-0.097	-0.105	0.206 *	0.176	0.188	0.128
LDMC x Vegetative reproduction	-0.055	0.184	0.062	0.203	0.215 *	0.179
Traits common garden						
LDMC	0.089	0.216 *	-0.214 *	-0.111	-0.096	0.292 **
Height	0.348 ***	0.162	0.162	0.131	0.255 *	-0.064
Leaf persistence in spring green	-0.185	0.057	-0.051	-0.097	-0.131	-0.256 *
Leaf persistence in summer green	0.169	0.102	0.198	0.100	0.151	0.117
Vegetative reproduction	0.035	0.157	-0.274 **	-0.044	-0.124	0.137
LDMC x Vegetative reproduction	0.117	0.264 *	-0.330 **	-0.097	-0.138	0.280 **

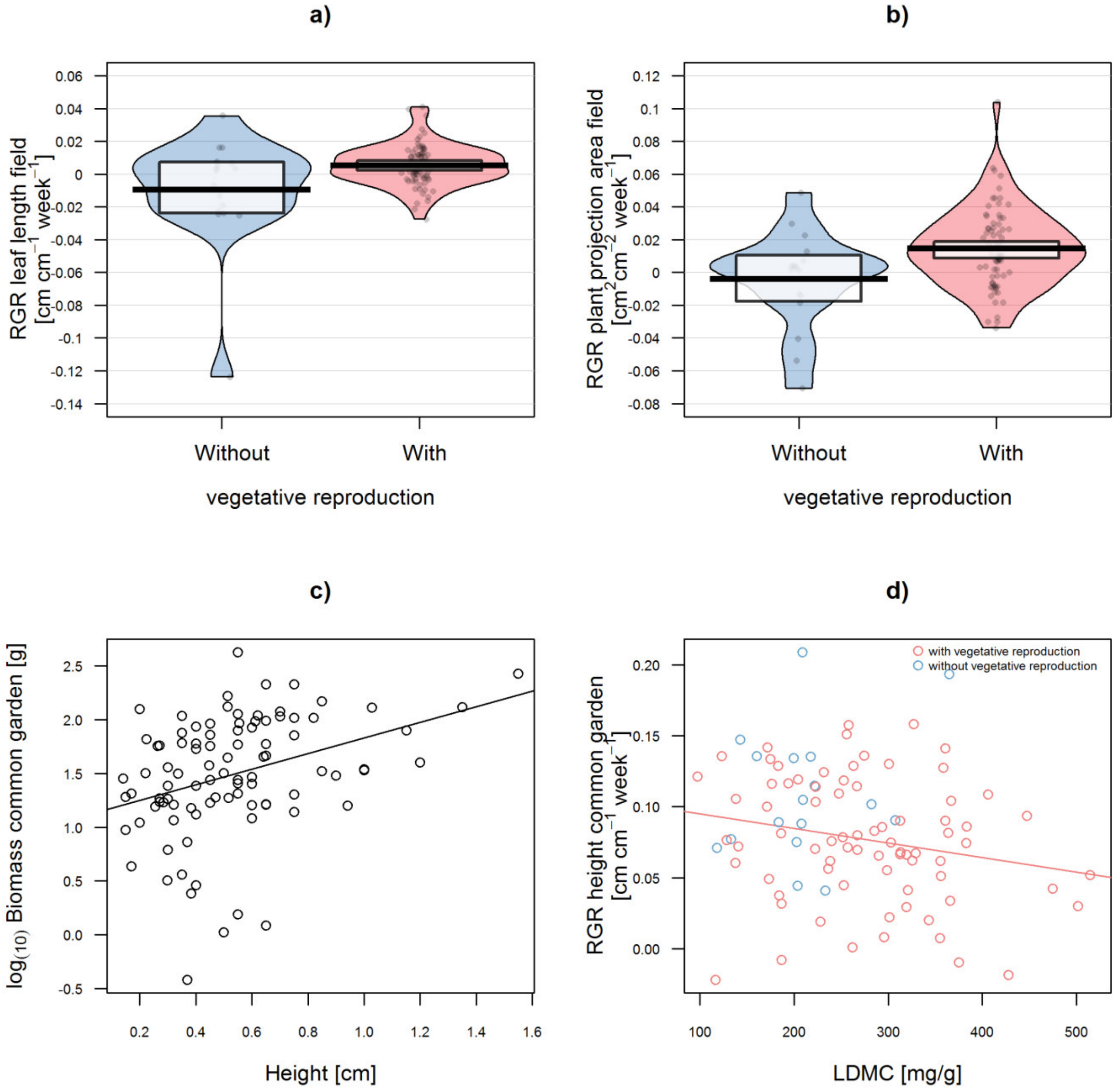


Figure 4.3 Correlations of a) RGR leaf length in the field with vegetative reproduction, b) RGR plant projection area in the field with the vegetative reproduction, c) biomass in the common garden with the trait height and d) RGR height in the common garden with the interaction trait LDMC-vegetative reproduction. Final traits were correlated in lm models with performance variables of field and common garden, respectively. The graphs show predictor variables with high correlation coeffients (for significance levels see Table 4.2).

4.5 Discussion

As expected, growth rates in the field were much smaller than under common garden conditions. Most aspects of growth as well as survival were species-specific to some degree, as revealed by the significant rank correlations between field and common garden variables. These findings are consistent with the high congruence of the two performance PCAs based on field and common garden observations. Our first hypothesis stated that the species' RGRs observed in the field experiment correspond to the species' RGRs grown under common garden conditions, which was clearly confirmed by our findings. In this aspect, our study is in accordance with results of previous studies that describe only minor impacts of different environments on interspecific rankings (Garnier et al. 2001; Roche et al. 2004; Al Haj Khaled et al. 2005; Kazakou et al. 2014). For example, Meziane & Shipley (1999) described that ranks of net assimilation rates, which are related to relative growth rates, were not much affected by differences in light and nutrient supply. Performance data of species obtained from garden experiments are therefore good predictors for performance under field conditions.

Procrustes optimization identified different trait constellations that explained performance in both experiments, thus confirming our second hypothesis. The differences in the optimized trait combinations show that some species characteristics are only relevant under realistic management regimes and others under favourable garden conditions. Leaf anatomical traits were only important under field conditions, probably because they reflect the species' photosynthetic capacity and are directly connected with growth rates and indirectly with recovery from defoliation by land-use, which was irrelevant in the common garden. In contrast, potential height was only important in the common garden, where the plants could attain large sizes without being grazed or mown. There were even traits with opposing effects on growth. While the ability to reproduce vegetatively characterized slow-growing species with respect to RGR leaf length in the common garden (e.g. *Festuca ovina, F. guestfalica* and *Silene flos-cuculi*) this trait was characteristic of fast-growing species in the field (e.g. *Galium mollugo and Scirpus sylvaticus).* In the field experiment, species with vegetative reproduction displayed increased RGR of height, leaf length and plant projection area, while in the common garden experiment species with vegetative reproduction decreased in RGR. The different role of vegetative reproduction under different land-use regimes has also been reported from studies in population ecology. Johansen et al. (2016) reported that with decreasing grazing intensity clonal regeneration increased in importance of population growth rates of *Knautia arvensis*. These findings explain why the final sets of traits found for our two experiments were not interchangeable.

Nevertheless, there were also traits that played important roles under both field and common garden conditions. LDMC and the interaction between LDMC and vegetative reproduction as well as leaf persistence were relevant under both conditions. The key role of these traits was also reported by Gross et al. (2007) who found that LDMC and lateral spread were suitable predictors of growth under different nutrient, shade and clipping intensities. The importance of LDMC supported our expectation that LES traits are key predictors for performance. However, we found LDMC to be a better predictor for plant biomass production than SLA, as was pointed out also in previous studies (Kröber et al. 2015; Smart et al. 2017). More generally, leaf traits seem to be better predictors when based on mass rather than area (Osnas et al. 2013; Lloyd et al. 2013). Overall, LES traits became only meaningful in combination with other traits. The final trait models in our study all included the ability to reproduce vegetatively, confirming previous findings that LES traits alone are poor predictors for plant growth (Paine et al. 2015). Similarly, LES traits were found to have a subordinate role in community assembly as response to land-use. For example, Dirks et al. (2017) found that size and reproduction traits rather than leaf economic traits drove the composition of Mediterranean annual vegetation along a land-use intensity gradient. This emphasizes the general importance of traits concerning clonal growth and vegetative reproduction for plant performance (Klimešová et al. 2016).

Furthermore, the interactions of LDMC with summer-persistent leaves and succulent leaf anatomy were only relevant in the field. Thus, LDMC was not relevant for growth when species only had green leaves in spring, such as for *Allium vineale*. Similarly, a low LDMC did not translate into increased growth rate when the leaves were succulent, as for example in *Sedum maximum.* This combination of traits is characteristic for species with crassulacean acid metabolism (CAM), adapted to harsh and dry environments.

Against expectations, defense traits were not included in any final model, neither in the field nor in the common garden. These findings match the observations that community-weighted physical defense traits did not respond to the land-use gradient in the Biodiversity Exploratories (Plath & Bruelheide unpublished results), pointing to a prevalence of plant strategies to tolerate grazing rather than to avoid the grazing impact in these grasslands. Instead, and unexpectedly, leaf anatomical traits turned out to be drivers of growth. Leaf anatomy traits are related to light absorption and photosynthetic rates, aspects also captured by LES traits. Comparing mesomorphic and scleromorphic leaves, the former display a higher membrane permeability and stromal conductance, leading to a higher photosynthetic capacity (Tomás et al. 2013). However, scleromorphic leaves were not advantageous in the field because species with mesomorphic leaves regrow more easily after mowing and grazing under real-world land-use conditions. As the field experiment was conducted in three different regions of Germany and contained grassland plots of different management regimes of grazing and mowing, future studies should aim at analyzing trait differences for particular land use types.

In conclusion, our study showed that species-specific traits were capable to predict different dimensions of plant performance, characterized by relative growth rates and survival both under field and controlled common garden conditions. We found a prominent role of vegetative reproduction for plant performance, albeit with opposing effects under common garden and field conditions, and of LDMC. Importantly, additional traits and trait interactions modified plant performance under realistic field conditions. Thus, trait constellations and their interactions are not transferable across different environments. Overall, our study supports the necessity of including trait interactions into trait-based plant growth models.

4.6 Acknowledgements

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4.7 References

Al Haj Khaled, R., Duru, M., Theau, J.P., Plantureux, S., & Cruz, P. 2005. Variation in leaf traits through seasons and N-availability levels and its consequences for ranking grassland species. *Journal of Vegetation Science* 16: 391–398.

Böhnke, M., & Bruelheide, H. 2013. How do evergreen and deciduous species respond to shade?—Tolerance and plasticity of subtropical tree and shrub species of South-East China. *Environmental and Experimental Botany* 87: 179–190.

Breitschwerdt, E., Jandt, U., & Bruelheide, H. 2015. Do newcomers stick to the rules of the residents? Designing trait-based community assembly tests. *Journal of Vegetation Science* 26: 219–232.

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S.M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V.D., Schrodt, F., Mahecha, M.D., Peet, R.K., Sandel, B., van Bodegom, P., Altman, J., Alvarez Davila, E., Arfin Khan, M.A.S., Attorre, F., Aubin, I., Baraloto, C., Barroso, J.G., Bauters, M., Bergmeier, E., Biurrun, I., Bjorkman, A.D., Blonder, B., Čarni, A., Cayuela, L., Černý, T., Cornelissen, J.H.C., Craven, D., Dainese, M., Derroire, G., De Sanctis, M., Díaz, S., Doležal, J., Farfan-Rios, W., Feldpausch, T.R., Fenton, N.J., Garnier, E., Guerin, G.R., Gutiérrez, A.G., Haider, S., Hattab, T., Henry, G., Hérault, B., Higuchi, P., Hölzel, N., Homeier, J., Jentsch, A., Jürgens, N., Kącki, Z., Karger, D.N., Kessler, M., Kleyer, M., Knollová, I., Korolyuk, A.Y., Kühn, I., Laughlin, D.C., Lens, F., Loos, J., Louault, F., Lyubenova, M.I., Malhi, Y., Marcenò, C., Mencuccini, M., Müller, J.V., Munzinger, J., Myers-Smith, I.H., Neill, D.A., Niinemets, Ü., Orwin, K.H., Ozinga, W.A., Penuelas, J., Pérez-Haase, A., Petřík, P., Phillips, O.L., Pärtel, M., Reich, P.B., Römermann, C., Rodrigues, A.V., Sabatini, F.M., Sardans, J., Schmidt, M., Seidler, G., Espejo, J.E.S., Silveira, M., Smyth, A., Sporbert, M., Svenning, J.-C., Tang, Z., Thomas, R., Tsiripidis, I., Vassilev, K., Violle, C., Virtanen, R., Weiher, E., Welk, E., Wesche, K., Winter, M., Wirth, C., & Jandt, U. 2018. Global trait–environment relationships of plant communities. *Nature Ecology and Evolution (in the press)*

Bullock, J.M., Franklin, J., Stevenson, M.J., Silvertown, J., Coulson, S.J., Gregory, S.J., & Tofts, R. 2001. A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology* 38: 253–267.

Bultynck, L., Fiorani, F., & Lambers, H. 1999. Control of leaf growth and its role in determining variation in plant growth rate from an ecological perspective. *Plant Biology* 1: 13–18.

Comas, L., Becker, S., Cruz, V.M.V., Byrne, P.F., & Dierig, D.A. 2013. Root traits contributing to plant productivity under drought. *Frontiers in Plant Science* 4:.

Craine, J.M., & Dybzinski, R. 2013. Mechanisms of plant competition for nutrients, water and light. *Functional Ecology* 27: 833–840.

Deng, L., Sweeney, S., & Shangguan, Z.-P. 2014. Grassland responses to grazing disturbance: plant diversity changes with grazing intensity in a desert steppe. *Grass and Forage Science* 69: 524–533.

Díaz, S., Cabido, M., & Casanoves, F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122.

Dirks, I., Dumbur, R., Lienin, P., Kleyer, M., & Grünzweig, J.M. 2017. Size and reproductive traits rather than leaf economic traits explain plant-community composition in species-rich annual vegetation along a gradient of land use intensity. *Frontiers in Plant Science* 8:.

Enquist, B.J., Kerkhoff, A.J., Stark, S.C., Swenson, N.G., McCarthy, M.C., & Price, C.A. 2007. A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature* 449: 218–222.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., & Weisser, W.W. 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology* 11: 473–485.

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., Roumet, C., & Navas, M.-L. 2001. Consistency of species ranking based on functional leaf traits. *New Phytologist* 152: 69–83.

Grime, J.P., & Hunt, R. 1975. Relative growth-rate: Its range and adaptive significance in a local Flora. *Journal of Ecology* 63: 393–422.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C., & Whitehouse, J. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79: 259–281.

Gross, N., Suding, K.N., & Lavorel, S. 2007. Leaf dry matter content and lateral spread predict response to land use change for six subalpine grassland species. *Journal of Vegetation Science* 18: 289–300.

Hanley, M.E., Lamont, B.B., Fairbanks, M.M., & Rafferty, C.M. 2007. Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 157–178.

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., & Bruelheide, H. 2017. Predicting individual plant performance in grasslands. *Ecology and Evolution* 7: 8958–8965.

Hoffmann, W.A., & Poorter, H. 2002. Avoiding bias in calculations of relative growth rate. *Annals of Botany* 90: 37–42.

Hunt, R., & Cornelissen, J.H.C. 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist* 135: 395–417.

Jäger, E., & Werner, K. 2001. *Exkursionsflora von Deutschland, Bd.4, Gefäßpflanzen, Kritischer Band*. Spektrum Akademischer Verlag.

Johansen, L., Wehn, S., & Hovstad, K.A. 2016. Clonal growth buffers the effect of grazing management on the population growth rate of a perennial grassland herb. *Flora - Morphology, Distribution, Functional Ecology of Plants* 223: 11–18.

Kazakou, E., Violle, C., Roumet, C., Navas, M.-L., Vile, D., Kattge, J., & Garnier, E. 2014. Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science* 25: 235–247.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. m., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. g., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W. a., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. j., Tackenberg, O., Wilmann, B., Cornelissen, J. h. c., Eriksson, O., Garnier, E., & Peco, B. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.

Klimešová, J., Latzel, V., de Bello, F., & van Groenendael, J.M. 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. *Preslia* 80: 245–253.

Klimešová, J., Tackenberg, O., & Herben, T. 2016. Herbs are different: clonal and bud bank traits can matter more than leaf–height–seed traits. *New Phytologist* 210: 13–17.

Klotz, S., Kühn, I., & Durka, W. 2002. *Biolflor: eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland*. Bundesamt für Naturschutz, Bonn.

Kröber, W., Li, Y., Härdtle, W., Ma, K., Schmid, B., Schmidt, K., Scholten, T., Seidler, G., Oheimb, G., Welk, E., Wirth, C., & Bruelheide, H. 2015. Early subtropical forest growth is driven by community mean trait values and functional diversity rather than the abiotic environment. *Ecology and Evolution* 5: 3541–3556.

Lambers, H., & Poorter, H. 1992. Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. In Begon, M. & Fitter, A.H. (eds.), *Advances in Ecological Research*, pp. 187–261. Academic Press.

Lienin, P., & Kleyer, M. 2012. Plant trait responses to the environment and effects on ecosystem properties. *Basic and Applied Ecology* 13: 301–311.

Lind, E.M., Borer, E., Seabloom, E., Adler, P., Bakker, J.D., Blumenthal, D.M., Crawley, M., Davies, K., Firn, J., Gruner, D.S., Stanley Harpole, W., Hautier, Y., Hillebrand, H., Knops, J., Melbourne, B., Mortensen, B., Risch, A.C., Schuetz, M., Stevens, C., & Wragg, P.D. 2013. Life-history constraints in grassland plant species: a growth-defence trade-off is the norm. *Ecology Letters* 16: 513–521.

Lloyd, J., Bloomfield, K., Domingues, T.F., & Farquhar, G.D. 2013. Photosynthetically relevant foliar traits correlating better on a mass vs an area basis: of ecophysiological relevance or just a case of mathematical imperatives and statistical quicksand? *New Phytologist* 199: 311–321.

Meziane, D., & Shipley, B. 1999. Interacting components of interspecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. *Functional Ecology* 13: 611–622.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. 2015. *vegan: Community Ecology Package*.

Osnas, J.L.D., Lichstein, J.W., Reich, P.B., & Pacala, S.W. 2013. Global leaf trait relationships: Mass, area, and the leaf economics spectrum. *Science* 340: 741–744.

Paine, C.E.T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide, H., Daïnou, K., Gouvenain, R.C. de, Doucet, J.-L., Doust, S., Fine, P.V.A., Fortunel, C., Haase, J., Holl, K.D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., Martínez-Garza, C., Messier, C., Paquette, A., Philipson, C., Piotto, D., Poorter, L., Posada, J.M., Potvin, C., Rainio, K., Russo, S.E., Ruiz-Jaen, M., Scherer-Lorenzen, M., Webb, C.O., Wright, S.J., Zahawi, R.A., & Hector, A. 2015. Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *Journal of Ecology* 103: 978–989.

Poorter, H. 1989. Interspecific variation in relative growth rate: On ecological causes and physiological consequences.

Poorter, L., & Bongers, F. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87: 1733–1743.

Poorter, H., & Remkes, C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83: 553–559.

Poschlod, P., Kleyer, M., Jackel, A.-K., Dannemann, A., & Tackenberg, O. 2003. BIOPOP — A database of plant traits and internet application for nature conservation. *Folia Geobotanica* 38: 263–271.

Roche, P., Díaz-Burlinson, N., & Gachet, S. 2004. Congruency analysis of species ranking based on leaf traits: which traits are the more reliable? *Plant Ecology* 174: 37–48.

Roscher, C., Scherer-Lorenzen, M., Schumacher, J., Temperton, V.M., Buchmann, N., & Schulze, E.-D. 2011. Plant resource-use characteristics as predictors for species contribution to community biomass in experimental grasslands. *Perspectives in Plant Ecology, Evolution and Systematics* 13: 1–13.

Smart, S.M., Glanville, H.C., Blanes, M. del C., Mercado, L.M., Emmett, B.A., Jones, D.L., Cosby, B.J., Marrs, R.H., Butler, A., Marshall, M.R., Reinsch, S., Herrero-Jáuregui, C., & Hodgson, J.G. 2017. Leaf dry matter content is better at predicting above-ground net primary production than specific leaf area. *Functional Ecology* 31: 1336–1344.

Suter, M., & Edwards, P.J. 2013. Convergent succession of plant communities is linked to species' functional traits. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 217–225.

Tomás, M., Flexas, J., Copolovici, L., Galmés, J., Hallik, L., Medrano, H., Ribas-Carbó, M., Tosens, T., Vislap, V., & Niinemets, Ü. 2013. Importance of leaf anatomy in determining mesophyll diffusion conductance to CO2 across species: quantitative limitations and scaling up by models. *Journal of Experimental Botany* 64: 2269–2281.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Zheng, S.X., Li, W.H., Lan, Z.C., Ren, H.Y., Wang, K.B., & Bai, Y.F. 2014. Testing functional trait-based mechanisms underpinning plant responses to grazing and linkages to ecosystem functioning in grasslands. *Biogeosciences Discuss.* 11: 13157–13186.

4.8 Supporting Information

Additional Supporting Information of this chapter may be found on the attached CD:

Table S4.1: Trait values (SLA, LDMC, height, leaf anatomy, leaf persistence, leaf distribution, physical defense and vegetative reproduction) of 93 species.

Table S4.2: The 93 species and their number of individuals planted per species, number of replicates per species used for calculation of mean values of survival rates, biomass and relative growth rates for the field and common garden experiment respectively.

Table S4.3: Species performance variables in the field and common garden experiment: Survial rates, biomass and RGRs (height, plant projection area, leaf length and number of leaves) and PCA species scores of first and second axis.

Table S4.4: Spearman correlation coefficients for performance variables between observations on mean species values in the field and the common garden experiment.

Figure S4.1: Principal component analysis (PCA) based on 14 traits (SLA, LDMC, height, leaf anatomy (succulent, scleromorphic, mesomorphic, hygromorphic and helomorphic), leaf persistence (in spring green and in summer green), leaf distribution (rosettes and semirosettes), physical defense and vegetative reproduction) and all 93 species.

Chapter 5 – Synthesis

5.1 Main results

This thesis focused on an enrichment planting experiment testing the survival and performance of transplant species belonging to four different scenarios (Random, Dissim, Sim and Beals) added to grassland communities under different land-use intensities and also in comparison to the species planted in a common garden experiment. An overall result of this thesis demonstrates that the enrichment planting experiment was successful and new species could become established with a total transplant survival rate of 44.6 % after two years.

The main results of the study presented in chapter 2 showed that the change of community mean trait distances brought about by adding species according to the four enrichment planting scenarios Random, Dissim, Sim and Beals to the subplots differed between scenarios. Adding species selected by the Dissim and Random scenarios increased mean trait distances of communities, however adding species selected by the Dissim scenario brought the strongest increase. Adding species according to the Sim scenario decreased mean trait distances of communities, while adding species selected by the Beals scenario did not result in any changes – mean trait distances remained the same as they were before enrichment planting was done. For all scenarios mean trait distances decreased with increasing land-use intensity.

The survival rates of the transplant species after 1.5 years were observed to be highest for plants of the Beals scenario followed by species of the Sim scenario. Survival rates were intermediate for plants of the Random scenario and lowest for those of the Dissim scenario. Survival rates decreased with increasing land-use intensity with similar magnitudes of decrease in all four scenarios.

Variance partitioning analyses in chapter 3 showed that among all predictor variables species identity explained most variance, followed by plot identity. Trait characteristics of the communities (FD or CWM) and Scenario explained exclusively a very low amount of variance in growth of transplants (beneath 1%). This was also obvious in the high proportion of explained variance by the random factors (species-, plot-, Exploratory- and subplot-identity) and the high differences between conditional and marginal R^2 of linear optimized models. However, looking in detail at the linear models for the different vegetation periods and performance variables of transplants (different RGRs and aboveground biomass production at time of harvest) we found that performance was most often influenced by LUI. LUI had positive impacts on transplants growth in winter and on aboveground biomass production at time of harvest and negative impact on growth in the following summer. FD characteristics of the community had mostly positive impacts on growth and were involved in more models as CWMs. Scenario was only important in interaction with FD or CWM, and in most cases the Beals scenario showed highest positive response in growth, followed by Sim, Dissim and Random. An additional effect of soil moisture was found to have a negative influence on growth in winter and a positive effect in the following summer. In general, growth variables in the different monitoring intervals were influenced by different predictors, showing that performance models are temporally restricted.

Analyses in chapter 4 found that the performance in both experiments – field experiment in the Biodiversity Exploratories and the common garden experiment conducted in the Botanical Garden of the Martin Luther University Halle-Wittenberg – were species-specific. Both experiments had similar rankings of species for most performance parameters. Moreover the procrustes analysis was significant between performance parameters in field and common garden experiment. However, the relationship between performance and traits differed in the common garden and field experiment, showing that the respective set of optimal final traits found during the optimization procedure for each experiment was not interchangeable. For example, vegetative reproduction and the interaction between vegetative reproduction and leaf dry matter content (LDMC) were positively correlated with growth under field conditions, whereas under common garden conditions the effect was contrary. Moreover, certain traits were found to be exclusively important in one experiment but not in the other, such as leaf anatomy in the field experiment and plant height in the common garden experiment.

5.2 General discussion

Community saturation

Empty habitats can be filled with species either of the local or regional species pool but also can be invaded by exotic species (Davis et al. 2000), which are a thread to many ecosystems (Gordon 1998; Pimentel et al. 2001). Furthermore dispersal limitations are considered a reason for diversity loss (Stampfli & Zeiter 1999; Ehrlen & Eriksson 2000; Stein et al. 2008; Riibak et al. 2017). Particularly for grasslands in Europe dispersal limitations are caused by a general decline of grasslands in combination with landscape fragmentation (Cousins 2009; Krauss et al. 2010) and the loss of former dispersal vectors through abandonment of historical practices like hay movement, transhumance and farmers sharing their equipment (Fischer et al. 1996; Poschlod & Bonn 1998; Poschlod et al. 1998; Wallin et al. 2009). Moreover, land-use intensification has been shown to cause species losses with declines in biodiversity worldwide (Sala et al. 2000; Foley et al. 2005). Zobel et al. (2006) declared that dispersal limitations affect ecosystem functions on local, regional and even global scale and calls for deeper investigations. In this respect, knowledge about the arrival and the establishment success of new species can give important insights on assembly rules (Zobel et al. 2006). In this thesis, an enrichment planting experiment was performed to test for assembly processes especially in respect to environmental filtering and niche differentiation. I asked firstly if the communities investigated are saturated with plant species or if new species can become established. Results showed that new species became established with a transplant survival rate of 44.6% until the end of the enrichment planting experiment after two years. The fact that new species were able to survive within the two years of the enrichment planting experiment indicates that the grassland communities were not saturated, thus confirming hypothesis H1 of this thesis. However, it has to be discussed that the unsaturation of communities has been considered not a special case but rather the rule (Mateo et al. 2017) and that even the existence of a theoretical upper limit to species richness has been questioned (Cornell 1999; Loreau 2000).

The enrichment planting experiment achieved a considerable high survival rate compared to seed addition experiments described in literature. A review including 43 seed addition experiments found that only 15% of seedlings successfully became established from seeds (Clark et al. 2007). Similarly, results of another review examining 27 seed addition experiments showed a high post germination mortality of seedlings, resulting in only 23 % of sites where species reached the adult stage (Turnbull et al. 2000). Other studies found that using young transplants nursed in the greenhouse represented a good method to integrate new species into existing communities (Drayton & Primack 2000; Wallin et al. 2009; Reckinger et al. 2010). For example, Wallin et al. (2009) found that using transplants was twice as successful compared to sowing seeds. However, the method of using young transplants to increase plant diversity is generally not recommended for grassland restoration purposes (Walker et al. 2004; Raabová et al. 2007; Hedberg & Kotowski 2010), because their survival and dispersal in the long-term was found to be low (Hopkins et al. 1999; Morgan 1999). This shows that colonization success only can be judged if the transplants reproduce and form stable populations within the communities over longer periods of time (Ebenhard 1991; Godefroid et al. 2011), which however was not investigated due to a relatively short duration of the experiment with a terminal harvest of all individuals after two years. However, the intention of this thesis was not to find a good restoration method but to test the processes behind the assembly of plant species and how dissimilar or similar in traits a new species needs to be in order to get integrated into existing grassland communities under varying land-use intensity.

Species effects

I hypothesized in H2 that species differences are connected with growth, survival and performance. Interspecific differences were found to be important indicators for species performance. Species effects were found to be relevant in chapter 3, where variance exclusively explained by species identity was very high (up to 37.6 %), and also in chapter 4 where species rankings in performance parameters were significantly correlated between the two different experiments in the field and common garden. Meziane & Shipley (1999) found for example that differences in light and nutrient supply had little influence on ranks of net assimilation rates, which are related to relative growth rates. Also other studies found that interspecific rankings were only marginally affected by different environments (Garnier et al. 2001; Roche et al. 2004; Al Haj Khaled et al. 2005; Kazakou et al. 2014), which is in accordance with the findings in this thesis. However, trait-performance relationships varied in chapter 4 between the field and common garden experiment. For example, the trait vegetative reproduction was connected with increased growth in the field but with slow growth in the common garden experiment.

A study in grasslands of Inner Mongolia found that two different species of *Stipa* were differently affected in their reproductive behavior by grazing as compared to mowing (Gao et al. 2014). The ratio of vegetative to reproductive tiller biomass under grazing decreased in

Stipa grandis, while it increased in *Stipa krylovii* (Gao et al. 2014), showing that the trait vegetative reproduction is species-specificly effected by grazing.

Other traits were only important in the field and not in the common garden, as for example leaf anatomy traits (chapter 4). In particular, species with mesomorphic leaves were connected to higher survival and higher growth rates in the field experiment. Mesomorphic leaves have higher membrane permeability and stromal conductance, which results in higher photosynthetic capacity, whereas the photosynthetic capacity of species with scleromorphic leaves was found to be limited by cell wall thickness (Tomás et al. 2013). The lower cell wall thickness and higher photosynthetic capacity of mesomorphic leaves might cause faster regrowth after mowing and grazing events and therefore could be an advantage under land-use management. Growth and performance were found to be species-specific in the two different environmental settings (field vs. common garden), but trait-performance relationships differed, thus confirming hypothesis H2 of this thesis only partly.

Differences between the four enrichment planting scenarios

The four enrichment planting scenarios Random, Dissim, Sim and Beals of this thesis were especially designed to investigate assembly rules. The Random scenario followed neutral theory by selecting transplant species randomly and irrespective of traits. The Dissim scenario and the Sim scenario were developed to test for niche differentiation and environmental filtering processes along the land-use intensity gradient, respectively. The Beals scenario represented species with highest probability of co-occurrence to existing communities. This scenario was used to find the degree between environmental filtering and niche differentiation a species needs to successfully become established in grassland communities of varying land-use intensity by comparing the mean trait distances of the Beals, Dissim and Sim scenarios.

In hypothesis H3 of this thesis it was assumed that the scenario, according to which the transplant species was selected, should also have major impact on its survival and performance. It was found that the scenarios significantly differed in survival rates (chapter 2). However, in chapter 3 it was found that scenario explained only a small proportion of variance in individual performance. The scenario effects in this case were only important in interaction with functional diversity or community weighted means of certain traits, hereby the trend was a higher positive effect of FD on growth for species of the Beals scenario (chapter 3). Testing the single effects of the scenarios for growth and biomass production without other predictors showed that significant differences between scenarios were only found for 3 out of 13 linear models. The Beals scenario had significantly higher RGR leaf length and number of leaves compared to the Random scenario in the first vegetation period, this effect however disappeared in the second vegetation period (number of leaves was published in Bruelheide et al. (2015)). Similarly, in the winter period the Beals and Sim scenario had significantly higher RGR height compared to the Random scenario, but this effect was also not persistent in the following summer vegetation period (unpublished data). Therefore, the third hypothesis (H3) of this thesis can be only partly confirmed: scenario differences have impact on survival rates but the effects on performance are not as clear. The strong scenario effects for survival rates compared to almost not notable scenario effects on growth parameters might be attributed to different reasons, described in the following. Survival rates represent a final state at a certain date, whereas RGR measurements are conducted over larger timespans that underlie changes; e.g. in chapter 3 different predictors were found to be important for the growth of transplants between the different observation intervals, which also points to the importance of temporal differences in performance. Moreover, RGR can only be measured for surviving individuals. The death of certain species might also represent a filtering process which might select for species with similar growth characteristics and though equalizing differences between scenarios. However, one main reason might be that the transplants were exposed to the ambient land-use and their growth was therefore interrupted by mowing and grazing events, which resulted also in negative values of RGR. Land-use intensity was the predictor with the highest explanatory power and the most often significant factor across all final models in all three seasons investigated (chapter 3). However, there was no effect of land-use intensity in interactions with scenario for survival rates (chapter 2), nor for performance (chapter 3). This indicates that land-use intensity is influencing species growth, but this influence is similar for all transplants regardless of the scenario according to which the transplanted species was selected.

Other studies have shown that survival and RGR are largely independent from each other and that RGR under field conditions were found to be strongly correlated with disturbance-generated abundance patterns (Suding et al. 2003). This finding is supported by Gross et al. (2009), who argued that the examination of growth and survival is difficult as their importance can change under different ecological conditions, e.g. survival indicated facilitation in grasslands under water-limitation, whereas growth was connected with competition only in less water-limited grasslands.

As hypothesis H3 is only fully confirmed for survival rates and not for performance, the following discussion of the sub-hypotheses H3a – H3d (see Fig. 5.1) will be based on survival rates only, except for hypothesis H3d concerning the Beals scenario, where positive performance responses to FD measures were found in chapter 3.

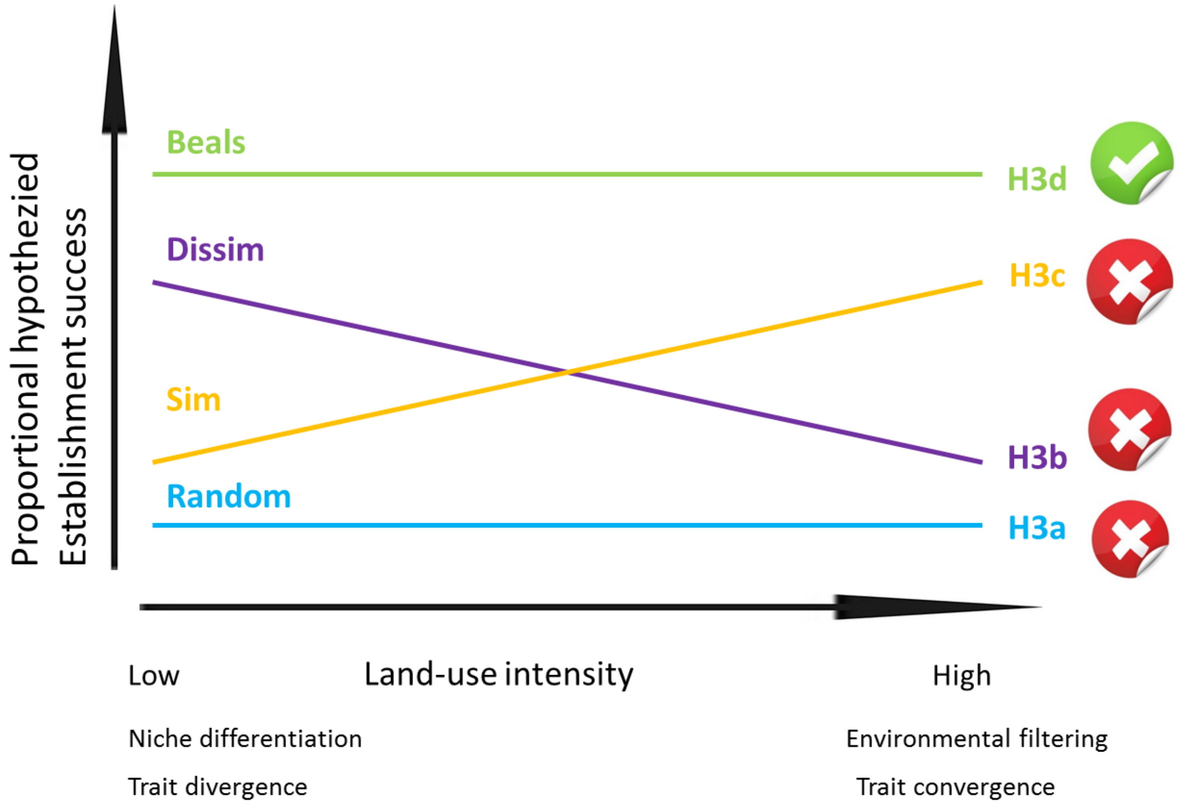

Figure 5.1 Recapitulation of Figure 1.1 from the introduction. Hypotheses H3a – H3d as stated in this thesis concerned the proportional hypothesized establishment success of transplant species of the four different enrichment planting scenarios Random, Dissim, Sim and Beals along the gradient of land-use intensity, including the supposedly underlying assembly processes niche differentiation and environmental filtering. This thesis could only confirm hypothesis H3d, but not H3a-c.

The Random scenario

Hypothesis H3a states that the Random scenario has the lowest success under all conditions (see Fig. 5.1). However, species of the Random scenario did not rank last with respect to survival rates; as the Dissim scenario ranked even lower. However, the survival rates of the Random scenario were much lower than those of the Beals and Sim scenario. As described in chapter 2, the mean trait distances of the experimental subplots increased by adding species of the Random scenario. Thus, the species of the Random scenario where more dissimilar to the resident community than the resident species among themselves, which points to a regional species pool containing more dissimilar species in comparison to the investigated communities. Zobel (1997) found that the species pool from which species are taken for species richness manipulation experiments can influence the establishment success of the species, whereby it does matter if the randomly chosen species is from the local, regional or other species pool (Zobel 1997). The species of the enrichment planting experiment of this thesis were chosen from the regional species pool, which was ensured by comparisons to the German Vegetation Reference Database (GVRD, Jandt & Bruelheide 2012). However the used species pool was apparently broader as the local species pools of the experimental plots investigated, which clearly demonstrates that despite the availability of information on species' habitat-preferences the definition of a species pool is not as easy (Pärtel et al. 2011). However, that the species of the Random scenario were very dissimilar in traits and though increased mean trait distances is in accordance with findings of Cornwell et al. (2006), who found that observed plant communities occupy less trait space than expected from a random assembly. The low survival rates of the species of the Random scenario and the high proportion of dissimilar species among the species of the Random scenario therefore suggest that dissimilar species had less advantage than similar species. This is confirmed by comparisons to the even lower survival success of species of the Dissim scenario and to the higher survival rates of the species of the Sim scenario. Therefore, the assembly of the species in the investigated grassland communities seems rather to be based on environmental filtering giving more similar species better chances of survival as compared to randomly chosen and more dissimilar species.

However, it has to be clarified that the Random scenario cannot be used to test neutral theory that predicts distributions patterns of species abundance and species-area curves but does not include community trait patterns considered in this thesis. However, Hubbell (2005) described that functional trait similarity may be a result of similar adaptations to the most common environmental conditions and further states that the coexistence of functionally similar species may be enhanced by a combination of dispersal and recruitment limitation as well as site heterogeneity. None of these factors were investigated within this thesis. Moreover, the species of the Random scenario were indeed chosen randomly, but they were more dissimilar to the resident community in trait values as discussed above, thus being not a good representation for testing neutral theory.

Niche differentiation and environmental filtering: The Dissim and Sim scenarios

Hypothesis H3b assumed an increase of establishment success for species of the Dissim scenario with decreasing land-use intensity and a higher establishment success under low land-use intensity conditions compared to the Sim scenario (see Fig. 5.1). This hypothesis could not be confirmed. Indeed, the species of the Dissim scenario had higher survival under low land-use intensity conditions (chapter 2). However, in relation to the other scenarios the survival rates of the Dissim scenario were lowest under all conditions (chapter 2), and never superior compared to the Sim scenario, also not under low land-use intensity conditions. Survival rates decreased similarly for all scenarios with increasing land-use intensity (chapter 2).

Likewise, against the expectation according to hypothesis H3c (see Fig. 5.1), the survival rates of the species of the Sim scenario did not increase with increasing land-use intensity. However, the survival rates of the most similar species of the Sim scenario were the second highest across all land-use intensity conditions after the species of the Beals scenario. It seems logic that the less favorable conditions at high land-use intensity resulted in lower survival rates of transplants. In the multi-trait approach of chapter 2 the investigation of the changes in mean trait distances brought about by adding the four enrichment planting scenarios to the experimental subplots showed that land-use intensity negatively influenced the mean trait distances of all scenarios to a similar degree. The decrease in trait diversity as well as decreasing survival rates of introduced transplants with increasing LUI in the investigated grassland communities consistently demonstrate that land-use intensification leads to diversity loss.

When comparing the proportional establishment success between the Dissim and Sim scenario along the land-use intensity gradient unexpectedly no differences were found (chapter 2). Species of the Sim scenario under all conditions were superior in survival rates compared to those of the Dissim scenario. This indicates that rather similar traits are advantageous, which most likely reflects adaptations to land-use management. Traits that are important to survive the harsh conditions are probably connected with a good ability to recover fast after disturbance and to quickly colonize newly created gaps, which is supported by results found in chapter 4. Hereby, the trait vegetative reproduction was positively linked to performance in the field experiment but not in the common garden experiment. This is confirmed by Suding et al. (2003), who found that tolerances to defoliation explain species responses to abundance patterns under disturbance better than species competitive ability. Furthermore, they argued that under field conditions fast growth might be connected with the capacity of regrowth after herbivory, whereas in the greenhouse fast growth is related to shade tolerance (Suding et al. 2003). Other studies have also shown that the ability to reproduce vegetatively is a good method of plants to cope with disturbances (Klimešová & Klimeš 2003; Klimešová et al. 2008; Fukui & Araki 2014; Klimešová et al. 2018).

The higher survival rates of the species of the Sim scenario in the studied communities point to a higher importance of environmental filtering, whereas niche differentiation seems to play a subordinate role, as for the Dissim scenario with species most dissimilar to the resident community survival rates were lowest. One explanation for the low establishment success of the species of the Dissim scenario could be that the influence of land-use is very strong even under low intensity conditions, though similarity rather than dissimilarity is required. Another explanation for the low survival rates of the species of the Dissim scenario even under low land-use intensity conditions could be that under these conditions other environmental filters are involved, which also select for rather similar traits. The low land-use intensity plots in the Schwäbische Alb and in the Hainich are mostly semi-dry grasslands grazed by sheep. Semi-dry grasslands are characterized by calcareous soils with low water and low nutrient availability. Therefore, on these plots drought and shortage of nutrients as well as soil pH can function as environmental filters. Drought and low nutrient availability favor plant species that are known to tolerate the stressful conditions as for example slow growing species with scleromorphic, evergreen leaves with high leaf dry matter content (LDMC) (Grime 1977; Reich 2014). In consequence, in the exploratory plots it cannot be generally assumed that environmental filtering does only depend on LUI, as other natural not human induced filters could interact. For example, in Mediterranean grassland it was found that low water availability could increase the influence of grazing (Carmona et al. 2012).

However, the general decline in mean trait distance with increasing LUI before and after enrichment planting (irrespective of scenario), provides a strong support for the increasing strength of environmental filtering with increasing LUI (Flynn et al. 2009; Pakeman 2011).

Furthermore, it has to be considered that for niche differentiation rather than being dissimilar in all traits, a species only needs to be different in one distinct trait, which we could have missed.

Firstly, instead of looking at many traits as in a multi-trait approach, single-trait relationships were additionally tested in chapter 2, but did not achieve better results as the multi-trait approach. Only for LDMC and leaf distribution the mean trait distances of the four scenarios decreased with increasing LUI after enrichment planting (chapter 2). For all other single trait approaches LUI after enrichment planting had either no effect at all or no scenario differences were found (chapter 2). The reason behind this might be that single traits are unresponsive to land-use intensity but in combination with other traits might show a relationship. For example, Li et al. (2017) found that sets of traits related to carbon assimilation at the leaf-level and to leaf distribution at the crown-level explained species-specific growth rates in combination better than did separate traits.

Secondly, de Bello et al. (2012) argued that the traits which are selected for the investigation of assembly rules matter in the sense that traits that are useful to detect environmental filtering might not be the same traits that are important to detect niche differentiation. In particular, traits that are related to plant productivity were found to rather show trait convergence at the community level whereas traits that are connected with disturbance and regeneration show divergence (Grime 2006; Swenson & Enquist 2009). This is confirmed by Díaz et al. (1998), who found that vegetative traits were filtered more often than regeneration traits. Reasons for detecting less evidence for niche differentiation in our approach might therefore be caused by not including the right traits, as stated above, and especially by potentially having missed regeneration and phenology traits. However, because of using young transplants in the experiments of this thesis the focus was on the adult life stage and seed and reproduction traits were therefore not considered. Instead, trait selection was based on their assumed importance for growth and persistence in the investigated grassland communities under influences of land-use management. Therefore, traits were chosen that represent a species' competitive ability and are connected with growth rates such as specific leaf area (SLA), leaf dry matter content (LDMC), height, leaf anatomy, leaf persistence and leaf distribution (Cornelissen et al. 2003; Kleyer et al. 2008). Furthermore, the trait vegetative reproduction is linked to a species ability to recover quickly after disturbance and to colonize newly created gaps. The trait 'physical defense mechanisms' relates to land-use as plants with physical defense traits such as thorns or hooks are less likely to be grazed. The questions how many traits and which traits to pick to describe mechanisms in ecology have been often discussed (Wright et al. 2004; Lepš et al. 2006). However, I assume the selection of the traits used in this thesis to be meaningful because many of them are known to play a major role in the life of plants and are recommended as core traits to investigate ecosystem functions (Weiher et al. 1999; Westoby et al. 2002; Lavorel & Garnier 2002). Nevertheless, some important traits were missing. Besides regeneration and phenology traits as mentioned before, especially root traits were found to be important for species performance and growth (Bardgett et al. 2014; Herz et al. 2017). Unfortunately, including root-traits was not manageable in the time before planting started, as the selection of the two scenarios Dissim and Sim was trait-based and therefore root traits for the whole species pool including species of the resident communities (in total 251 species) would have been needed. Nevertheless, root-traits should be included in future studies. In order to be able to use these for a large number of species it would be helpful to include these traits in trait databases. Additionally, special attention should be paid to the selection of traits in order to avoid unwanted data redundancy. The ten traits used for species selection of the plot-specific scenarios Dissim and Sim were also used to investigate the changes in mean trait distances brought about by adding the four enrichment planting scenarios to the different grassland communities in chapter 2. However, in the subsequent studies (chapter 3 and 4) the traits clonal growth organs and lateral spread were neglected. This was done because these traits were redundant with the trait 'vegetative reproduction' and because these variables contained mistakes. To avoid such data errors trait data of different sources need to be thoroughly checked prior to analysis.

Moreover, the relationship between environmental filtering and niche differentiation might also be a matter of scale. While environmental filtering is thought to act on a broader scale, competition and niche differentiation are assumed to be relevant on a smaller scale (de Bello et al. 2013). For example, for a 10 × 10 cm² subplot de Bello et al. (2013) found trait divergence assuming niche differentiation, whereas for a 50 × 50 cm² plot they found trait convergence assuming environmental filtering. This shows that the experimental subplots of 1 m² used in the approach of this thesis might have been too big to demonstrate niche differentiation. However, several studies have shown that environmental filtering and niche differentiation act simultaneously and jointly at similar scales to structure plant communities but may influence different trait dimensions (Mason et al. 2011; Maire et al. 2012; Gross et al. 2013), which was already discussed above. Moreover, opposing to the assumption that competition through limiting similarity leads to trait divergence, it can lead sometimes also to trait convergence by elimination of more dissimilar species (Mayfield & Levine 2010; Gerhold et al. 2013; Loughnan & Gilbert 2017). Similarly, environmental filtering can lead also sometimes, against assumptions, to trait divergence by favoring for instance species with stress avoidance and with stress tolerance traits at the same time (Freschet et al. 2011). All this shows that trait-based approaches have shortcomings which might be minimized by the combination with other approaches as it was realized in this thesis by using an additional co-occurrence based scenario. To increase knowledge in community assembly theory in the future it would be interesting to combine co-occurrence- and trait-based approaches furthermore with phylogenetic ones, to identify the historical and deterministic processes that influence the composition of plant communities (Pavoine et al. 2011; Pavoine & Bonsall

2011), which would also open links between ecology and evolution (He et al. 2005; Vanoverbeke et al. 2016).

Using co-occurrence information: The Beals scenario

The species of the Beals scenario were selected based on co-occurrence information. Comparisons between the mean trait distances of the Beals, Sim and Dissim scenarios in chapter 2 resulted in a degree of trait similarity for the species of the Beals scenario with mean trait distances being closer to the most similar species compared to the most dissimilar species. This degree of the species of the Beals scenario was about 70% similar and about 30% dissimilar in traits and did not change along the land-use intensity gradient. This indicates that despite changing environmental filtering intensities the relationship between similarity and dissimilarity in traits stayed constant. It should be tested if this is a universal principle that exists also in different ecosystems and along other environmental gradients.

The species of the Beals scenario had highest survival rates compared to all other scenarios under all land-use intensity conditions, which is in accordance with the expectation of hypothesis H3d (see Fig. 5.1). The even higher survival of the Beals scenario compared to the Sim scenario points to the fact that some dissimilarity in traits might be beneficial and might have caused higher chances of survival. The positive growth response of transplants of the Beals scenario to FD measures (chapter 3) might also point to niche differentiation processes. However, environmental filtering through land-use intensity seems to be the strongest filter influencing all transplants similarly, whereas trait characteristics of the community as FD or CWM have only positive effects if the species are already adapted to the conditions. For that reason the Beals scenario showed highest positive responses to FD. Comparisons between species with high and low Beals index introduced as seeds into communities with and without removal of competitive neighbors showed that the species that did not fit well into the community (low Beals index) could only become established if the competitors were removed (Švamberková et al. 2017). Švamberková et al. (2017) drew the conclusion that biotic filtering was limiting their growth and not the abiotic conditions and that species pool-based co-occurrence measures often underestimate the importance of biotic filtering. These findings support the results of this thesis that land-use intensity was similar for all species, whereas community-based characteristics such as FD or CWM had only positive effects for the species that already fitted well (high Beals index) into the community.

Moreover, the successful establishment of the species of the Beals scenario might also be a result of their adaptations to the community in form of positive community-specific interactions either with other plants (facilitation) or with other life forms. Gerz et al. (2018) found for example that niche differentiation of plants is connected with symbiosis with mycorrhizal fungi. Furthermore, the positive diversity effects on productivity in biodiversity experiments were found to be delayed in time because interactions with soil biota first had to be developed (Eisenhauer et al. 2012), showing that soil biota play an important role in more diverse communities. Other studies also confirming this connection of positive interactions, showed that facilitation has more input in more diverse communities or even increases species diversity (Valiente-Banuet & Verdú 2007; McIntire & Fajardo 2014). The positive growth response of the species of the Beals scenario to FD could therefore also be a hint to positive interactions. Moreover, the positive effects of facilitation were found to increase under environmental stress (Pugnaire & Luque 2001; Callaway et al. 2002), from which the species of the Beals scenario might have benefitted under the harsh and stressful conditions both caused by intensive land-use or water and nutrient limitation. However, biotic interactions and especially the effect of facilitation were not addressed in this thesis, but should get more attention in further investigations.

Environmental filters

This thesis focused on the environmental filter land-use intensity and also on trait characteristics of the different grassland communities. Land-use intensity was found to be more often explaining growth than FD or CWM measures (chapter 2), thus confirming hypothesis H4. However, land-use intensity expressed as the LUI was the only environmental filter tested. As the LUI is a compound of factors (fertilization, grazing and mowing) it enables generalizations of different effects. However, the index also has the disadvantage that some effects might not be visible or be disguised by others, as for example differences between meadows, pastures and meadow-pastures might get lost, or the effects of disturbance and fertilization are not separated. In addition to LUI the influence of climatic parameters (air temperature and humidity, and soil temperature and moisture) was analyzed and soil moisture was found to be additionally important (chapter 3). This leads to the assumption that soil conditions might have a large impact on species' survival und performance. This was visible on the plots in the Schorfheide with its particularly wet soils (histosols), which caused high mortality of transplants. Including species' soil preferences as a trait when selecting species for the enrichment planting scenarios would have been additionally necessary and could have led to better results concerning performance differences of the four scenarios. The only scenario which included this issue indirectly through high co-occurrence probability was the Beals scenario.

5.3 Conclusion

Community assembly theory either focuses on the species present in a community (e.g. niche theory (Leibold 1995; Leibold et al. 2004)), or on immigration/extinction processes (Hubbell 2001; Volkov et al. 2003; Rosindell et al. 2011). In this thesis, both approaches were combined by asking how new immigrants fit into the resident community. Asking this question is not only important for current colonizers, but also gives information about the processes that occurred in the past and resulted in the resident communities. Linking the fate of individuals new to the community to assembly theory showed that especially the combination of trait-based with co-occurrence-based approaches has a large predictive power. In particular, the finding that the most successful species of the Beals scenario were constantly about 70% similar and about 30% dissimilar in traits along the gradient of land-use intensity was unexpected. The fact that species with more similar traits (Beals scenario) and most similar traits (Sim scenario) had higher success rates indicates that the impact of environmental filtering was stronger, whereas the low success of most and more dissimilar species (Dissim and Random scenario) implies a low impact of niche differentiation.

5.4 References

Al Haj Khaled, R., Duru, M., Theau, J.P., Plantureux, S., & Cruz, P. 2005. Variation in leaf traits through seasons and N-availability levels and its consequences for ranking grassland species. *Journal of Vegetation Science* 16: 391–398.

Bardgett, R.D., Mommer, L., & De Vries, F.T. 2014. Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* 29: 692–699.

de Bello, F., Price, J.N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W., Gerhold, P., Götzenberger, L., Lavergne, S., Lepš, J., Zobel, K., & Pärtel, M. 2012. Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93: 2263–2273.

de Bello, F., Vandewalle, M., Reitalu, T., Lepš, J., Prentice, H.C., Lavorel, S., & Sykes, M.T. 2013. Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology* 101: 1237–1244.

Bruelheide, H., Breitschwerdt, E., & Jandt, U. 2015. Sociology of plants – a so-far untapped potential for predicting plant performance in temperate grasslands. *Bericht der Reinhold-Tüxen Gesellschaft* 27: 64–78.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., & Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844–848.

Carmona, C.P., Azcárate, F.M., Bello, F. de, Ollero, H.S., Lepš, J., & Peco, B. 2012. Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. *Journal of Applied Ecology* 49: 1084–1093.

Clark, C.J., Poulsen, J.R., Levey, D.J., & Osenberg, C.W. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Naturalist* 170: 128–142.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H. ter, Morgan, H.D., Heijden, M.G.A. van der, Pausas, J.G., & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Cornell, H.V. 1999. Unsaturation and regional influences on species richness in ecological communities: A review of the evidence. *Écoscience* 6: 303–315.

Cornwell, W.K., Schwilk, D.W., & Ackerly, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* 87: 1465–1471.

Cousins, S.A.O. 2009. Landscape history and soil properties affect grassland decline and plant species richness in rural landscapes. *Biological Conservation* 142: 2752–2758.

Davis, M.A., Grime, J.P., & Thompson, K. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology* 88: 528–534.

Díaz, S., Cabido, M., & Casanoves, F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122.

Drayton, B., & Primack, R.B. 2000. Rates of success in the reintroduction by four methods of several perennial plant species in eastern Massachusetts. *Rhodora* 102: 299–331.

Ebenhard, T. 1991. Colonization in metapopulations: a review of theory and observations. *Biological Journal of the Linnean Society* 42: 105–121.

Ehrlen, J., & Eriksson, O. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81: 1667–1674.

Eisenhauer, N., Reich, P.B., & Scheu, S. 2012. Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants. *Basic and Applied Ecology* 13: 571–578.

Fischer, S.F., Poschlod, P., & Beinlich, B. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology* 33: 1206–1222.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., & DeClerck, F. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12: 22–33.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., & Snyder, P.K. 2005. Global consequences of land use. *Science* 309: 570–574.

Freschet, G.T., Dias, A.T.C., Ackerly, D.D., Aerts, R., van Bodegom, P.M., Cornwell, W.K., Dong, M., Kurokawa, H., Liu, G., Onipchenko, V.G., Ordoñez, J.C., Peltzer, D.A., Richardson, S.J., Shidakov, I.I., Soudzilovskaia, N.A., Tao, J., & Cornelissen, J.H.C. 2011. Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. *Global Ecology and Biogeography* 20: 755–765.

Fukui, S., & Araki, K.S. 2014. Spatial niche facilitates clonal reproduction in seed plants under temporal disturbance. *PLOS ONE* 9: e116111.

Gao, H., Gao, Y., & He, X. 2014. Impacts of grazing and mowing on reproductive behaviors of Stipa grandis and Stipa krylovii in a semi-arid area. *Journal of Arid Land* 6: 97–104.

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., Roumet, C., & Navas, M.-L. 2001. Consistency of species ranking based on functional leaf traits. *New Phytologist* 152: 69–83.

Gerhold, P., Price, J.N., Püssa, K., Kalamees, R., Aher, K., Kaasik, A., & Pärtel, M. 2013. Functional and phylogenetic community assembly linked to changes in species diversity in a long-term resource manipulation experiment. *Journal of Vegetation Science* 24: 843–852.

Gerz, M., Bueno, C.G., Ozinga, W.A., Zobel, M., & Moora, M. 2018. Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology* 106: 254–264.

Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A.-D., Aguraiuja, R., Cowell, C., Weekley, C.W., Vogg, G., Iriondo, J.M., Johnson, I., Dixon, B., Gordon, D., Magnanon, S., Valentin, B., Bjureke, K., Koopman, R., Vicens, M., Virevaire, M., & Vanderborght, T. 2011. How successful are plant species reintroductions? *Biological Conservation* 144: 672–682.

Gordon, D.R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: Lessons from Florida. *Ecological Applications* 8: 975–989.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169–1194.

Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science* 17: 255–260.

Gross, N., Börger, L., Soriano-Morales, S.I., Le Bagousse-Pinguet, Y., Quero, J.L., García-Gómez, M., Valencia-Gómez, E., & Maestre, F.T. 2013. Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. *Journal of Ecology* 101: 637–649.

Gross, N., Kunstler, G., Liancourt, P., De Bello, F., Suding, K.N., & Lavorel, S. 2009. Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology* 23: 1167–1178.

He, F., Gaston, K.J., Connor, E.F., & Srivastava, D.S. 2005. The local–regional relationship: Immigration, extinction, and scale. *Ecology* 86: 360–365.

Hedberg, P., & Kotowski, W. 2010. New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead. *Journal for Nature Conservation* 18: 304–308.

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., & Bruelheide, H. 2017. Predicting individual plant performance in grasslands. *Ecology and Evolution* 7: 8958–8965.

Hopkins, Pywell, Peel, Johnson, & Bowling. 1999. Enhancement of botanical diversity of permanent grassland and impact on hay production in Environmentally Sensitive Areas in the UK. *Grass and Forage Science* 54: 163–173.

Hubbell, S.P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19: 166–172.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, USA.

Jandt, U., & Bruelheide, H. 2012. German Vegetation Reference Database (GVRD). *Biodiversity & Ecology* 4: 355–355.

Kazakou, E., Violle, C., Roumet, C., Navas, M.-L., Vile, D., Kattge, J., & Garnier, E. 2014. Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science* 25: 235–247.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. m., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. g., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W. a., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. j., Tackenberg, O., Wilmann, B., Cornelissen, J. h. c., Eriksson, O., Garnier, E., & Peco, B. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.

Klimešová, J., & Klimeš, L. 2003. Resprouting of herbs in disturbed habitats: is it adequately described by Bellingham–Sparrow's model? *Oikos* 103: 225–229.

Klimešová, J., Latzel, V., de Bello, F., & van Groenendael, J.M. 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. *Preslia* 80: 245–253.

Klimešová, J., Martínková, J., & Herben, T. 2018. Horizontal growth: An overlooked dimension in plant trait space. *Perspectives in Plant Ecology, Evolution and Systematics* 32: 18–21.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters* 13: 597–605.

Lavorel, S., & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.

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

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.

Lepš, J., De Bello, F., Lavorel, S., & Berman, S. 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* 78: 481–501.

Li, Y., Kröber, W., Bruelheide, H., Härdtle, W., & von Oheimb, G. 2017. Crown and leaf traits as predictors of subtropical tree sapling growth rates. *Journal of Plant Ecology* 10: 136–145.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. *Ecology Letters* 3: 73–76.

Loughnan, D., & Gilbert, B. 2017. Trait-mediated community assembly: distinguishing the signatures of biotic and abiotic filters. *Oikos* 126: 1112–1122.

Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. da S., Soussana, J.-F., & Louault, F. 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist* 196: 497–509.

Mason, N.W.H., De Bello, F., Doležal, J., & Lepš, J. 2011. Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology* 99: 788–796.

Mateo, R.G., Mokany, K., & Guisan, A. 2017. Biodiversity models: What if unsaturation is the rule? *Trends in Ecology & Evolution* 32: 556–566.

Mayfield, M.M., & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.

McIntire, E.J.B., & Fajardo, A. 2014. Facilitation as a ubiquitous driver of biodiversity. *New Phytologist* 201: 403–416.

Meziane, D., & Shipley, B. 1999. Interacting components of interspecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. *Functional Ecology* 13: 611–622.

Morgan, J.W. 1999. Have tubestock plantings successfully established populations of rare grassland species into reintroduction sites in western Victoria? *Biological Conservation* 89: 235–243.

Pakeman, R.J. 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology* 99: 1143–1151.

Pärtel, M., Szava-Kovats, R., & Zobel, M. 2011. Dark diversity: shedding light on absent species. *Trends in Ecology & Evolution* 26: 124–128.

Pavoine, S., & Bonsall, M.B. 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews* 86: 792–812.

Pavoine, S., Vela, E., Gachet, S., de Bélair, G., & Bonsall, M.B. 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *Journal of Ecology* 99: 165–175.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., & Tsomondo, T. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems & Environment* 84: 1–20.

Poschlod, P., & Bonn, S. 1998. Changing dispersal processes in the central European landscape since the last ice age: an explanation for the actual decrease of plant species richness in different habitats? *Acta botanica neerlandica* 47: 27–44.

Poschlod, P., Kiefer, S., Tränkle, U., Fischer, S., & Bonn, S. 1998. Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Applied Vegetation Science* 1: 75–91.

Pugnaire, F.I., & Luque, M.T. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93: 42–49.

Raabová, J., Münzbergová, Z., & Fischer, M. 2007. Ecological rather than geographic or genetic distance affects local adaptation of the rare perennial herb, Aster amellus. *Biological Conservation* 139: 348–357.

Reckinger, C., Colling, G., & Matthies, D. 2010. Restoring populations of the endangered plant Scorzonera humilis: Influence of site conditions, seed Source, and plant stage. *Restoration Ecology* 18: 904–913.

Reich, P.B. 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.

Riibak, K., Ronk, A., Kattge, J., & Pärtel, M. 2017. Dispersal limitation determines large-scale dark diversity in Central and Northern Europe. *Journal of Biogeography* 44: 1770–1780.

Roche, P., Díaz-Burlinson, N., & Gachet, S. 2004. Congruency analysis of species ranking based on leaf traits: which traits are the more reliable? *Plant Ecology* 174: 37–48.

Rosindell, J., Hubbell, S.P., & Etienne, R.S. 2011. The Unified Neutral Theory of Biodiversity and Biogeography at age ten. *Trends in Ecology & Evolution* 26: 340–348.

Sala, O.E., Chapin, F.S., Iii, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Stampfli, A., & Zeiter, M. 1999. Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. A case study from the southern Alps. *Journal of Vegetation Science* 10: 151–164.

Stein, C., Auge, H., Fischer, M., Weisser, W.W., & Prati, D. 2008. Dispersal and seed limitation affect diversity and productivity of montane grasslands. *Oikos* 117: 1469–1478.

Suding, K.N., Goldberg, D.E., & Hartman, K.M. 2003. Relationships among species traits: Separating levels of response and identifying linkages to abundance. *Ecology* 84: 1–16.

Švamberková, E., Vítová, A., & Lepš, J. 2017. The role of biotic interactions in plant community assembly: What is the community species pool? *Acta Oecologica* 85: 150–156.

Swenson, N.G., & Enquist, B.J. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology* 90: 2161–2170.

Tomás, M., Flexas, J., Copolovici, L., Galmés, J., Hallik, L., Medrano, H., Ribas-Carbó, M., Tosens, T., Vislap, V., & Niinemets, Ü. 2013. Importance of leaf anatomy in determining mesophyll diffusion conductance to CO2 across species: quantitative limitations and scaling up by models. *Journal of Experimental Botany* 64: 2269–2281.

Turnbull, L.A., Crawley, M.J., & Rees, M. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88: 225–238.

Valiente-Banuet, A., & Verdú, M. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters* 10: 1029–1036.

Vanoverbeke, J., Urban, M.C., & Meester, L.D. 2016. Community assembly is a race between immigration and adaptation: eco-evolutionary interactions across spatial scales. *Ecography* 39: 858–870.

Volkov, I., Banavar, J.R., Hubbell, S.P., & Maritan, A. 2003. Neutral theory and relative species abundance in ecology. *Nature* 424: 1035–1037.

Walker, K.J., Stevens, P.A., Stevens, D.P., Mountford, J.O., Manchester, S.J., & Pywell, R.F. 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biological Conservation* 119: 1–18.

Wallin, L., Svensson, B.M., & Lönn, M. 2009. Artificial dispersal as a restoration tool in meadows: Sowing or planting? *Restoration Ecology* 17: 270–279.

Weiher, E., Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. 1999. Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., & Wright, I.J. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution* 12: 266–269.

Zobel, M., Öpik, M., Moora, M., & Pärtel, M. 2006. Biodiversity and ecosystem functioning: It is time for dispersal experiments. *Journal of Vegetation Science* 17: 543–547.

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Appendix

Curriculum vitae

Eva Breitschwerdt

Date and place of birth: 02.08.1980, Mühlacker
Nationality: German
Address: Dryanderstr. 17, 06110 Halle (Saale), Germany

Education:

05.2011 – present	PhD student, Martin Luther University Halle-Wittenberg Research topic: 'Using enrichment planting to test for environmental filtering and niche differentiation in grassland communities', supervisors: Prof. Dr. Helge Bruelheide, Dr. Ute Jandt
10.2002 – 11.2008	Studies in biology, Georg-August University of Göttingen Major subject: Botany, Vegetation Science Minor subjects: Microbiology, Spanish Diploma thesis: 'Kleinräumige Muster in der Diversität von Kalkmagerrasen-Komplexen', supervisors: Prof. Dr. Erwin Bergmeier, Dr. Heike Culmsee
08.1997 – 06.2000	Abitur: Gymnasium Uslar

Stayings abroad:

09.2005 – 07.2006	Erasmus exchange program, University of Salamanca, Spain
08.2001 – 09.2002	Helper on a Farm, Iceland
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Halle, den 7.11.2018

List of publications

Publications of this thesis:

Breitschwerdt, E., Jandt, U., & Bruelheide, H. 2015. Do newcomers stick to the rules of the residents? Designing trait-based community assembly tests. *Journal of Vegetation Science* 26: 219–232.

Breitschwerdt, E., Jandt, U., & Bruelheide, H. 2018. Using co-occurrence information and trait composition to understand individual plant performance in grassland communities. *Scientific Reports* 8: 9076.

Breitschwerdt, E., Jandt, U., & Bruelheide, H. (under review) Trait-performance relationships of grassland plant species differ between common garden and field conditions. *Ecology and Evolution*

Other publications by the author:

Bruelheide, H., Breitschwerdt, E., & Jandt, U. 2015. Sociology of plants – a so-far untapped potential for predicting plant performance in temperate grasslands. *Bericht der Reinhold-Tüxen Gesellschaft* 27: 64–78.

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „Using enrichment planting to test for environmental filtering and niche differentiation in grassland communities“ bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den 7.11.2018

Eva Breitschwerdt

Attachment

Using enrichment planting to test for environmental filtering and niche differentiation in grassland communities

by Eva Breitschwerdt

Supporting Information of chapters 2 – 4

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Chapter 2 – 2.8 Supporting Information

Table S2.1 ANOVA results of the mixed linear models for the response in mean pairwise trait distances to the four different scenarios (Beals, Dissim, Random and Sim) and land-use intensity, expressed as *LUI* for the years 2006 to 2010, separately for all single traits (SLA, LDMC, Height, Leaf anatomy, Leaf persistence, Leaf distribution, Vegetative reproduction, Clonal growth organs, Lateral spread and Physical defence) before, after and the level of change through enrichment planting. For variance of random factors see Table S2.2.

1. SLA	SLA distances before enrichment planting				SLA distances after enrichment planting				Change in SLA distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	0.783	0.504	3	372	19.944	<0.001	3	372	33.483	<0.001
LUI	1	50	0.069	0.794	1	50	0.075	0.785	1	50	0.021	0.886
Senario x LUI	3	372	0.628	0.597	3	372	0.365	0.779	3	372	0.541	0.655
2. LDMC	LDMC distances before enrichment planting				LDMC distances after enrichment planting				Change in LDMC distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	1.667	0.174	3	372	17.381	<0.001	3	372	10.308	<0.001
LUI	1	50	17.676	<0.001	1	50	20.985	<0.001	1	50	0.018	0.895
Senario x LUI	3	372	0.087	0.967	3	372	6.244	<0.001	3	372	8.575	<0.001
3. Height	Height distances before enrichment planting				Height distances after enrichment planting				Change in Height distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	0.709	0.547	3	372	92.468	<0.001	3	372	121.943	<0.001
LUI	1	50	0.058	0.81	1	50	0.333	0.567	1	50	2.331	0.133
Senario x LUI	3	372	0.623	0.601	3	372	0.669	0.571	3	372	2.94	0.033
4. Leaf anatomy	Leaf anatomy distances before enrichment planting				Leaf anatomy distances after enrichment planting				Change in Leaf anatomy distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	0.173	0.915	3	372	365.618	<0.001	3	372	454.582	<0.001
LUI	1	50	5.146	0.028	1	50	3.809	0.057	1	50	5.824	0.02
Senario x LUI	3	372	1.785	0.149	3	372	11.329	<0.001	3	372	10.655	<0.001

Continued

5. Leaf persistence	Leaf persistence distances before enrichment planting				Leaf persistence distances after enrichment planting				Change in Leaf persistence distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	0.131	0.942	3	372	39.531	<0.001	3	372	45.342	<0.001
LUI	1	50	0.072	0.789	1	50	<0.001	0.996	1	50	0.292	0.591
Senario x LUI	3	372	1.081	0.357	3	372	0.562	0.641	3	372	3.125	0.026
6. Leaf distribution	Leaf distribution distances before enrichment planting				Leaf distribution distances after enrichment planting				Change in Leaf distribution distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	1.345	0.259	3	372	61.077	<0.001	3	372	76.089	<0.001
LUI	1	50	6.831	0.012	1	50	7.999	0.007	1	50	3.056	0.087
Senario x LUI	3	372	0.689	0.559	3	372	1.21	0.306	3	372	2.256	0.082
7. Vegetative reproduction	Veg. repro. distances before enrichment planting				Veg. repro. distances after enrichment planting				Change in Veg. repro. distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	0.018	0.997	3	372	119.19	<0.001	3	372	144.694	<0.001
LUI	1	50	0.005	0.946	1	50	0.026	0.874	1	50	0.003	0.959
Senario x LUI	3	372	1.739	0.158	3	372	1.492	0.216	3	372	2.655	0.048
8. Clonal Growth Organs	CGO distances before enrichment planting				CGO distances after enrichment planting				Change in CGO distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	0.668	0.572	3	372	42.45	<0.001	3	372	44.266	<0.001
LUI	1	50	0.303	0.585	1	50	0.193	0.663	1	50	1.609	0.21
Senario x LUI	3	372	0.541	0.655	3	372	0.174	0.914	3	372	0.222	0.881
9. Lateral spread	Lateral spread distances before enrichment planting				Lateral spread distances after enrichment planting				Change in Lateral spread distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	0.291	0.832	3	372	21.263	<0.001	3	372	51.993	<0.001
LUI	1	50	4.205	0.046	1	50	1.842	0.181	1	50	10.415	0.002
Senario x LUI	3	372	0.509	0.677	3	372	1.919	0.126	3	372	11.206	<0.001

Continued

10. Physical defence	Physical defence distances before enrichment planting				Physical defence distances after enrichment planting				Change in Physical defence distances			
	nDF	dDF	F	p	nDF	dDF	F	p	nDF	dDF	F	p
Scenario	3	372	1.144	0.331	3	372	133.07	<0.001	3	372	178.762	<0.001
LUI	1	50	4.89	0.032	1	50	2.865	0.097	1	50	3.789	0.057
Senario x LUI	3	372	0.335	0.8	3	372	1.22	0.302	3	372	1.628	0.183

Table S2.2 Variance of random factors in the mixed linear models for the response of mean pairwise trait distances and survival rates to the four different scenarios (Beals, Dissim, Random and Sim) and land-use intensity, expressed as *LUI* for the years 2006 to 2010. Variances of random factors are shown for the multi-trait approaches and all single traits separately (SLA, LDMC, Height, Leaf anatomy, Leaf persistence, Leaf distribution, Vegetative reproduction, Clonal growth organs, Lateral spread and Physical defence) before, after and the level of change through enrichment planting.

Survival rates:	Survival rates one year after planting			Survival rates in the second year					
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals			
Variance of random factors	8.02E-04	2.22E-02	4.25E-02	2.08E-03	2.88E-02	4.20E-02			
Multi-Trait Approaches:	Trait distances before enrichment planting			Trait distances after enrichment planting			Change in trait distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	1.32E-05	3.70E-04	2.59E-04	1.39E-05	1.52E-04	2.12E-04	1.75E-12	6.17E-05	1.20E-04
Single Trait Approaches:									
1. SLA	SLA distances before enrichment planting			SLA distances after enrichment planting			Change in SLA distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	1.46E-04	7.47E-04	4.27E-04	6.40E-05	3.54E-04	4.18E-04	1.64E-05	1.12E-04	2.15E-04
2. LDMC	LDMC distances before enrichment planting			LDMC distances after enrichment planting			Change in LDMC distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	1.24E-04	3.49E-04	2.92E-04	4.50E-05	2.95E-04	2.91E-04	1.87E-05	9.63E-05	2.35E-04
3. Height	Height distances before enrichment planting			Height distances after enrichment planting			Change in height distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	5.23E-07	3.73E-06	1.74E-06	3.52E-07	1.72E-06	1.45E-06	5.63E-14	6.25E-07	1.10E-06

Continued

4. Leaf anatomy	Leaf anatomy distances before enrichment planting			Leaf anatomy distances after enrichment planting			Change in leaf anatomy distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	6.26E-03	8.59E-03	2.65E-03	3.25E-03	4.18E-03	2.33E-03	4.71E-04	9.81E-04	1.85E-03
5. Leaf persistence	Leaf persistence distances before enrichment planting			Leaf persistence distances after enrichment planting			Change in leaf persistence distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	8.22E-04	3.53E-03	1.83E-03	5.62E-04	1.97E-03	1.48E-03	4.15E-06	5.40E-04	1.23E-03
6. Leaf distribution	Leaf distribution distances before enrichment planting			Leaf distribution distances after enrichment planting			Change in leaf distribution distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	2.10E-11	6.94E-03	2.54E-03	3.52E-12	2.93E-03	2.28E-03	3.63E-13	1.02E-03	2.00E-03
7. Vegetative reproduction	Veg. reproduction distances before enrichment planting			Veg. reproduction distances after enrichment planting			Change in veg. reproduction distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	7.66E-12	5.29E-03	1.91E-03	9.39E-13	2.35E-03	1.75E-03	6.05E-13	7.55E-04	1.47E-03
8. Clonal growth organs	CGO distances before enrichment planting			CGO distances after enrichment planting			Change in CGO distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	9.97E-12	1.86E-03	1.36E-03	1.26E-04	5.04E-04	1.96E-03	5.23E-14	4.63E-04	2.05E-03
9. Lateral spread	Lateral spread distances before enrichment planting			Lateral spread distances after enrichment planting			Change in lateral spread distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	9.36E-04	5.89E-03	4.14E-03	2.10E-04	3.00E-03	2.84E-03	3.43E-04	5.77E-04	1.18E-03
10. Physical defence	Physical defence distances before enrichment planting			Physical defence distances after enrichment planting			Change in physical defence distances		
	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals	Exploratory	Plot	Residuals
Variance of random factors	1.18E-04	2.41E-03	2.50E-03	6.41E-04	1.20E-03	2.74E-03	1.34E-04	2.87E-04	1.76E-03

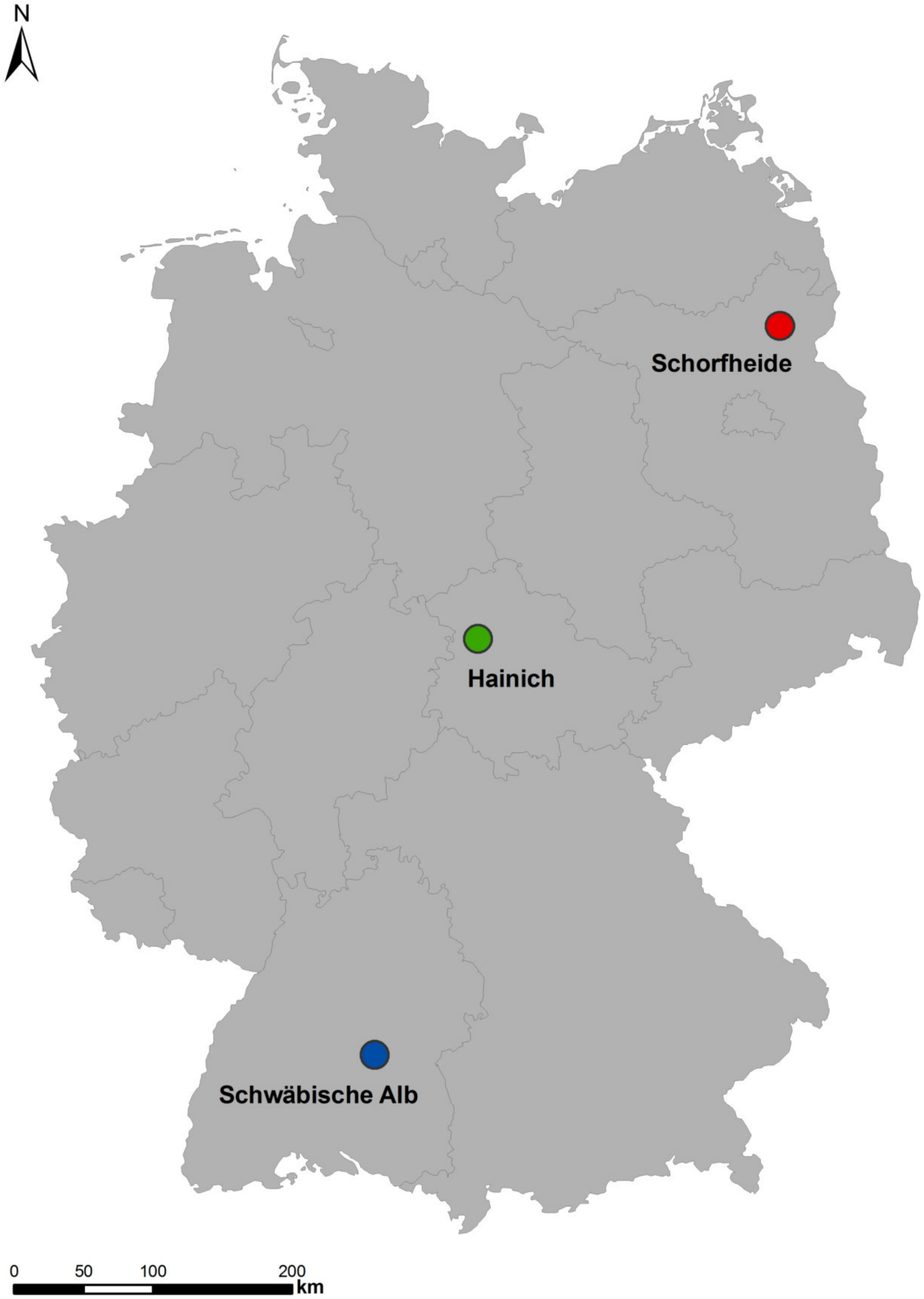

Figure S2.1 The three study regions in Germany. In each of the three regions, 18 grassland plots were selected, as shown in Fig. S2.2 – S2.4.

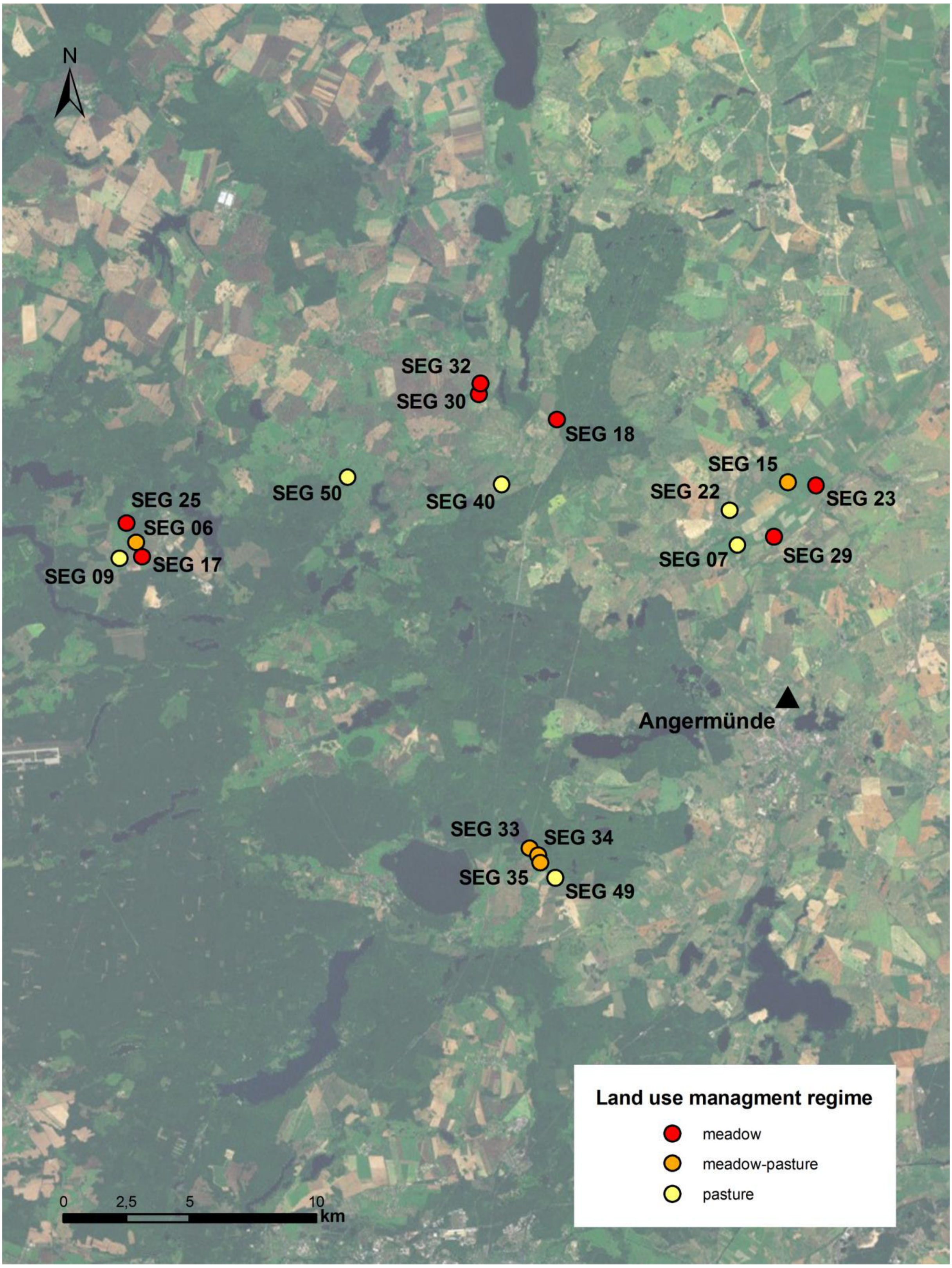

Figure S2.2 The distribution of 18 plots in the study region Schorfheide near Angermünde (Brandenburg). Meadows are shown in red, meadow-pastures in orange and pastures in yellow.

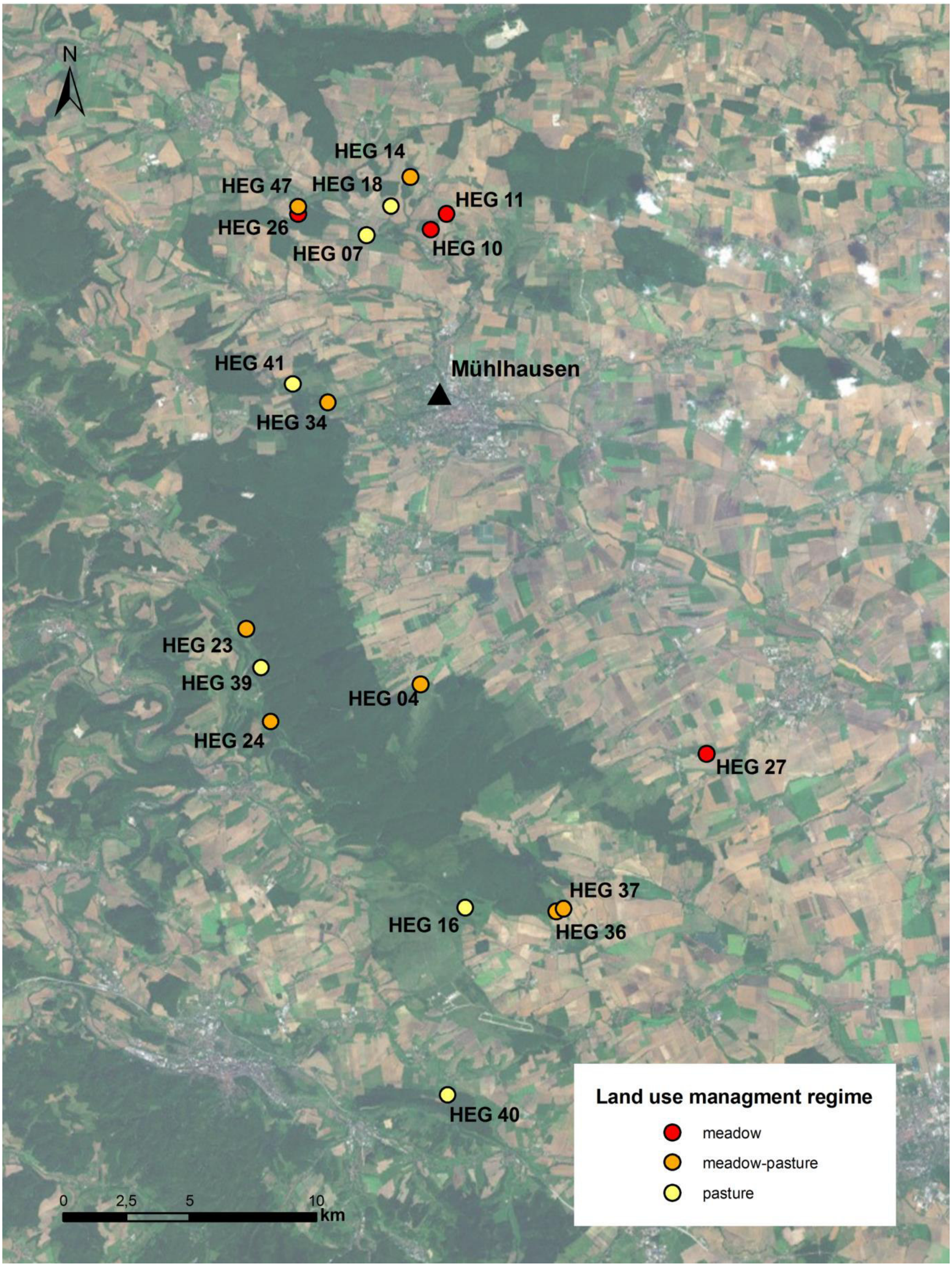

Figure S2.3 The distribution of 18 plots in the study region Hainich near Mühlhausen (Thüringen). Meadows are shown in red, meadow-pastures in orange and pastures in yellow.

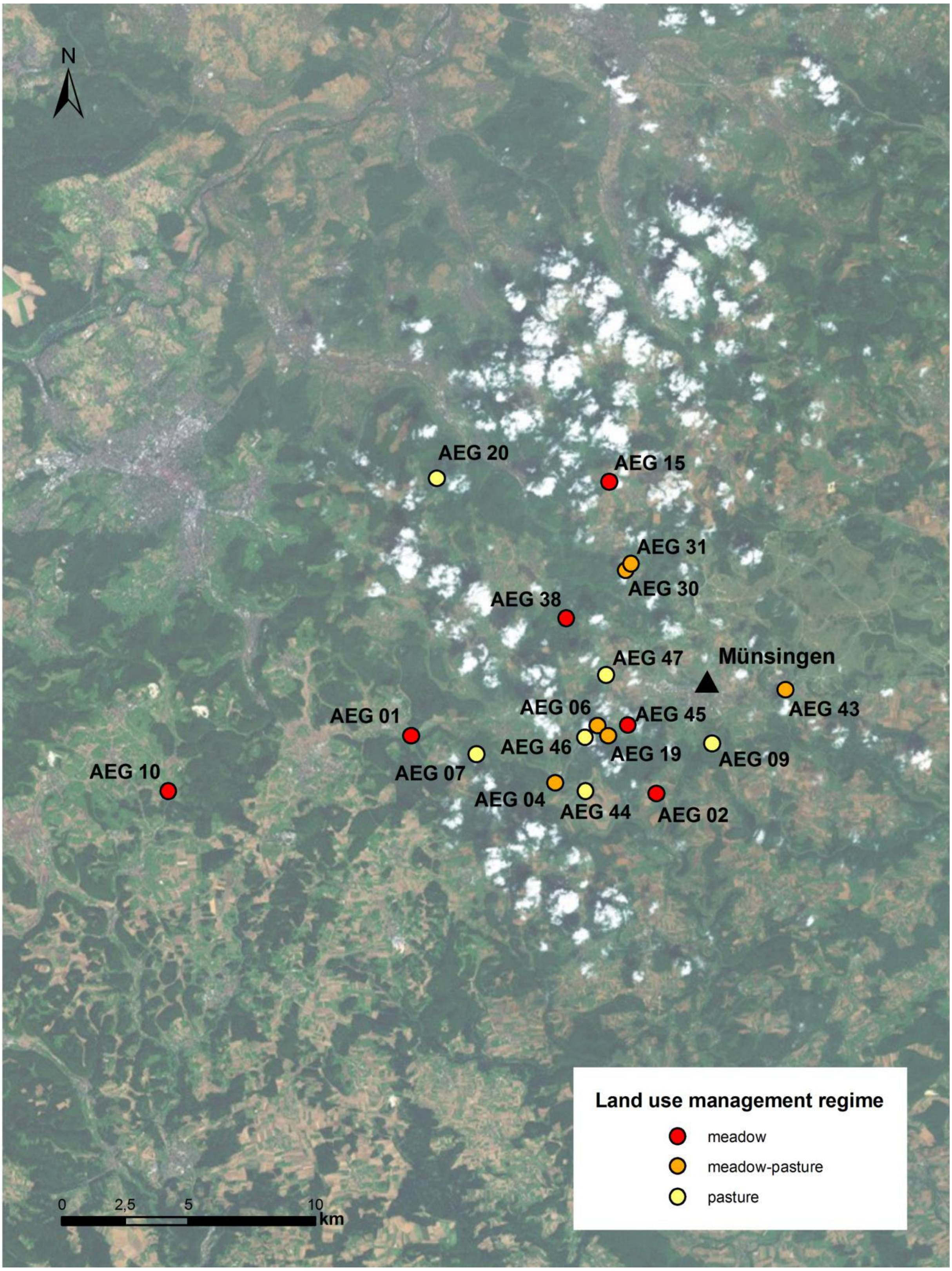

Figure S2.4 The distribution of 18 plots in the study region Schwäbische Alb near Münsingen (Baden-Württemberg). Meadows are shown in red, meadow-pastures in orange and pastures in yellow.

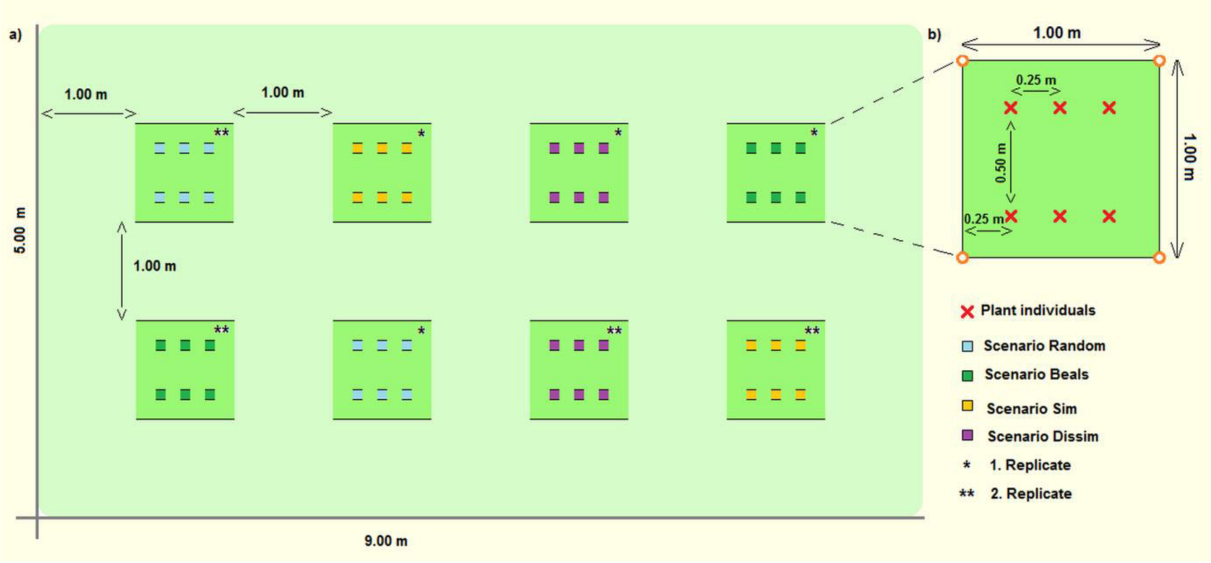

Figure S2.5 Plot design of (a) plots (5 m by 9 m) containing 8 x 1 m² subplots. Each scenario (Beals, Dissim, Random, and Sim) was replicated twice. Each Subplot (b) received 6 transplants. Subplots and transplant positions were arranged randomly.

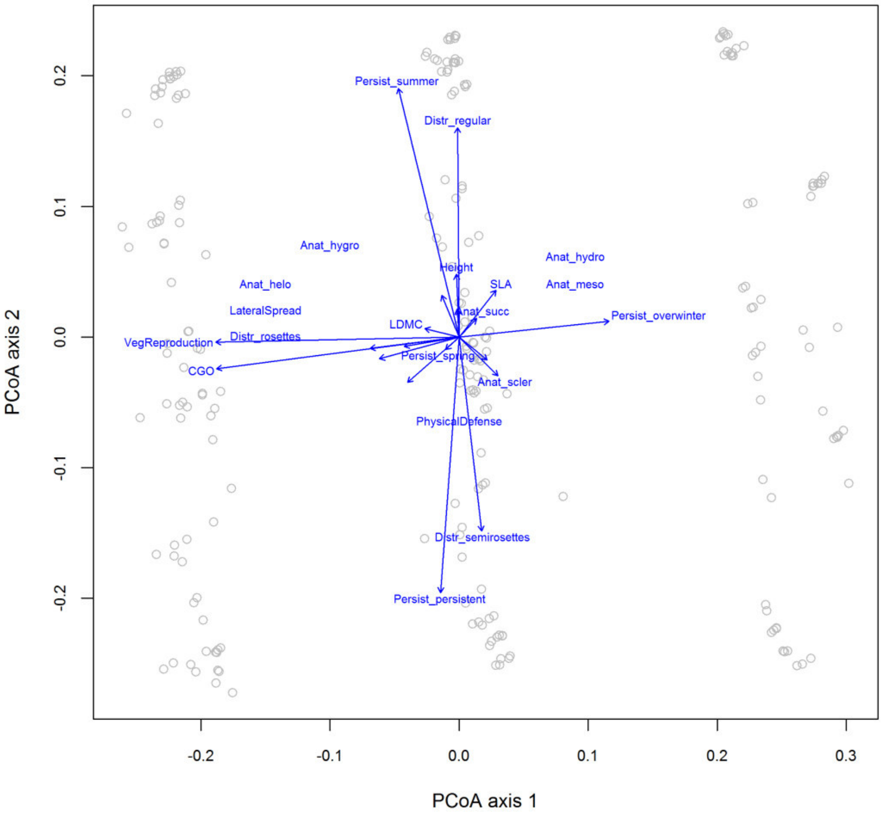

Figure S2.6 Principal coordinate analysis (PCoA) on multi-trait distances based on all 10 traits. Trait correlations with the first and second PCoA axes were derived from a post-hoc regression. For trait name abbreviations see Table 2.1.

Figure S2.7 Planting campaign in spring 2012 Schorfheide, plot SEG50. The photograph shows the six transplant individuals per subplot shortly before being planted in the grassland

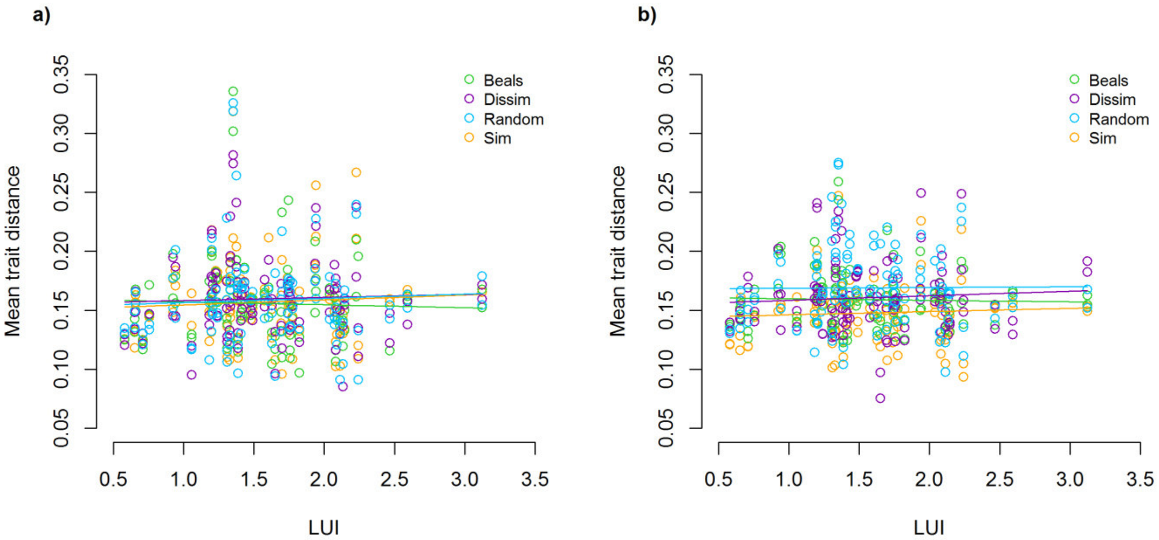

Figure S2.8 SLA distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

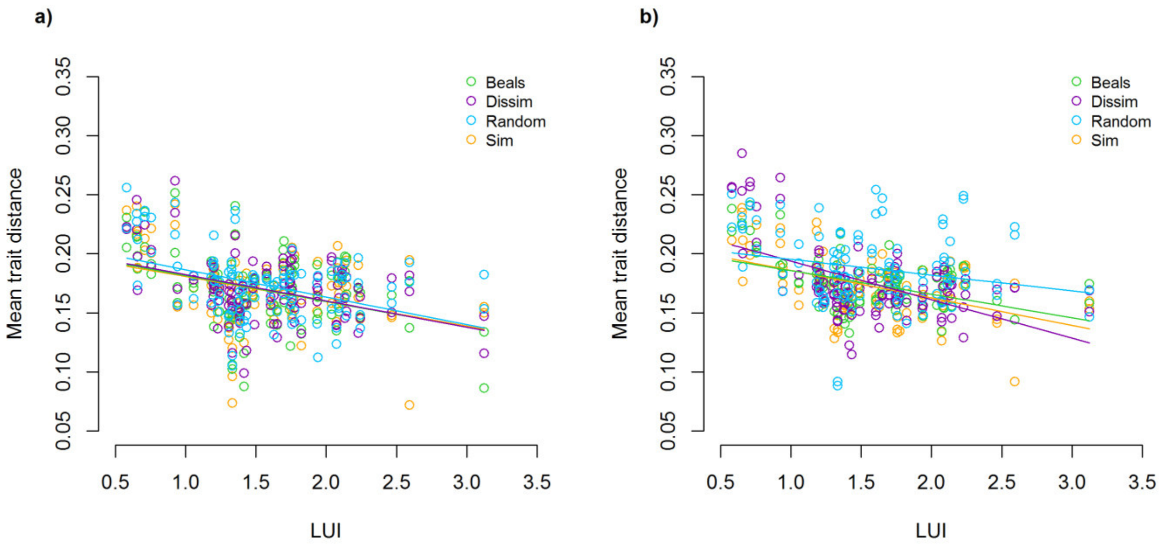

Figure S2.9 LDMC distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

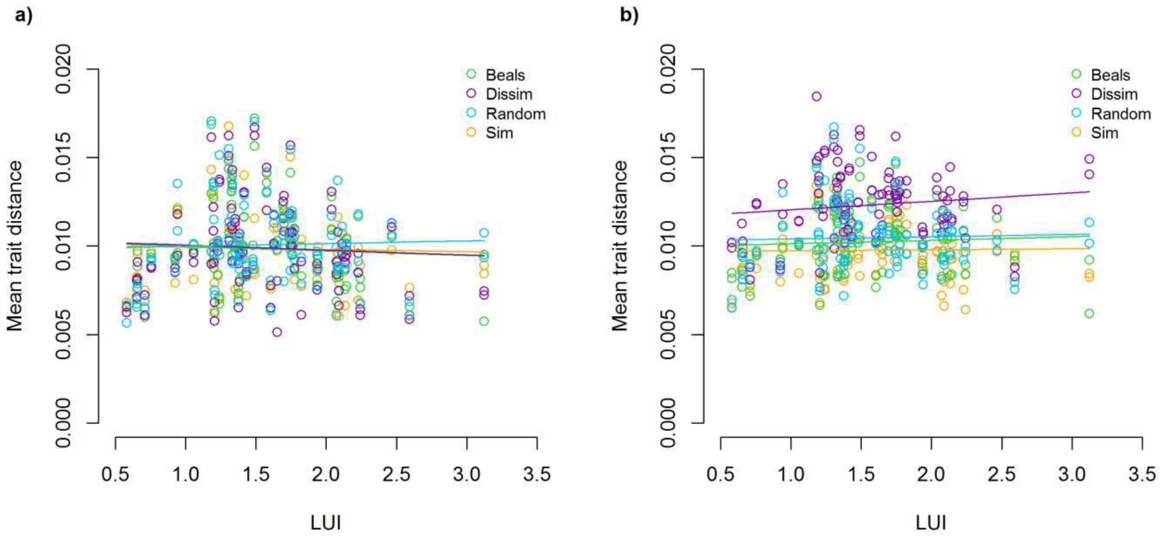

Figure S2.10 Height distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

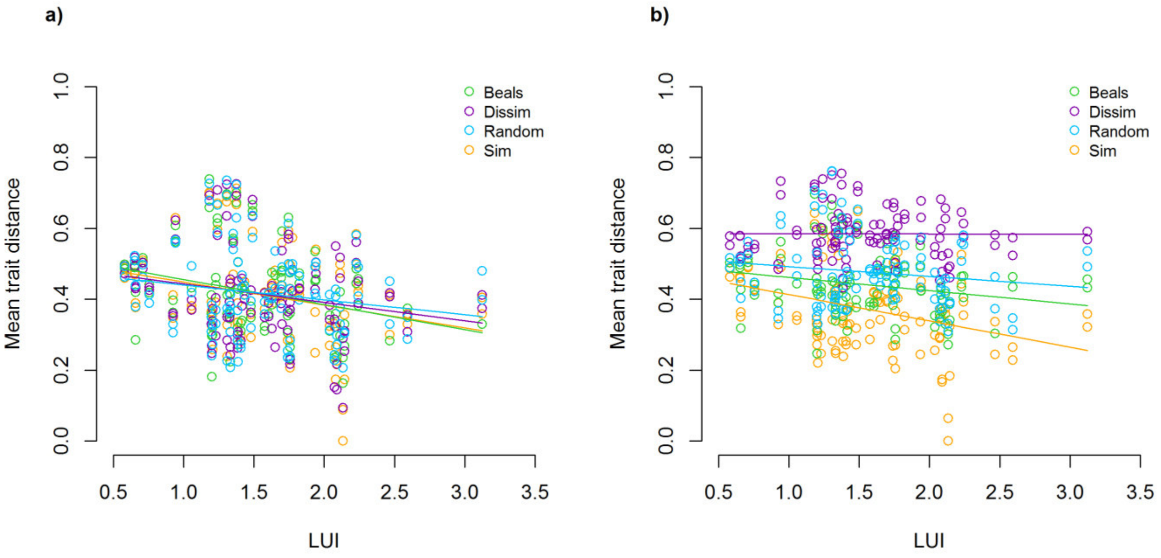

Figure S2.11 Leaf anatomy distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

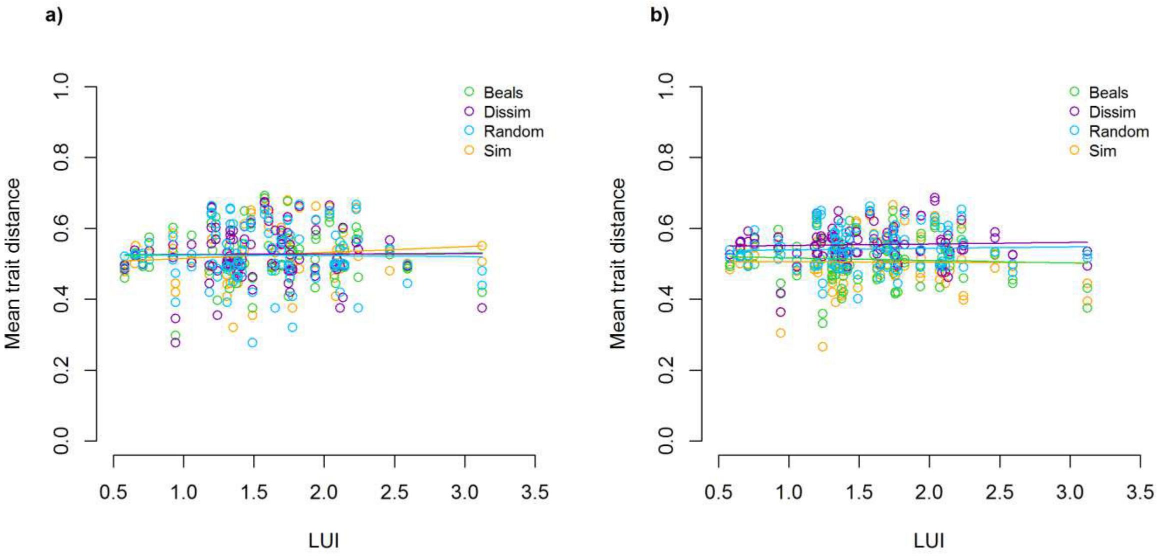

Figure S2.12 Leaf persistence distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

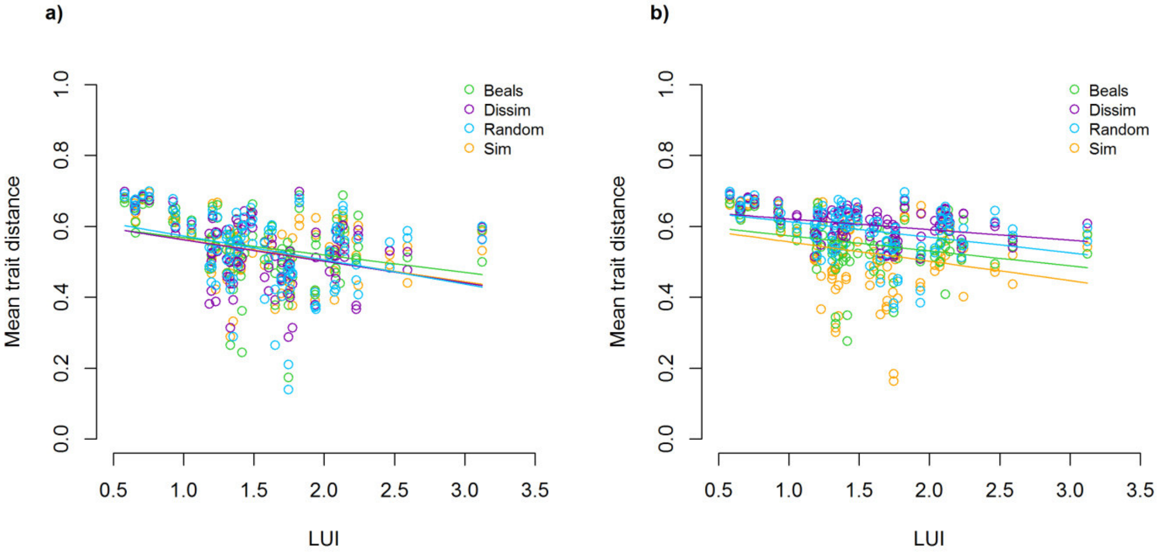

Figure S2.13 Leaf distribution distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

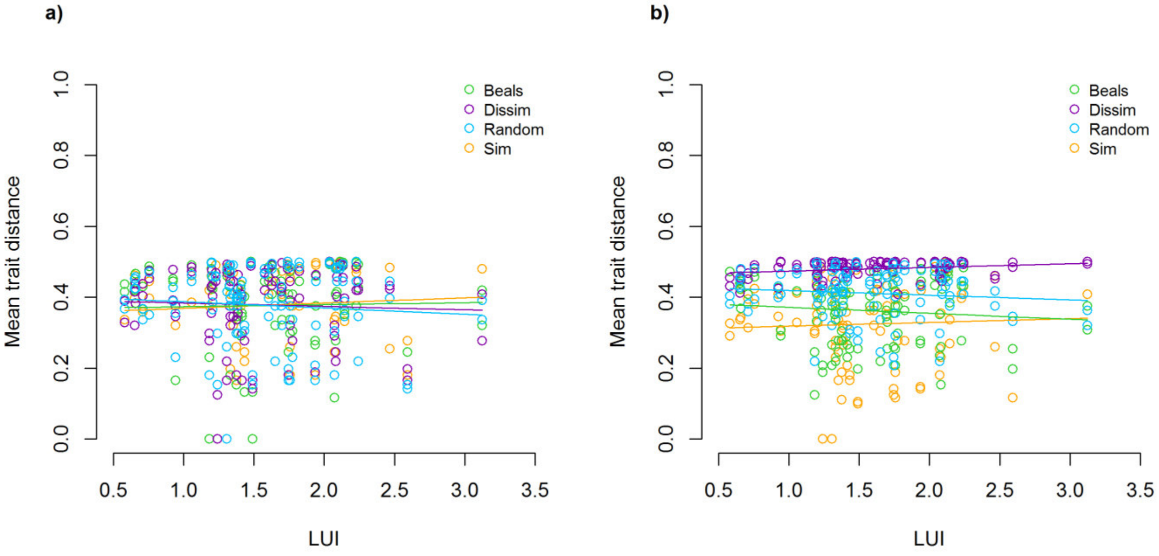

Figure S2.14 Vegetative reproduction distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

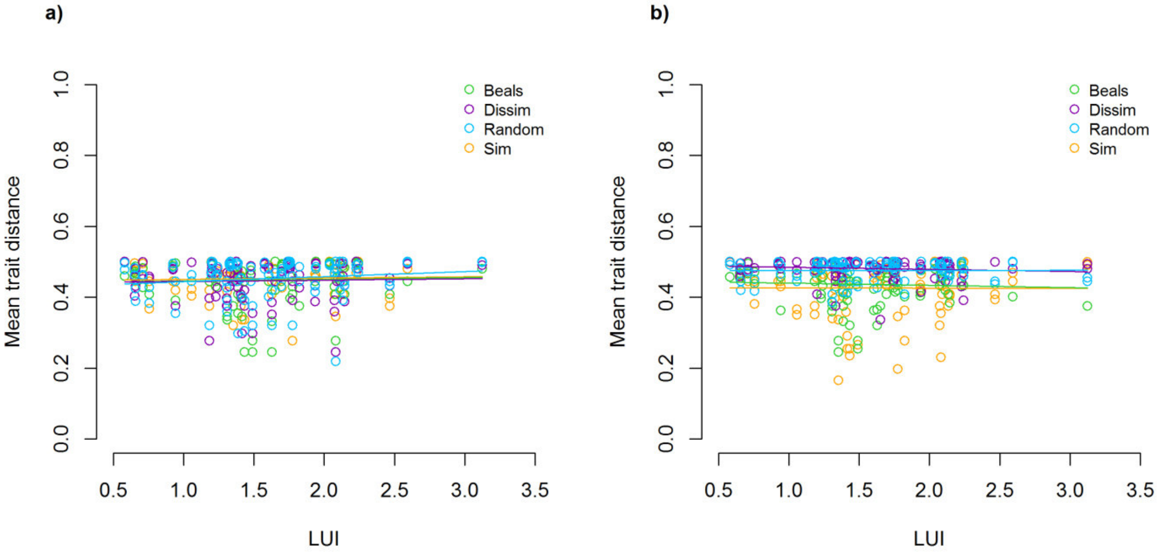

Figure S2.15 Clonal growth organs distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

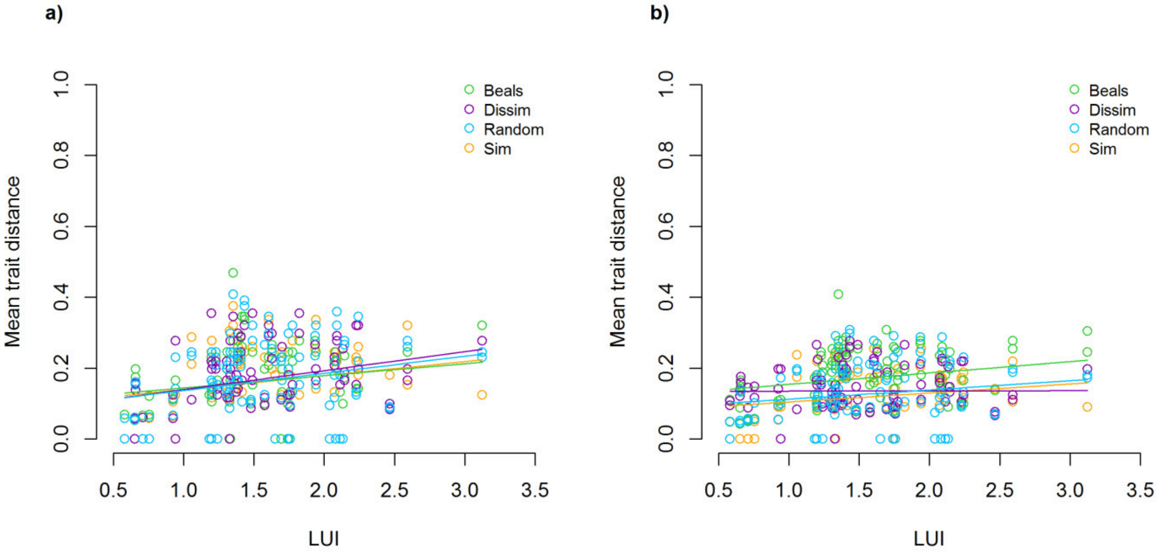

Figure S2.16 Lateral spread distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

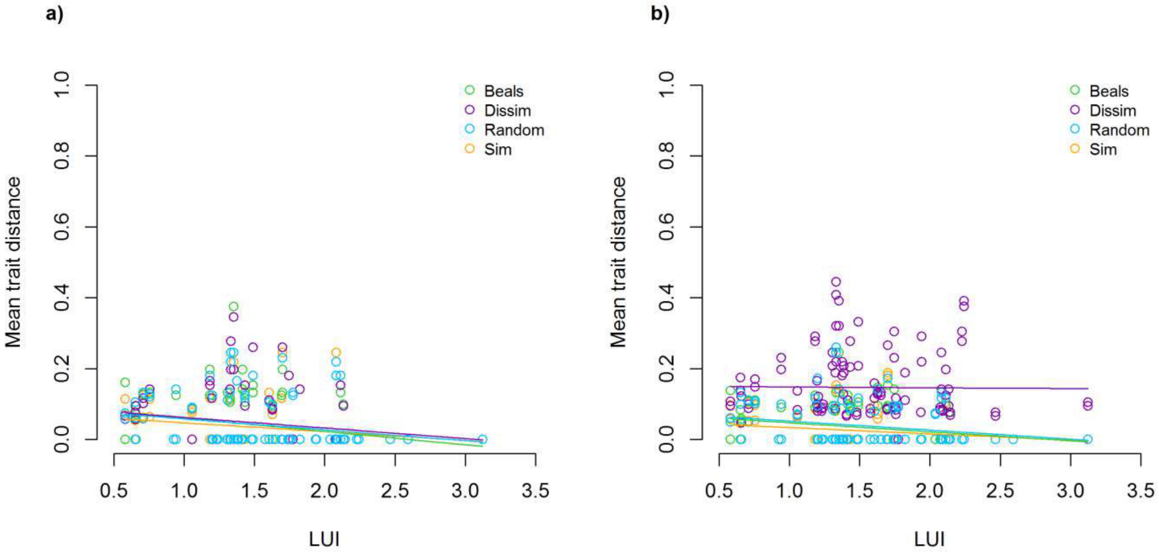

Figure S2.17 Physical defence distances as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim) (a) before and (b) after enrichment planting.

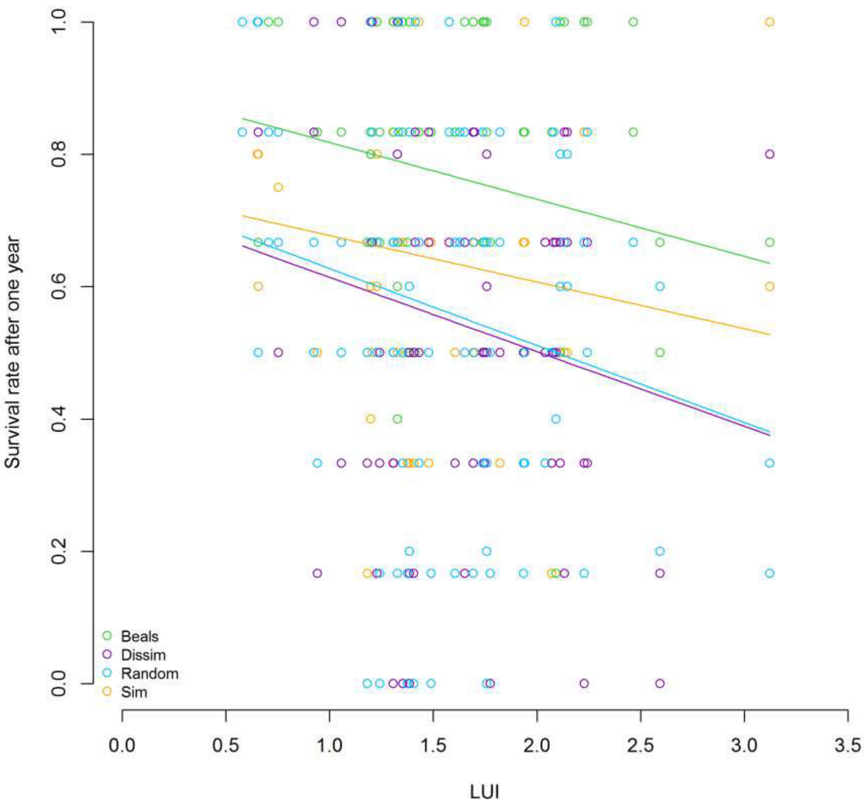

Figure S2.18 Survival rates of transplanted individuals after one year as a function of land-use intensity (*LUI*) of the four scenarios (Beals, Dissim, Random, Sim). Regression lines were obtained from a mixed model with random factors plot-nested in Exploratory (see Table 2.3).

Chapter 3 – 3.8 Supplementary Information

Table S3.1 Differences in trait values between the different scenarios. F and p refer to an ANOVA. Est. = estimated trait value for the different scenarios. Small letters refer to statistically significant differences among scenarios according to a Tukey post-hoc test.

Trait	Trait description	**F**	**P**	**Est. Beals**	**Tukey**	**Est. Dissim**	**Tukey**	**Est. Random**	**Tukey**	**Est. Sim**	**Tukey**
Specific leaf area (SLA)	Leaf area per dry mass [m²/kg]	1.76	0.15	20.36	a	20.45	a	20.44	a	21.06	a
Leaf dry matter content (LDMC)	Leaf dry mass per leaf fresh mass [mg/g]	42.98	0.00	248.18	b	223.52	d	264.06	a	235.10	c
Height	[m]	39.67	0.00	0.51	b	0.65	a	0.52	b	0.49	b
Leaf anatomy 01	leaf succulent	12.21	0.00	0.00	b	0.02	a	0.00	b	0.00	b
Leaf anatomy 02	scleromorphic	546.29	0.00	0.19	c	0.85	a	0.47	b	0.06	d
Leaf anatomy 03	mesomorphic	588.85	0.00	0.94	b	0.31	d	0.81	c	1.00	a
Leaf anatomy 04	hygromorphic	33.66	0.00	0.12	a	0.03	c	0.07	b	0.00	d
Leaf anatomy 05	helomorphic	10.10	0.00	0.05	b	0.02	c	0.04	cb	0.08	a
Leaf persistence 01	green before summer	16.82	0.00	0.00	b	0.04	a	0.03	a	0.00	b
Leaf persistence 02	green in summer	24.11	0.00	0.33	b	0.38	b	0.52	a	0.32	b
Leaf persistence 03	green in winter	50.56	0.00	0.00	c	0.10	a	0.03	b	0.00	c
Leaf persistence 04	evergreen	48.98	0.00	0.67	a	0.48	b	0.42	b	0.68	a
Leaf distribution 01	leaves distributed regularly	51.51	0.00	0.40	b	0.19	c	0.33	b	0.51	a
Leaf distribution 02	rosette	22.92	0.00	0.10	a	0.01	b	0.08	a	0.03	b
Leaf distribution 03	semi-rosette	64.55	0.00	0.50	c	0.80	a	0.59	b	0.46	c
Physical defense	Presence of hooks, spines, thorns, stinging hairs	148.05	0.00	0.01	b	0.22	a	0.02	b	0.00	b
Vegetative reproduction	Presence of stolons, rhizome, bulb, etc.	411.47	0.00	0.99	a	0.38	c	0.72	b	0.96	a

Table S3.2 Trait values of the 130 species transplanted into subplots and information on which of the four tested Scenarios the species were planted (B = Beals, D = Dissim, R = Random, S = Sim). The survival rate (Surv.) is the percentage of individuals alive at end of the experiment compared to the amount of individuals transplanted at the start. As an example of growth rate, RGR h4-5 is given. RGRh4-5 is the species mean across all individuals´ RGR height in the winter time interval (4 – 5) [cm cm $^{-1}$ week^{-1}]. NA (= not available) values for RGR height indicate that no individual of that species survived until the 5th monitoring interval. Trait values for each species include: L.A. = Leaf anatomy (categories 1 – 6); L.P. = Leaf persistence (categories 1 – 4); L.D. = Leaf distribution (categories 1 – 3); Veg. R. = Vegetative reproduction, and Phys. D. = Physical defense. For an explanation of trait categories, see SI Table S3.1.

Species	Freq.	Scen.	RGRh4-5	Surv.	SLA	LDMC	Height	L.A.1	L.A.2	L.A.3	L.A.4	L.A.5	L.A.6	L.P.1	L.P.2	L.P.3	L.P.4	L.D.1	L.D.2	L.D.3	Phys. D.	Veg. R.
Achillea millefolium	50	B,R	0.0033	0.78	11.86	274.50	0.45	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Agrimonia eupatoria	6	B,R	-0.0143	0.50	13.15	383.12	0.38	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1
Allium scorodoprasum	30	D,R	NA	0.00	11.57	255.09	0.56	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1
Allium vineale	16	D,R	NA	1.00	17.61	137.75	0.30	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1
Alopecurus pratensis	30	B,R	0.0142	0.17	16.82	355.17	0.70	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Angelica sylvestris	6	R	NA	0.00	16.54	221.31	1.15	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0
Anthoxanthum odoratum	56	B	0.0102	0.82	21.08	262.12	0.22	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Anthyllis vulneraria	16	B,S	0.0223	0.19	13.58	227.61	0.32	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Armeria maritima	6	R	-0.0122	0.00	15.89	247.83	0.27	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
Arrhenatherum elatius	46	B,R,S	0.0201	0.33	23.92	313.30	1.03	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Artemisia campestris	8	R	NA	0.00	17.15	255.77	0.45	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0
Artemisia vulgaris	12	D,R	0.0093	0.42	39.75	142.72	1.55	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0
Asperula cynanchica	8	R	-0.0343	0.00	15.88	325.06	0.17	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1
Astragalus glycyphyllos	12	S	-0.0135	0.33	32.51	184.27	1.00	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Bellis perennis	52	B,R	0.0027	0.46	29.71	180.71	0.10	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1
Betonica officinalis	14	R	0.0268	0.43	24.90	360.45	0.65	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Brachypodium pinnatum	6	R,S	-0.0036	0.67	15.04	474.77	0.55	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1
Briza media	60	B,D,R	0.0044	0.64	29.56	320.63	0.35	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Bromus erectus	12	R	0.0044	0.67	13.04	342.88	0.60	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Campanula patula	10	D,R	-0.0113	0.10	38.22	179.75	0.45	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Campanula rotundifolia	4	B	0.0284	0.75	21.12	405.83	0.20	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Carex flacca	8	R	-0.0105	0.25	10.71	514.33	0.40	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Carlina vulgaris	26	D	-0.0233	0.12	12.34	312.85	0.37	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0

Continued

Species	Freq.	Scen.	RGRh4-5	Surv.	SLA	LDMC	Height	L.A.1	L.A.2	L.A.3	L.A.4	L.A.5	L.A.6	L.P.1	L.P.2	L.P.3	L.P.4	L.D.1	L.D.2	L.D.3	Phys. D.	Veg. R.
Carum carvi	2	R	0.0185	0.50	19.14	248.72	0.55	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Centaurea jacea	42	B,R	0.0179	0.60	10.60	255.55	0.82	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Centaurea nigra	18	S	0.0261	0.50	14.81	300.81	0.45	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1
Centaurea scabiosa	28	B,D,R	0.0056	0.50	30.07	140.55	0.85	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1
Centaurea stoebe	72	D,R	-0.0016	0.22	18.28	198.45	0.85	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0
Cerastium holosteoides	18	B,S	0.0133	0.36	23.35	250.92	0.27	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Cichorium intybus	50	D,R	0.0216	0.40	22.73	174.86	0.62	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1
Cirsium acaule	8	D,R	-0.0135	0.50	8.72	222.50	0.14	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1
Cirsium arvense	4	B	-0.0354	0.25	12.03	203.27	0.90	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1
Crepis biennis	6	R	0.0309	0.17	23.02	170.46	0.85	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Crepis tectorum	22	D	0.0003	0.00	26.31	144.09	0.35	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Cynosurus cristatus	8	B,R	0.0139	0.75	23.00	302.62	0.40	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Daucus carota	4	R	-0.0055	0.50	15.11	262.57	0.55	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Dianthus carthusianorum	36	D,R	0.0263	0.36	16.44	207.73	0.30	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0
Dipsacus fullonum	98	D	0.0043	0.21	17.16	209.34	1.35	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0
Echium vulgare	6	D	-0.0269	0.17	30.73	113.18	0.56	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0
Erigeron acris	20	D,R	-0.0039	0.00	18.11	251.09	0.35	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0
Euphorbia esula	42	R,S	NA	0.00	30.42	263.27	0.45	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Festuca arundinacea	8	R	0.0037	0.50	20.27	382.86	1.20	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1
Festuca guestfalica	2	R	-0.0130	1.00	9.62	501.39	0.30	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1
Festuca nigrescens	6	R	NA	0.00	10.21	365.90	0.47	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Festuca ovina	14	D,R	0.0060	0.71	14.01	301.00	0.26	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1
Festuca pratensis	24	B,R	-0.0023	0.77	18.17	329.28	0.70	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Festuca rubra	16	B	0.0085	0.79	10.21	365.90	0.51	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Filipendula ulmaria	10	B,R	-0.0065	0.60	41.20	194.00	1.00	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1

Continued

Species	Freq.	Scen.	RGRh4-5	Surv.	SLA	LDMC	Height	L.A.1	L.A.2	L.A.3	L.A.4	L.A.5	L.A.6	L.P.1	L.P.2	L.P.3	L.P.4	L.D.1	L.D.2	L.D.3	Phys. D.	Veg. R.
Galium mollugo	10	R,S	-0.0081	0.17	29.62	231.33	0.51	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Galium pumilum	10	R	-0.0153	0.50	25.95	447.06	0.20	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Geranium pratense	2	R	0.0251	1.00	14.47	266.40	0.40	0	0	1	1	0	0	0	1	0	0	0	0	1	0	1
Geranium pusillum	6	R	NA	0.00	25.48	205.14	0.22	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Geranium pyrenaicum	2	R	0.0386	0.50	24.65	183.62	0.47	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Geranium sylvaticum	2	R	-0.0171	1.00	18.31	247.53	0.40	0	0	1	1	0	0	0	1	0	0	0	0	1	0	1
Geum rivale	12	R	0.0109	0.67	25.29	221.98	0.50	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1
Geum urbanum	12	R	-0.0059	0.83	14.15	312.29	0.75	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1
Helianthemum nummularium	6	B,R	0.0112	0.33	15.19	252.92	0.15	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1
Helichrysum arenarium	4	R	0.0000	0.00	18.17	265.53	0.20	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1
Helictotrichon pubescens	8	R	0.0015	0.50	12.60	354.92	0.65	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1
Hieracium pilosella	26	B,R,S	0.0170	0.50	14.18	295.25	0.17	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1
Holcus lanatus	82	B,R,S	0.0155	0.83	28.19	267.25	0.65	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Hypericum perforatum	14	B,R	-0.0003	0.64	18.23	366.68	0.56	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1
Hypochaeris radicata	4	R	-0.0054	1.00	33.85	97.53	0.37	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1
Jasione montana	6	R	0.0280	0.00	17.27	253.09	0.27	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Knautia arvensis	14	B,R	0.0088	0.50	21.52	176.14	0.55	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1
Koeleria pyramidata	4	R	-0.0065	1.00	13.71	325.52	0.65	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Lathyrus pratensis	10	B	-0.0039	0.30	29.84	289.71	0.65	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Leontodon autumnalis	16	B,R,S	-0.0005	0.50	26.07	171.37	0.30	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1
Leontodon hispidus	12	B,R,S	0.0157	0.50	14.97	285.42	0.28	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1
Leucanthemum vulgare	6	R	0.0476	0.50	22.67	138.10	0.50	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Linum austriacum	18	R,S	0.0083	0.33	17.84	247.85	0.45	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1
Lolium perenne	28	B,S	0.0084	0.44	18.86	251.79	0.35	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Lotus corniculatus	72	B,R,S	-0.0041	0.56	20.03	252.42	0.22	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1

Continued

Species	Freq.	Scen.	RGRh4-5	Surv.	SLA	LDMC	Height	L.A.1	L.A.2	L.A.3	L.A.4	L.A.5	L.A.6	L.P.1	L.P.2	L.P.3	L.P.4	L.D.1	L.D.2	L.D.3	Phys. D.	Veg. R.
Luzula campestris	30	B,R,S	0.0195	0.62	20.01	227.85	0.15	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Malva alcea	4	R	-0.0175	0.25	23.12	214.01	0.82	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Medicago falcata	4	S	0.0199	0.50	20.67	360.59	0.35	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1
Medicago lupulina	12	R,S	0.0213	0.08	24.20	319.07	0.37	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Medicago x varia	6	R	0.0046	0.83	24.56	239.90	0.55	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Melilotus officinalis	14	R	-0.0353	0.00	17.33	218.30	0.65	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0
Oenothera biennis	4	D	NA	0.00	15.93	238.30	1.00	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Ononis spinosa	10	D,R	-0.0405	0.50	15.91	333.94	0.45	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1
Origanum vulgare	10	R,S	-0.0116	0.60	13.24	358.58	0.40	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1
Pastinaca sativa	28	D,R	0.0146	0.27	18.12	221.48	0.94	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0
Petrorhagia prolifera	22	D	NA	0.00	17.96	268.57	0.30	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0
Peucedanum officinale	4	R	NA	0.00	13.06	303.40	1.30	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Phleum phleoides	10	D,R	0.0277	0.40	17.90	319.28	0.45	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1
Picris hieracioides	20	R,S	0.0101	0.35	21.00	327.09	0.61	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Pimpinella major	6	S	0.0174	0.67	17.93	233.00	0.60	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Pimpinella saxifraga	8	B,R	-0.0169	0.25	12.00	364.91	0.32	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0
Plantago lanceolata	12	B	0.0470	0.70	17.61	204.11	0.30	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1
Plantago major	8	D,R	NA	0.00	15.38	201.99	0.21	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1
Plantago media	6	R	0.0019	0.67	15.85	183.22	0.27	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1
Poa angustifolia	4	R	-0.0075	0.25	13.37	427.66	0.60	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Poa pratensis	4	B	-0.0011	0.75	12.04	374.79	0.55	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Potentilla argentea	74	D,R	0.0018	0.39	19.10	281.85	0.34	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
Prunella vulgaris	56	B,R,S	0.0096	0.68	23.29	222.56	0.17	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Pseudolysimachion spicatum	22	D,R	0.0167	0.50	41.11	128.24	0.27	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1
Ranunculus acris	76	B,R,S	0.0131	0.61	14.50	256.95	0.75	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1

Continued

Species	Freq.	Scen.	RGRh4-5	Surv.	SLA	LDMC	Height	L.A.1	L.A.2	L.A.3	L.A.4	L.A.5	L.A.6	L.P.1	L.P.2	L.P.3	L.P.4	L.D.1	L.D.2	L.D.3	Phys. D.	Veg. R.
Ranunculus bulbosus	2	R	0.0246	0.00	21.46	190.57	0.25	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1
Ranunculus repens	40	B,R	0.0270	0.66	20.58	186.01	0.27	0	0	0	1	1	0	0	0	0	1	0	0	1	0	1
Rumex acetosa	126	B,R,S	0.0355	0.76	23.10	116.20	0.52	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Rumex crispus	4	R,S	0.0399	0.75	15.36	199.38	0.90	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0
Rumex obtusifolius	16	D,R	0.0161	0.63	23.98	160.04	0.85	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0
Rumex thyrsiflorus	12	R,S	0.0285	0.67	18.36	208.54	0.75	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Salvia pratensis	26	D,R	0.0190	0.35	20.38	186.37	0.45	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Sanguisorba minor	8	B,R	-0.0008	0.25	13.63	307.29	0.32	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0
Saponaria officinalis	6	R	0.0173	0.67	20.09	363.46	0.55	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Scabiosa columbaria	18	B,R	-0.0073	0.33	16.00	217.36	0.45	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0
Scirpus sylvaticus	52	S	-0.0068	0.25	21.60	267.20	0.65	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1
Sedum maximum	12	D	0.0475	0.17	17.74	172.98	0.55	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1
Senecio jacobaea	56	R,S	-0.0008	0.64	13.40	258.00	0.51	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Silaum silaus	2	S	0.0017	1.00	13.93	293.66	0.65	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Silene dioica	4	R	0.0117	0.50	37.11	133.14	0.60	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Silene flos-cuculi	64	B,R,S	0.0358	0.63	20.07	186.34	0.55	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1
Silene latifolia	66	R,S	0.0191	0.39	19.93	170.90	0.64	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Silene otites	30	D,R	0.0050	0.30	15.41	263.07	0.40	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1
Silene vulgaris	4	R	-0.0114	0.50	22.70	202.72	0.35	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0
Symphytum officinale	6	R	0.0171	0.33	16.73	117.82	0.75	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0
Tanacetum vulgare	2	R	0.0163	0.00	17.25	262.16	0.90	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1
Thymus pulegioides	12	R,S	-0.0066	0.25	17.05	355.82	0.25	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1
Torilis japonica	10	R	0.0016	0.10	22.45	399.73	0.75	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Tragopogon pratensis	6	R	0.0145	0.33	34.42	203.53	0.38	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Trifolium dubium	10	D,R	NA	0.00	35.00	236.22	0.17	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0

Continued

Species	Freq.	Scen.	RGRh4-5	Surv.	SLA	LDMC	Height	L.A.1	L.A.2	L.A.3	L.A.4	L.A.5	L.A.6	L.P.1	L.P.2	L.P.3	L.P.4	L.D.1	L.D.2	L.D.3	Phys. D.	Veg. R.
Trifolium montanum	2	R	NA	0.00	21.65	281.33	0.27	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0
Trisetum flavescens	50	B,R,S	0.0092	0.58	25.05	312.49	0.55	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Valeriana officinalis	18	D,R	0.0098	0.44	30.56	122.96	1.15	0	0	0	1	1	0	0	1	0	0	0	0	1	0	1
Veronica teucrium	4	R	-0.0229	0.50	20.34	238.47	0.60	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1
Vicia cracca	18	B,R	0.0051	0.11	20.81	298.67	0.75	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
Vicia sepium	4	S	0.0360	1.00	23.41	236.04	0.45	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1
Vicia villosa	4	D,R	0.0237	0.00	42.45	234.87	0.35	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0

Table S3.3 Number of included plots for calculating the mean of climatic variables.

	Air temperature	Soil temperature	Relative air humidity	Soil moisture
Veg. Period 2012	n = 48	n = 41	n = 46	n = 49
Winter 2012/2013	n = 51	n = 50	n = 51	n = 53
Veg. Period 2013	n = 52	n = 50	n = 52	n = 52

Table S3.4 Variance partitioning of RGR for all variables at all time intervals (1 – 4 = vegetation period 2012; 4 – 5 = winter 2012/2013; 5 – 7 = vegetation period 2013), and aboveground biomass, LDMC and SLA at the final harvest in September 2013), exclusively explained by plot (a), scenario (b), species (c) traits (d), and jointly by two (e, f, g, h, i, j) or three of these factors (k, l, m, n) or all of them (o), as well as residual variance (p). For an illustration of variance components a to p see Fig. 3.1. All components add up to 1. p. proj. area = plant projection area. Traits included Multi-trait FD, SLA FD/CWM, LDMC FD/CWM and Height FD /CWM.

	a	**b**	**c**	**d**	**e**	**f**	**g**	**h**	**i**	**j**	**k**	**l**	**m**	**n**	**o**	**p**	**Plot**	**Scenario**	**Species**	**Trait**
RGR height 1 - 4 ~ Multi-trait FD	0.126	0	0.375	0	0	0.042	0	0.001	0	0.001	0	0.003	0.008	0.004	0	0.452	0.123	0.051	0.422	0.012
RGR height 1 - 4 ~ SLA FD	0.127	0	0.375	0	0	0.049	0	0	0	0.001	0	0.003	0.001	0	0	0.452	0.123	0.051	0.422	0.001
RGR height 1 - 4 ~ LDMC FD	0.128	0	0.376	0	0	0.048	0	0	0	0	0	0.002	0.001	0.002	0	0.452	0.123	0.051	0.422	0.003
RGR height 1 - 4 ~ Height FD	0.109	0	0.376	0	0	0.049	0	0.017	0	0	0	0	0.001	0	0.005	0.452	0.123	0.051	0.422	0.018
RGR height 1 - 4 ~ SLA CWM	0.127	0	0.375	0	0	0.049	0	0	0	0	0	0.002	0	0.001	0	0.452	0.123	0.051	0.422	0.003
RGR height 1 - 4 ~ LDMC CWM	0.127	0	0.376	0	0	0.05	0	0	0	0	0	0.002	0	0	0	0.452	0.123	0.051	0.422	0
RGR height 1 - 4 ~ Height CWM	0.125	0	0.376	0	0	0.05	0	0.002	0	0	0	0.001	0	0	0	0.452	0.123	0.051	0.422	0

Continued

	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	Plot	Scenario	Species	Trait
RGR p. proj. area 1 - 4 ~ Multi-trait FD	0.126	0.001	0.199	0.005	0	0	0.01	0	0	0.004	0	0.001	0.001	0	0	0.665	0.127	0	0.209	0
RGR p. proj. area 1 - 4 ~ SLA FD	0.122	0	0.2	0.001	0	0	0.009	0	0	0.003	0	0	0	0	0	0.669	0.127	0	0.209	0
RGR p. proj. area 1 - 4 ~ LDMC FD	0.123	0.001	0.2	0.002	0	0	0.008	0	0	0.003	0	0	0	0	0	0.668	0.127	0	0.209	0
RGR p. proj. area 1 - 4 ~ Height FD	0.098	0	0.203	0	0	0	0.012	0.024	0	0	0	0	0	0	0.001	0.67	0.127	0	0.209	0.018
RGR p. proj. area 1 - 4 ~ SLA CWM	0.122	0	0.203	0	0	0	0.001	0	0	0	0	0	0	0.005	0	0.67	0.127	0	0.209	0.004
RGR p. proj. area 1 - 4 ~ LDMC CWM	0.122	0.001	0.202	0.002	0	0	0	0	0	0.001	0	0	0	0.006	0	0.667	0.127	0	0.209	0.008
RGR p. proj. area 1 - 4 ~ Height CWM	0.109	0	0.202	0	0	0	0.008	0.012	0	0.001	0	0	0	0	0	0.669	0.127	0	0.209	0.013
RGR leaf length 1 - 4 ~ Multi-trait FD	0.129	0.004	0.205	0.002	0	0.002	0.003	0	0	0.001	0.001	0.004	0.002	0	0	0.656	0.13	0.008	0.213	0
RGR leaf length 1 - 4 ~ SLA FD	0.126	0.003	0.205	0	0	0.004	0.003	0	0	0	0	0.002	0	0	0	0.658	0.13	0.008	0.213	0
RGR leaf length 1 - 4 ~ LDMC FD	0.126	0.004	0.205	0	0	0.004	0.001	0.001	0	0	0	0.002	0	0.001	0	0.658	0.13	0.008	0.213	0.003
RGR leaf length 1 - 4 ~ Height FD	0.105	0.003	0.206	0.001	0	0.003	0.004	0.022	0	0	0	0	0	0	0.002	0.657	0.13	0.008	0.213	0.021
RGR leaf length 1 - 4 ~ SLA CWM	0.129	0.003	0.206	0.002	0	0.003	0.002	0	0	0	0	0.002	0	0	0	0.656	0.13	0.008	0.213	0
RGR leaf length 1 - 4 ~ LDMC CWM	0.126	0.003	0.206	0	0	0.004	0	0.001	0	0	0	0.002	0	0.002	0	0.658	0.13	0.008	0.213	0.003
RGR leaf length 1 - 4 ~ Height CWM	0.114	0.003	0.206	0	0	0.004	0.001	0.012	0	0	0	0	0	0.001	0.001	0.658	0.13	0.008	0.213	0.015
RGR leaf number 1 - 4 ~ Multi-trait FD	0.043	0.002	0.202	0	0	0.009	0.014	0	0	0	0	0	0	0	0	0.731	0.057	0.01	0.224	0
RGR leaf number 1 - 4 ~ SLA FD	0.044	0.002	0.202	0	0	0.009	0.014	0	0	0	0	0	0	0	0	0.731	0.057	0.01	0.224	0
RGR leaf number 1 - 4 ~ LDMC FD	0.044	0.002	0.202	0	0	0.009	0.014	0	0	0	0	0	0	0	0	0.731	0.057	0.01	0.224	0
RGR leaf number 1 - 4 ~ Height FD	0.044	0.002	0.202	0	0	0.009	0.014	0	0	0	0	0	0	0	0	0.731	0.057	0.01	0.224	0
RGR leaf number 1 - 4 ~ SLA CWM	0.044	0.001	0.203	0.002	0	0.008	0.015	0	0	0	0	0	0	0	0	0.729	0.057	0.01	0.224	0
RGR leaf number 1 - 4 ~ LDMC CWM	0.043	0.001	0.202	0	0	0.009	0.015	0.001	0	0	0	0	0	0	0	0.73	0.057	0.01	0.224	0
RGR leaf number 1 - 4 ~ Height CWM	0.043	0.002	0.202	0	0	0.009	0.015	0	0	0	0	0	0	0	0	0.731	0.057	0.01	0.224	0
RGR height 4 - 5 ~ Multi-trait FD	0.351	0.002	0.145	0	0.001	0.033	0	0.006	0	0	0	0	0	0	0	0.479	0.342	0.022	0.163	0.003
RGR height 4 - 5 ~ SLA FD	0.353	0.001	0.146	0	0.001	0.033	0	0.003	0	0	0	0	0	0	0	0.479	0.342	0.022	0.163	0.003
RGR height 4 - 5 ~ LDMC FD	0.348	0.001	0.145	0	0	0.033	0	0.008	0	0.001	0.001	0	0	0	0	0.479	0.342	0.022	0.163	0.007
RGR height 4 - 5 ~ Height FD	0.334	0.001	0.146	0.001	0.001	0.033	0	0.022	0	0	0	0	0	0.003	0.002	0.477	0.342	0.022	0.163	0.027
RGR height 4 - 5 ~ SLA CWM	0.359	0.001	0.146	0.002	0.001	0.033	0	0	0	0	0	0	0	0	0	0.477	0.342	0.022	0.163	0

Continued

	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	Plot	Scenario	Species	Trait
RGR height 4 - 5 ~ LDMC CWM	0.352	0.002	0.146	0	0.001	0.033	0	0.005	0	0	0	0	0	0	0.001	0.478	0.342	0.022	0.163	0.004
RGR height 4 - 5 ~ Height CWM	0.352	0.001	0.146	0	0.001	0.032	0	0.004	0	0	0	0	0	0.001	0	0.479	0.342	0.022	0.163	0.006
RGR p. proj. area 4 - 5 ~ Multi-trait FD	0.204	0	0.135	0.001	0.001	0.049	0.012	0.001	0	0	0	0	0	0	0	0.61	0.206	0.038	0.185	0
RGR p. proj. area 4 - 5 ~ SLA FD	0.206	0	0.136	0.001	0	0.049	0.01	0	0	0	0	0	0	0.002	0	0.61	0.206	0.038	0.185	0
RGR p. proj. area 4 - 5 ~ LDMC FD	0.205	0	0.135	0.003	0	0.05	0.011	0	0	0	0	0	0	0.001	0	0.608	0.206	0.038	0.185	0.002
RGR p. proj. area 4 - 5 ~ Height FD	0.204	0	0.135	0.003	0.001	0.051	0.01	0.001	0	0	0	0	0	0.003	0.003	0.607	0.206	0.038	0.185	0.007
RGR p. proj. area 4 - 5 ~ SLA CWM	0.203	0	0.136	0.004	0	0.049	0.014	0.001	0	0	0	0	0	0	0	0.607	0.206	0.038	0.185	0.001
RGR p. proj. area 4 - 5 ~ LDMC CWM	0.199	0	0.135	0	0.001	0.049	0.015	0.005	0	0	0	0	0	0	0.001	0.611	0.206	0.038	0.185	0.002
RGR p. proj. area 4 - 5 ~ Height CWM	0.203	0	0.135	0	0.001	0.049	0.011	0.001	0	0	0	0	0	0.002	0.001	0.611	0.206	0.038	0.185	0.003
RGR leaf length 4 - 5 ~ Multi-trait FD	0.27	0	0.106	0	0	0.025	0.032	0.005	0	0	0	0	0	0.006	0	0.565	0.305	0.016	0.161	0.009
RGR leaf length 4 - 5 ~ SLA FD	0.273	0	0.106	0	0	0.025	0.035	0.003	0	0	0	0	0	0.003	0	0.566	0.305	0.016	0.161	0.005
RGR leaf length 4 - 5 ~ LDMC FD	0.266	0	0.105	0	0	0.025	0.025	0.009	0	0	0	0	0	0.012	0	0.565	0.305	0.016	0.161	0.022
RGR leaf length 4 - 5 ~ Height FD	0.265	0	0.106	0.001	0	0.026	0.033	0.011	0	0	0	0	0	0.004	0.003	0.564	0.305	0.016	0.161	0.018
RGR leaf length 4 - 5 ~ SLA CWM	0.278	0	0.107	0.002	0	0.025	0.035	0	0	0	0	0	0	0.003	0	0.563	0.305	0.016	0.161	0.001
RGR leaf length 4 - 5 ~ LDMC CWM	0.274	0	0.106	0	0	0.025	0.039	0.002	0	0	0	0	0	0	0	0.565	0.305	0.016	0.161	0
RGR leaf length 4 - 5 ~ Height CWM	0.272	0	0.106	0	0	0.025	0.031	0.004	0	0	0	0	0	0.006	0.002	0.566	0.305	0.016	0.161	0.011
RGR leaf number 4 - 5 ~ Multi-trait FD	0.091	0	0.202	0	0.001	0.019	0.049	0.001	0	0	0	0	0	0.004	0.001	0.642	0.139	0.012	0.266	0.005
RGR leaf number 4 - 5 ~ SLA FD	0.087	0	0.201	0	0.001	0.019	0.046	0.005	0	0	0	0	0	0.007	0	0.642	0.139	0.012	0.266	0.011
RGR leaf number 4 - 5 ~ LDMC FD	0.089	0	0.201	0	0.001	0.019	0.048	0.003	0	0	0	0	0	0.005	0.001	0.642	0.139	0.012	0.266	0.008
RGR leaf number 4 - 5 ~ Height FD	0.093	0	0.202	0.002	0.001	0.02	0.053	0	0	0	0	0	0	0	0	0.64	0.139	0.012	0.266	0.001
RGR leaf number 4 - 5 ~ SLA CWM	0.09	0	0.202	0	0.001	0.019	0.054	0.002	0	0	0	0	0	0	0	0.642	0.139	0.012	0.266	0.001
RGR leaf number 4 - 5 ~ LDMC CWM	0.089	0	0.202	0	0.001	0.019	0.053	0.003	0	0	0	0	0	0	0	0.642	0.139	0.012	0.266	0.003
RGR leaf number 4 - 5 ~ Height CWM	0.091	0	0.202	0	0.001	0.019	0.051	0.001	0	0	0	0	0	0.002	0	0.642	0.139	0.012	0.266	0.001
RGR height 5 - 7 ~ Multi-trait FD	0.375	0.002	0.16	0	0.004	0.016	0.017	0.016	0	0	0	0	0	0	0	0.423	0.4	0.012	0.182	0.01
RGR height 5 - 7 ~ SLA FD	0.379	0.002	0.159	0	0.004	0.016	0.01	0.011	0	0.001	0	0	0.001	0.005	0	0.422	0.4	0.012	0.182	0.017

Continued

	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	Plot	Scenario	Species	Trait
RGR height 5 - 7 ~ LDMC FD	0.36	0.002	0.16	0	0.002	0.016	0.014	0.031	0	0	0.002	0	0	0.001	0	0.422	0.4	0.012	0.182	0.029
RGR height 5 - 7 ~ Height FD	0.388	0.002	0.16	0	0.004	0.016	0.013	0.003	0	0	0	0	0	0.003	0	0.422	0.4	0.012	0.182	0.005
RGR height 5 - 7 ~ SLA CWM	0.387	0.002	0.16	0	0.004	0.016	0.012	0.003	0	0	0	0	0	0.003	0	0.422	0.4	0.012	0.182	0.005
RGR height 5 - 7 ~ LDMC CWM	0.391	0.002	0.16	0	0.004	0.016	0.015	0	0	0	0	0	0	0	0.001	0.423	0.4	0.012	0.182	0.001
RGR height 5 - 7 ~ Height CWM	0.39	0.002	0.159	0	0.003	0.017	0.014	0.001	0	0	0	0	0	0.002	0.001	0.422	0.4	0.012	0.182	0.004
RGR p. proj. area 5 - 7 ~ Multi-trait FD	0.181	0	0.159	0.001	0.001	0.003	0	0.007	0	0	0	0	0	0.002	0.001	0.656	0.183	0	0.155	0.01
RGR p. proj. area 5 - 7 ~ SLA FD	0.177	0	0.157	0	0.001	0.002	0	0.011	0	0.002	0	0	0	0.007	0	0.657	0.183	0	0.155	0.019
RGR p. proj. area 5 - 7 ~ LDMC FD	0.176	0	0.159	0	0	0.002	0	0.012	0	0	0.001	0	0	0.004	0	0.658	0.183	0	0.155	0.015
RGR p. proj. area 5 - 7 ~ Height FD	0.187	0	0.159	0	0.001	0.002	0	0.001	0	0	0	0	0	0.001	0	0.658	0.183	0	0.155	0.001
RGR p. proj. area 5 - 7 ~ SLA CWM	0.183	0	0.159	0	0.001	0.002	0	0.005	0	0	0	0	0	0.006	0	0.658	0.183	0	0.155	0.01
RGR p. proj. area 5 - 7 ~ LDMC CWM	0.189	0	0.158	0.001	0.001	0.002	0	0	0	0.001	0	0	0	0	0	0.657	0.183	0	0.155	0
RGR p. proj. area 5 - 7 ~ Height CWM	0.184	0	0.158	0	0.001	0.002	0	0.004	0	0.001	0	0	0	0.003	0	0.658	0.183	0	0.155	0.007
RGR leaf length 5 - 7 ~ Multi-trait FD	0.312	0	0.097	0.004	0	0.001	0.043	0	0	0	0	0.005	0.001	0.008	0	0.533	0.365	0.003	0.152	0.01
RGR leaf length 5 - 7 ~ SLA FD	0.289	0	0.095	0.004	0	0.002	0.038	0.023	0	0.002	0	0.001	0	0.013	0.001	0.533	0.365	0.003	0.152	0.043
RGR leaf length 5 - 7 ~ LDMC FD	0.295	0	0.098	0.001	0	0.002	0.029	0.017	0	0	0	0.004	0	0.022	0	0.536	0.365	0.003	0.152	0.038
RGR leaf length 5 - 7 ~ Height FD	0.311	0	0.097	0	0	0.002	0.049	0.001	0	0	0	0.002	0	0.003	0	0.538	0.365	0.003	0.152	0.003
RGR leaf length 5 - 7 ~ SLA CWM	0.307	0	0.097	0	0	0.003	0.041	0.005	0	0	0	0.003	0	0.01	0	0.537	0.365	0.003	0.152	0.014
RGR leaf length 5 - 7 ~ LDMC CWM	0.313	0	0.096	0	0	0.003	0.051	0	0	0.001	0	0.002	0	0.001	0	0.537	0.365	0.003	0.152	0
RGR leaf length 5 - 7 ~ Height CWM	0.32	0	0.094	0.007	0	0.002	0.052	0	0	0.003	0	0.002	0	0	0	0.53	0.365	0.003	0.152	0.002
RGR leaf number 5 - 7 ~ Multi-trait FD	0.079	0	0.193	0	0	0.007	0.014	0.004	0	0	0	0	0	0	0	0.711	0.092	0.002	0.209	0.001
RGR leaf number 5 - 7 ~ SLA FD	0.08	0	0.188	0	0	0.007	0.008	0.003	0	0.005	0	0	0	0.004	0	0.711	0.092	0.002	0.209	0.011
RGR leaf number 5 - 7 ~ LDMC FD	0.083	0	0.193	0	0	0.007	0.011	0	0	0	0	0	0	0.001	0	0.711	0.092	0.002	0.209	0
RGR leaf number 5 - 7 ~ Height FD	0.083	0	0.193	0	0	0.007	0.012	0	0	0	0	0	0	0	0	0.711	0.092	0.002	0.209	0
RGR leaf number 5 - 7 ~ SLA CWM	0.08	0	0.189	0	0	0.006	0.013	0.003	0	0.003	0	0	0.001	0	0	0.711	0.092	0.002	0.209	0.006
RGR leaf number 5 - 7 ~ LDMC CWM	0.083	0	0.191	0	0	0.007	0.014	0	0	0.002	0	0	0	0	0	0.711	0.092	0.002	0.209	0
RGR leaf number 5 - 7 ~ Height CWM	0.079	0	0.193	0	0	0.007	0.013	0.003	0	0	0	0	0	0	0	0.711	0.092	0.002	0.209	0.002

Continued

	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	Plot	Scenario	Species	Trait
Biomass ~ Multi-trait FD	0.101	0	0.222	0.001	0	0.002	0.053	0.02	0	0	0	0	0	0.008	0.001	0.593	0.184	0.002	0.285	0.03
Biomass ~ SLA FD	0.12	0	0.22	0	0	0.001	0.057	0.001	0	0.002	0	0	0	0.004	0.001	0.595	0.184	0.002	0.285	0.008
Biomass ~ LDMC FD	0.098	0	0.222	0	0	0.001	0.052	0.023	0	0	0.001	0.001	0	0.009	0	0.595	0.184	0.002	0.285	0.032
Biomass ~ Height FD	0.121	0	0.223	0	0	0.001	0.058	0	0	0	0	0	0	0.003	0	0.594	0.184	0.002	0.285	0.003
Biomass ~ SLA CWM	0.091	0	0.222	0	0.001	0.001	0.026	0.03	0	0	0	0	0	0.035	0.001	0.595	0.184	0.002	0.285	0.065
Biomass ~ LDMC CWM	0.11	0	0.22	0	0.001	0.001	0.031	0.011	0	0.002	0	0	0	0.029	0.001	0.594	0.184	0.002	0.285	0.043
Biomass ~ Height CWM	0.102	0	0.222	0.002	0	0.001	0.053	0.02	0	0	0	0.002	0	0.008	0	0.592	0.184	0.002	0.285	0.029
LDMC ~ Multi-trait FD	0.134	0.002	0.298	0	0	0.016	0.043	0	0	0.001	0	0.014	0	0	0.004	0.492	0.192	0.032	0.373	0.004
LDMC ~ SLA FD	0.13	0.002	0.298	0.001	0	0.015	0.04	0.004	0	0.001	0	0.017	0	0.003	0.001	0.491	0.192	0.032	0.373	0.008
LDMC ~ LDMC FD	0.128	0.002	0.3	0	0	0.014	0.035	0.006	0	0	0	0.015	0	0.008	0.002	0.492	0.192	0.032	0.373	0.015
LDMC ~ Height FD	0.132	0.002	0.299	0	0	0.014	0.045	0.002	0	0	0	0.018	0.001	0	0	0.492	0.192	0.032	0.373	0
LDMC ~ SLA CWM	0.131	0.002	0.299	0	0	0.014	0.034	0.003	0	0	0	0.016	0	0.009	0.001	0.493	0.192	0.032	0.373	0.011
LDMC ~ LDMC CWM	0.13	0.002	0.298	0	0	0.013	0.042	0.004	0	0.001	0	0.015	0.001	0.001	0.002	0.492	0.192	0.032	0.373	0.008
LDMC ~ Height CWM	0.134	0.002	0.299	0	0	0.014	0.041	0	0	0	0	0.018	0	0.002	0	0.493	0.192	0.032	0.373	0
SLA ~ Multi-trait FD	0.19	0	0.224	0	0	0.023	0.008	0.001	0	0	0	0.023	0.001	0.007	0.003	0.522	0.231	0.048	0.289	0.012
SLA ~ SLA FD	0.181	0	0.224	0	0	0.024	0.018	0.01	0	0	0	0.027	0	0	0	0.522	0.231	0.048	0.289	0.005
SLA ~ LDMC FD	0.186	0	0.225	0	0	0.024	0.005	0.006	0	0	0	0.024	0	0.01	0.002	0.522	0.231	0.048	0.289	0.017
SLA ~ Height FD	0.193	0	0.225	0.003	0	0.024	0.015	0	0	0	0	0.026	0.001	0	0	0.519	0.231	0.048	0.289	0
SLA ~ SLA CWM	0.187	0	0.224	0	0	0.024	0	0.004	0	0	0	0.025	0	0.021	0.001	0.522	0.231	0.048	0.289	0.025
SLA ~ LDMC CWM	0.187	0	0.224	0	0	0.024	0.005	0.004	0	0	0	0.02	0	0.01	0.006	0.522	0.231	0.048	0.289	0.019
SLA ~ Height CWM	0.198	0	0.224	0.006	0	0.026	0.012	0	0	0	0	0.026	0	0.003	0	0.516	0.231	0.048	0.289	0.001

Table S3.5 Final models and their relative proportion of variances explained by the random factors Exploratory, plot (nested in Exploratory), subplot (nested in plot) and species identity (crossed with the other random factors) as well as residual variance. p. proj. area = plant projection area.

Responses	**Predictors**	**Variance of random factors %**				
Veg. period 2012		**Explo**	**Plot**	**Subplot**	**Species**	**Residuals**
RGR height	Multi-trait FD	0.066	0.098	0.031	0.340	0.466
RGR p. proj. area	Multi-trait FD	0.011	0.113	0.036	0.254	0.586
RGR leaf length	Height FD + Scen	0.028	0.090	0.019	0.241	0.622
RGR leaf number	SLA FD * Scen	0.006	0.047	0.009	0.257	0.681
Winter 2012/2013						
RGR height	LUI + Height FD * Scen + Height CWM * Scen	0.285	0.163	0.039	0.120	0.393
RGR p. proj. area	LUI + Height FD * Scen + SLA CWM + LDMC CWM + Height CWM	0.123	0.124	0.021	0.191	0.541
RGR leaf length	LUI + Height FD * Scen + Height CWM * Scen	0.245	0.126	0.042	0.107	0.481
RGR leaf number	LUI + Height FD + SLA CWM * Scen	0.029	0.077	0.000	0.326	0.567
Veg. period 2013						
RGR height	LUI	0.375	0.135	0.019	0.150	0.322
RGR p. proj. area	SLA FD	0.127	0.102	0.005	0.160	0.605
RGR leaf length	SLA FD + Height CWM	0.331	0.130	0.002	0.093	0.443
RGR leaf number	Multi-trait FD + SLA FD	0.017	0.058	0.022	0.251	0.652
Harvest 2013						
Biomass	LUI + Multi-trait FD * Scen + LDMC FD * Scen + SLA CWM * Scen	0.000	0.097	0.001	0.286	0.617
SLA	Height CWM + LDMC CWM * Scen	0.102	0.173	0.001	0.209	0.514
LDMC	SLA FD + LDMC FD + SLA CWM * Scen + LDMC CWM * Scen	0.000	0.148	0.009	0.383	0.460

Table S3.6 Final models that were improved with respect to AIC by adding climate variables: soil moisture (SM) and relative air humidity (rH). These models were only calculated for plots, for which climate data were available (for number of plots see SI Table S3.3). In all cases, the predictors remained significant after the climate variable had been added.

Responses	Predictors	Added c. variable	AIC without c. variable	AIC with c. variable	Estimate c. variable	P-value c. variable
Winter 2012/2013						
RGR height	LUI + Height FD * Scen + Height CWM * Scen	SM	3340.5	3334.6	-0.0206	0.0050
RGR p. proj. area	LUI + Height FD * Scen + SLA CWM + LDMC CWM + Height CWM	SM	3724.4	3712.4	-0.0232	0.0002
RGR leaf length	LUI + Height FD * Scen + Height CWM * Scen	SM	3551.3	3543	-0.0210	0.0014
RGR leaf number	LUI + Height FD + SLA CWM * Scen	SM	3781.1	3765.3	-0.0208	0.0000
Veg. period 2013						
RGR height	LUI	SM	2529.3	2525.7	0.0157	0.0183
RGR p. proj. Area	SLA FD	SM	2943.6	2941.5	0.0123	0.0431
RGR leaf length	SLA FD + Height CWM	SM	2614.6	2609.4	0.0177	0.0074
Harvest 2013						
SLA	Height CWM + LDMC CWM * Scen	SM	2634.3	2620	0.0274	0.0001
LDMC	SLA FD + LDMC FD + SLA CWM * Scen + LDMC CWM * Scen	rH	2616	2613.1	0.0284	0.0296

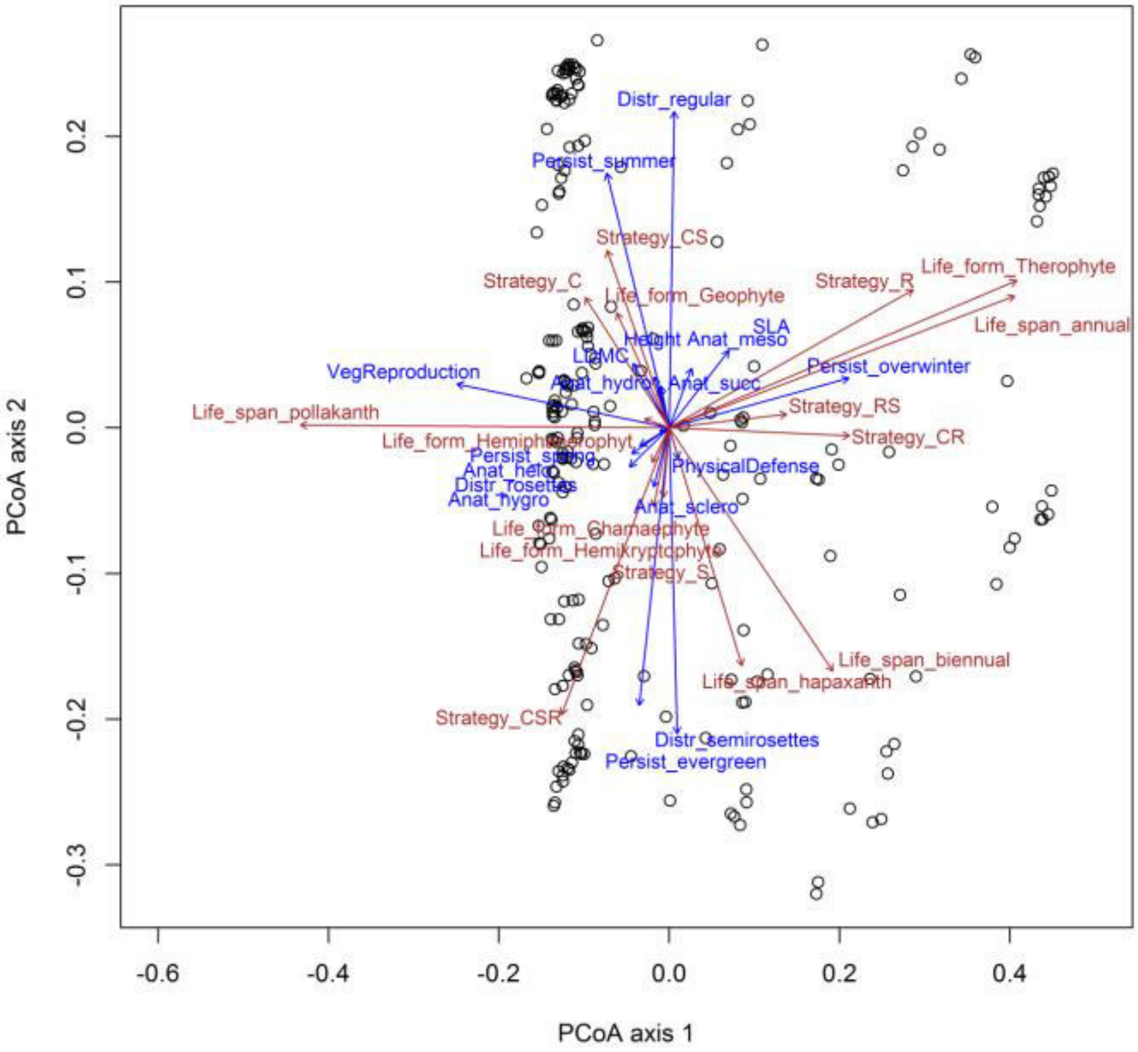

Figure S3.1 Principal coordinate analysis (PCoA) on multi-trait distances based on 11 traits (SLA, LDMC, height, anatomy, persistence, leaf distribution, vegetative reproduction, physical defense, life span, life form, strategy type) and all species, either planted as phytometers or resident species (n= 227). Traits included in the multi-trait distance used for selecting species in the different scenarios (see SI Table S3.1) are shown in blue, further traits are shown in brown. Trait correlations with the first and second PCoA axes were derived from a post-hoc regression. The further axes are captured by traits included in our multi-trait measure (3rd axis: leaf distribution, 4th axis leaf anatomy).

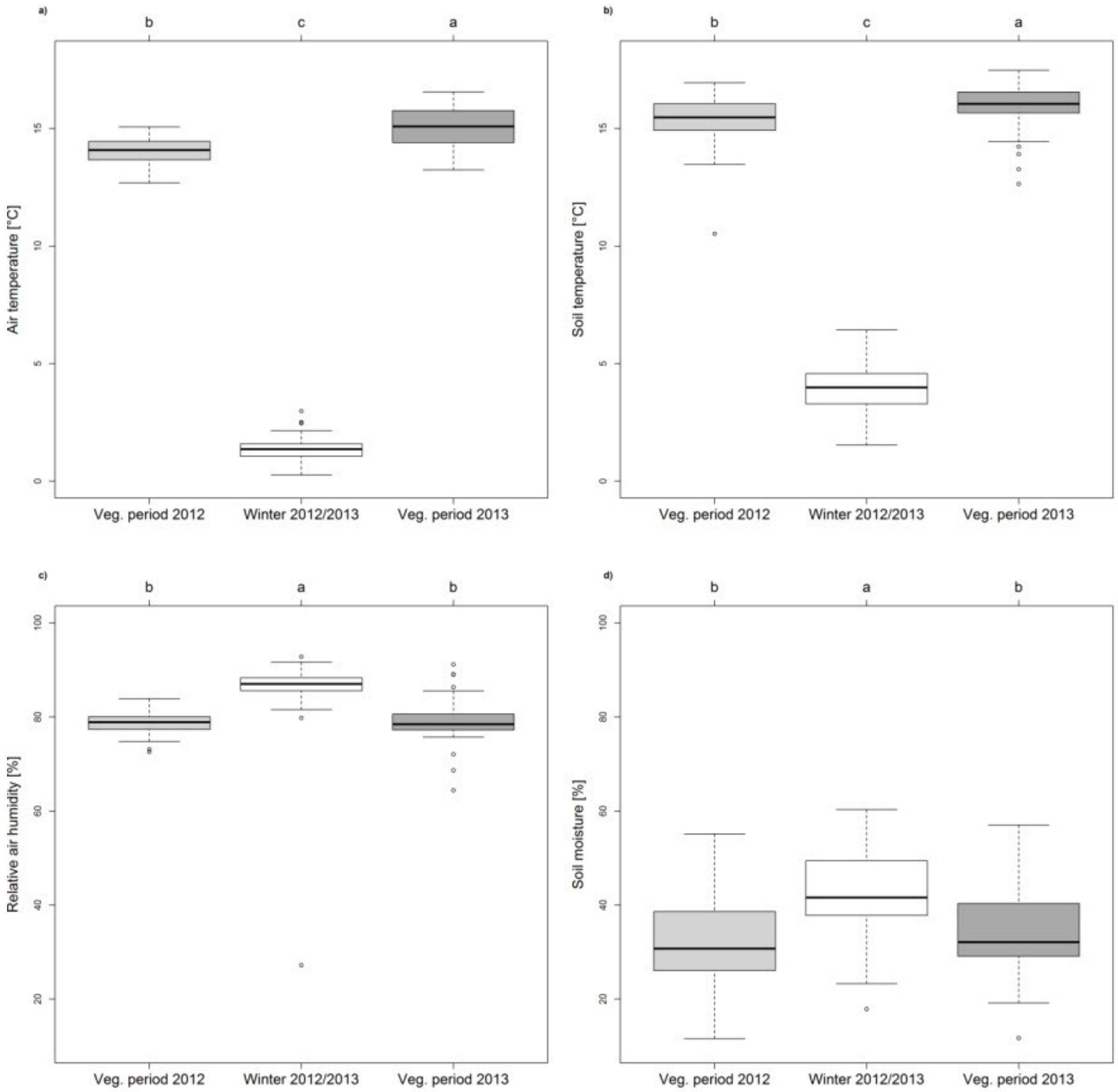

Figure S3.2 Mean climate data during the time of our experiment. Air temperature a) and relative air humidity c) were measured at two meters above ground level; soil temperature b) and soil moisture d) were measured at 10 cm below-ground. All climate data were measured at 10 minutes intervals by data loggers installed near the experimental plots and then aggregated to monthly mean values. Here, we present mean values aggregated to thethree investigated time spans (vegetation period 2012, winter 2012/2013 and vegetation period 2013) in our study plots (n= 54). Small letters refer to statistically significant differences according to a post-hoc Tukey test. Due to logger failure, in some plots the climate data were not complete and plot number differed among time periods for the different variables (see SI Table S3.3).

Chapter 4 – 4.8 Supporting Information

Table S4.1 Species and traits. Trait values without missing values are for 93 species available. Trait values for each species are: SLA = specific leaf are, LDMC = leaf dry matter content, height, L.A. = leaf anatomy (suc = succulent, scler = scleromorphic, meso = mesomorphic, hygro = hygromorphic, helo = helomorphic), L.P. = leaf persistence (spri = green in spring, sum = green in summer, species with 0 in both categories have evergreen leaves), L.D. = leaf distribution (ros = rosettes, s-ros = semi-rosettes, species with 0 in both categories have evenly spread leaves), Phys. d. = physical defense, Veg. r. = vegetative reproduction.

Species	Spec ID	SLA	LDMC	Height	L.A.suc	L.A.scler	L.A.meso	L.A.hygro	L.A.helo	L.P. spri	L.P. sum	L.D.ros	L.D.s-ros	Phys. d.	Veg. r.
Achillea millefolium	AchMil	11.86	274.50	0.45	0	1	1	0	0	0	0	0	1	0	1
Agrimonia eupatoria	AgrEup	13.15	383.12	0.38	0	0	1	0	0	0	1	0	1	0	1
Allium vineale	AllVin	17.61	137.75	0.30	0	0	1	0	0	1	0	0	0	0	1
Alopecurus pratensis	AloPra	16.82	355.17	0.70	0	0	1	0	0	0	1	0	0	0	1
Anthoxanthum odoratum	AntOdo	21.08	262.12	0.22	0	0	1	0	0	0	0	0	0	0	1
Arrhenatherum elatius	ArrEla	23.92	313.30	1.03	0	0	1	0	0	0	1	0	0	0	1
Artemisia vulgaris	ArtVul	39.75	142.72	1.55	0	1	1	0	0	0	1	0	0	0	0
Astragalus glycyphyllos	AstGly	32.51	184.27	1.00	0	0	1	0	0	0	1	0	0	0	1
Betonica officinalis	BetOff	24.90	360.45	0.65	0	0	1	0	0	0	1	0	0	0	1
Brachypodium pinnatum	BraPin	15.04	474.77	0.55	0	1	1	0	0	0	1	0	0	0	1
Briza media	BriMed	29.56	320.63	0.35	0	1	1	0	0	0	0	0	1	0	1
Bromus erectus	BroEre	13.04	342.88	0.60	0	1	1	0	0	0	0	0	1	0	1
Campanula rotundifolia	CamRot	21.12	405.83	0.20	0	0	1	0	0	0	0	0	1	0	1
Carex flacca	CarFla	10.71	514.33	0.40	0	0	1	0	0	0	0	0	1	0	1
Centaurea jacea	CenJac	10.60	255.55	0.82	0	1	1	0	0	0	1	0	1	0	1
Centaurea nigra	CenNig	14.81	300.81	0.45	0	0	1	0	0	0	1	0	1	0	1
Centaurea scabiosa	CenSca	30.07	140.55	0.85	0	1	0	0	0	0	1	0	1	0	1
Cichorium intybus	CicInt	22.73	174.86	0.62	0	1	0	0	0	0	1	0	1	0	1
Cirsium acaule	CirAca	8.72	222.50	0.14	0	1	1	0	0	0	1	0	1	1	1
Cynosurus cristatus	CynCri	23.00	302.62	0.40	0	0	1	0	0	0	0	0	1	0	1
Dianthus carthusianorum	DiaCar	16.44	207.73	0.30	0	1	0	0	0	0	1	0	1	0	0
Dipsacus fullonum	DipFul	17.16	209.34	1.35	0	1	0	0	0	0	0	0	1	1	0
Festuca arundinacea	FesAru	20.27	382.86	1.20	0	1	1	0	0	0	1	0	0	0	1
Festuca guestfalica	FesGue	9.62	501.39	0.30	0	1	0	0	0	0	0	0	1	0	1
Festuca ovina	FesOvi	14.01	301.00	0.26	0	1	0	0	0	0	0	0	1	0	1
Festuca pratensis	FesPra	18.17	329.28	0.70	0	0	1	0	0	0	0	0	0	0	1

Continued

Species	Spec ID	SLA	LDMC	Height	L.A.suc	L.A.scler	L.A.meso	L.A.hygro	L.A.helo	L.P. spri	L.P. sum	L.D.ros	L.D.s-ros	Phys. d.	Veg. r.
Festuca rubra	FesRub	10.21	365.90	0.51	0	0	1	0	0	0	0	0	1	0	1
Filipendula ulmaria	FilUlm	41.20	194.00	1.00	0	0	1	0	0	0	1	0	1	0	1
Galium mollugo	GalMol	29.62	231.33	0.51	0	0	1	0	0	0	1	0	0	0	1
Galium pumilum	GalPum	25.95	447.06	0.20	0	0	1	0	0	0	1	0	0	0	1
Geranium pratense	GerPra	14.47	266.40	0.40	0	0	1	1	0	0	1	0	1	0	1
Geranium pyrenaicum	GerPyr	24.65	183.62	0.47	0	0	1	0	0	0	0	0	1	0	0
Geranium sylvaticum	GerSyl	18.31	247.53	0.40	0	0	1	1	0	0	1	0	1	0	1
Geum rivale	GeuRiv	25.29	221.98	0.50	0	0	1	0	0	0	1	0	1	0	1
Geum urbanum	GeuUrb	14.15	312.29	0.75	0	0	1	1	0	0	0	0	1	0	1
Helianthemum nummularium	HelNum	15.19	252.92	0.15	0	1	0	0	0	0	0	0	0	0	1
Helictotrichon pubescens	HelPub	12.60	354.92	0.65	0	0	1	0	0	0	1	0	1	0	1
Hieracium pilosella	HiePil	14.18	295.25	0.17	0	0	1	0	0	0	0	1	0	0	1
Holcus lanatus	HolLan	28.19	267.25	0.65	0	0	1	0	0	0	0	0	0	0	1
Hypericum perforatum	HypPer	18.23	366.68	0.56	0	1	1	0	0	0	1	0	0	0	1
Hypochaeris radicata	HypRad	33.85	97.53	0.37	0	0	1	0	0	0	0	1	0	0	1
Knautia arvensis	KnaArv	21.52	176.14	0.55	0	0	1	0	0	0	1	0	1	0	1
Koeleria pyramidata	KoePyr	13.71	325.52	0.65	0	1	1	0	0	0	1	0	1	0	1
Lathyrus pratensis	LatPra	29.84	289.71	0.65	0	0	1	0	0	0	1	0	0	0	1
Leontodon autumnalis	LeoAut	26.07	171.37	0.30	0	0	1	0	0	0	0	1	0	0	1
Leontodon hispidus	LeoHis	14.97	285.42	0.28	0	0	1	0	0	0	1	1	0	0	1
Leucanthemum vulgare	LeuVul	22.67	138.10	0.50	0	1	1	0	0	0	0	0	1	0	1
Lolium perenne	LolPer	18.86	251.79	0.35	0	0	1	0	0	0	0	0	1	0	1
Lotus corniculatus	LotCor	20.03	252.42	0.22	0	0	1	0	0	0	1	0	0	0	1
Luzula campestris	LuzCam	20.01	227.85	0.15	0	1	1	0	0	0	1	0	1	0	1
Medicago falcata	MedFal	20.67	360.59	0.35	0	1	1	0	0	0	1	0	0	0	1
Medicago lupulina	MedLup	24.20	319.07	0.37	0	0	1	0	0	0	0	0	0	0	1
Medicago x varia	MedXva	24.56	239.90	0.55	0	0	1	0	0	0	0	0	0	0	1
Origanum vulgare	OriVul	13.24	358.58	0.40	0	1	1	0	0	0	1	0	0	0	1
Pastinaca sativa	PasSat	18.12	221.48	0.94	0	1	1	0	0	0	1	0	1	0	0
Phleum phleoides	PhlPhl	17.90	319.28	0.45	0	1	0	0	0	0	0	0	1	0	1
Picris hieracioides	PicHie	21.00	327.09	0.61	0	1	1	0	0	0	1	0	1	0	1
Pimpinella major	PimMaj	17.93	233.00	0.60	0	0	1	0	0	0	1	0	1	0	0

Continued

Species	Spec ID	SLA	LDMC	Height	L.A.suc	L.A.scler	L.A.meso	L.A.hygro	L.A.helo	L.P. spri	L.P. sum	L.D.ros	L.D.s-ros	Phys. d.	Veg. r.
Pimpinella saxifraga	PimSax	12.00	364.91	0.32	0	1	1	0	0	0	1	0	1	0	0
Plantago lanceolata	PlaLan	17.61	204.11	0.30	0	1	1	0	0	0	1	1	0	0	1
Plantago media	PlaMed	15.85	183.22	0.27	0	1	1	0	0	0	1	1	0	0	1
Poa angustifolia	PoaAng	13.37	427.66	0.60	0	1	1	0	0	0	0	0	1	0	1
Poa pratensis	PoaPra	12.04	374.79	0.55	0	0	1	0	0	0	0	0	0	0	1
Potentilla argentea	PotArg	19.10	281.85	0.34	0	1	0	0	0	0	1	0	0	0	0
Prunella vulgaris	PruVul	23.29	222.56	0.17	0	0	1	0	0	0	0	0	0	0	1
Pseudolysimachion spicatum	PseSpi	41.11	128.24	0.27	0	1	0	0	0	0	0	0	0	0	1
Ranunculus acris	RanAcr	14.50	256.95	0.75	0	0	1	0	0	0	1	0	1	0	1
Ranunculus repens	RanRep	20.58	186.01	0.27	0	0	0	1	1	0	0	0	1	0	1
Rumex acetosa	RumAce	23.10	116.20	0.52	0	0	1	0	0	0	0	0	1	0	1
Rumex crispus	RumCri	15.36	199.38	0.90	0	0	1	0	1	0	0	0	1	0	0
Rumex obtusifolius	RumObt	23.98	160.04	0.85	0	0	1	1	0	0	0	0	1	0	0
Rumex thyrsiflorus	RumThy	18.36	208.54	0.75	0	0	1	0	0	0	0	0	1	0	0
Salvia pratensis	SalPra	20.38	186.37	0.45	0	1	1	0	0	0	1	0	1	0	1
Sanguisorba minor	SanMin	13.63	307.29	0.32	0	1	1	0	0	0	0	0	1	0	0
Saponaria officinalis	SapOff	20.09	363.46	0.55	0	0	1	0	0	0	1	0	0	0	1
Scabiosa columbaria	ScaCol	16.00	217.36	0.45	0	1	1	0	0	0	0	0	1	0	0
Scirpus sylvaticus	SciSyl	21.60	267.20	0.65	0	0	1	0	1	0	0	0	1	0	1
Sedum maximum	SedMax	17.74	172.98	0.55	1	0	0	0	0	0	1	0	0	0	1
Senecio jacobaea	SenJac	13.40	258.00	0.51	0	0	1	0	0	0	0	0	1	0	1
Silaum silaus	SilSil	13.93	293.66	0.65	0	1	1	0	0	0	1	0	1	0	1
Silene dioica	SilDio	37.11	133.14	0.60	0	0	1	0	0	0	0	0	1	0	0
Silene flos-cuculi	SilFlo	20.07	186.34	0.55	0	0	1	0	0	0	0	0	1	0	1
Silene latifolia	SilLat	19.93	170.90	0.64	0	0	1	0	0	0	0	0	0	0	1
Silene otites	SilOti	15.41	263.07	0.40	0	1	0	0	0	0	0	0	1	0	1
Silene vulgaris	SilVul	22.70	202.72	0.35	0	1	1	0	0	0	0	0	0	0	0
Symphytum officinale	SymOff	16.73	117.82	0.75	0	0	0	1	1	0	1	0	1	1	0
Thymus pulegioides	ThyPul	17.05	355.82	0.25	0	1	0	0	0	0	0	0	0	0	1
Tragopogon pratensis	TraPra	34.42	203.53	0.38	0	0	1	0	0	0	1	0	1	0	0
Trisetum flavescens	TriFla	25.05	312.49	0.55	0	0	1	0	0	0	0	0	0	0	1
Valeriana officinalis	ValOff	30.56	122.96	1.15	0	0	0	1	1	0	1	0	1	0	1

Continued

Species	Spec ID	SLA	LDMC	Height	L.A.suc	L.A.scler	L.A.meso	L.A.hygro	L.A.helo	L.P. spri	L.P. sum	L.D.ros	L.D.s-ros	Phys. d.	Veg. r.
Veronica teucrium	VerTeu	20.34	238.47	0.60	0	1	1	0	0	0	1	0	0	0	1
Vicia cracca	VicCra	20.81	298.67	0.75	0	0	1	0	0	0	1	0	0	0	1
Vicia sepium	VicSep	23.41	236.04	0.45	0	0	1	0	0	0	0	0	0	0	1

Table S4.2 The 93 species and number of replicates per species (n) used in aggregation to mean values of relative growth rates (RGR) of height, plant projection area, leaf length and number of leaves obtained from field experiment (Field) and common garden experiment (CG). Furthermore the amount of individuals (ind.) of each species planted, alive at end of experiment and obtained biomass in both experiments. Abbreviations of species names are used in figures of PCA.

			n ind. planted		n ind. Survival		n ind. Biomass		n mean RGR height		n mean RGR plant proj. area		n mean RGR leaf length		n mean RGR no. of leaves	
no.	Species	Abbr.	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG
1	Achillea millefolium	AchMil	50	3	36	3	36	3	230	15	230	15	229	15	229	15
2	Agrimonia eupatoria	AgrEup	6	3	3	3	4	3	28	15	28	15	27	15	27	15
3	Allium vineale	AllVin	16	3	3	3	1	3	12	9	12	9	10	10	10	9
4	Alopecurus pratensis	AloPra	30	3	5	3	5	3	81	13	81	13	81	15	81	15
5	Anthoxanthum odoratum	AntOdo	56	3	46	3	46	3	285	9	285	15	285	15	285	13
6	Arrhenatherum elatius	ArrEla	46	3	15	3	15	3	137	13	137	15	137	15	137	15
7	Artemisia vulgaris	ArtVul	12	3	5	3	5	3	46	13	46	13	40	13	40	13
8	Astragalus glycyphyllos	AstGly	12	3	4	3	4	3	32	12	32	12	32	12	32	12
9	Betonica officinalis	BetOff	14	3	6	3	6	3	58	15	58	15	58	15	58	15
10	Brachypodium pinnatum	BraPin	6	3	4	3	4	3	26	13	26	13	26	13	26	15
11	Briza media	BriMed	60	3	37	3	37	3	263	13	263	15	263	15	263	15
12	Bromus erectus	BroEre	12	3	8	3	8	3	55	9	55	13	55	15	55	13
13	Campanula rotundifolia	CamRot	4	3	3	3	3	3	18	15	18	15	18	15	18	15
14	Carex flacca	CarFla	8	3	2	2	2	2	16	11	16	11	16	11	16	11
15	Centaurea jacea	CenJac	42	3	25	3	25	3	186	13	186	15	186	15	186	15
16	Centaurea nigra	CenNig	18	3	9	3	9	3	68	13	68	13	66	13	66	13
17	Centaurea scabiosa	CenSca	28	3	14	2	14	2	109	13	109	11	107	13	107	13
18	Cichorium intybus	CicInt	50	3	20	2	20	2	181	11	181	11	181	11	179	11

Continued

			n ind. planted		n ind. Survival		n ind. Biomass		n mean RGR height		n mean RGR plant proj. area		n mean RGR leaf length		n mean RGR no. of leaves	
no.	Species	Abbr.	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG
19	Cirsium acaule	CirAca	8	3	4	3	4	3	31	15	31	15	31	15	31	15
20	Cynosurus cristatus	CynCri	8	3	6	3	6	3	43	13	43	11	43	15	43	15
21	Dianthus carthusianorum	DiaCar	36	3	13	3	13	3	112	15	112	13	112	15	112	15
22	Dipsacus fullonum	DipFul	98	3	21	3	30	3	393	15	393	15	386	15	386	15
23	Festuca arundinacea	FesAru	8	3	4	3	4	3	38	13	38	11	36	15	36	15
24	Festuca guestfalica	FesGue	2	3	2	3	2	3	12	13	12	15	12	15	10	15
25	Festuca ovina	FesOvi	14	3	10	3	10	3	67	13	67	13	67	13	56	15
26	Festuca pratensis	FesPra	24	3	17	3	16	3	115	15	115	13	115	15	115	15
27	Festuca rubra	FesRub	16	3	11	3	11	3	69	11	69	15	68	15	69	15
28	Filipendula ulmaria	FilUlm	10	3	6	3	6	3	37	15	37	15	37	15	37	11
29	Galium mollugo	GalMol	10	3	1	3	1	3	13	13	13	15	13	13	7	15
30	Galium pumilum	GalPum	10	3	3	3	3	3	23	15	23	15	23	13	17	15
31	Geranium pratense	GerPra	2	3	2	3	2	3	12	15	12	15	12	15	12	15
32	Geranium pyrenaicum	GerPyr	2	3	1	1	1	1	5	12	5	12	5	12	5	12
33	Geranium sylvaticum	GerSyl	2	3	2	3	2	3	12	15	12	15	12	15	12	15
34	Geum rivale	GeuRiv	12	3	8	3	8	3	52	15	52	11	52	15	52	15
35	Geum urbanum	GeuUrb	12	3	10	3	10	3	66	15	66	15	66	13	66	13
36	Helianthemum nummularium	HelNum	6	3	2	1	2	1	18	9	18	9	18	9	18	9
37	Helictotrichon pubescens	HelPub	8	3	4	3	4	3	31	9	31	13	31	13	31	13
38	Hieracium pilosella	HiePil	26	3	13	2	13	2	99	7	99	11	99	10	99	10
39	Holcus lanatus	HolLan	82	3	68	3	68	3	423	13	423	15	423	15	423	15
40	Hypericum perforatum	HypPer	14	3	9	3	9	3	60	15	60	15	60	15	60	13
41	Hypochaeris radicata	HypRad	4	3	4	1	4	1	24	11	24	11	24	11	24	11
42	Knautia arvensis	KnaArv	14	3	7	3	7	3	61	13	59	15	59	15	59	13
43	Koeleria pyramidata	KoePyr	4	3	4	3	4	3	24	15	24	11	24	15	24	15
44	Lathyrus pratensis	LatPra	10	3	3	3	3	3	34	11	34	10	34	9	34	11

Continued

			n ind. planted		n ind. Survival		n ind. Biomass		n mean RGR height		n mean RGR plant proj. area		n mean RGR leaf length		n mean RGR no. of leaves	
no.	Species	Abbr.	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG
45	Leontodon autumnalis	LeoAut	16	3	8	1	8	1	62	10	62	10	62	9	62	9
46	Leontodon hispidus	LeoHis	12	3	6	2	6	2	48	13	48	13	48	13	48	13
47	Leucanthemum vulgare	LeuVul	6	3	3	1	3	1	28	7	28	9	28	9	28	9
48	Lolium perenne	LolPer	28	3	12	3	12	3	119	15	119	15	119	15	119	15
49	Lotus corniculatus	LotCor	72	3	40	3	40	3	301	15	301	15	299	15	272	15
50	Luzula campestris	LuzCam	30	3	16	3	16	3	129	9	129	11	129	15	129	15
51	Medicago falcata	MedFal	4	3	2	3	2	3	15	15	15	15	15	15	13	13
52	Medicago lupulina	MedLup	12	3	1	1	1	1	26	10	26	6	26	9	20	9
53	Medicago x varia	MedXva	6	3	5	3	5	3	30	15	30	15	30	15	26	15
54	Origanum vulgare	OriVul	10	3	6	3	6	3	38	15	38	15	38	15	38	15
55	Pastinaca sativa	PasSat	28	3	7	1	7	1	86	11	86	11	79	11	79	11
56	Phleum phleoides	PhlPhl	10	3	4	3	4	3	40	9	40	15	40	15	40	15
57	Picris hieracioides	PicHie	20	3	7	2	9	2	83	13	83	13	82	13	82	13
58	Pimpinella major	PimMaj	6	3	4	2	4	2	25	6	25	8	25	8	25	8
59	Pimpinella saxifraga	PimSax	8	3	2	2	2	2	24	7	24	9	24	8	24	7
60	Plantago lanceolata	PlaLan	12	3	7	2	7	2	50	11	50	13	48	12	48	12
61	Plantago media	PlaMed	6	3	4	3	4	3	31	13	31	15	31	13	31	15
62	Poa angustifolia	PoaAng	4	3	1	3	1	3	6	9	6	15	6	15	6	15
63	Poa pratensis	PoaPra	4	3	3	3	3	3	19	9	19	13	19	15	19	15
64	Potentilla argentea	PotArg	74	3	29	3	29	3	313	15	313	15	311	15	311	15
65	Prunella vulgaris	PruVul	56	3	38	3	38	3	246	15	246	15	246	15	246	15
66	Pseudolysimachion spicatum	PseSpi	22	3	11	3	11	3	96	15	96	15	96	15	96	15
67	Ranunculus acris	RanAcr	76	3	46	3	46	3	309	13	309	15	301	15	299	15
68	Ranunculus repens	RanRep	40	3	25	3	25	3	170	15	170	15	165	15	165	15
69	Rumex acetosa	RumAce	126	3	93	3	92	3	608	9	608	11	607	11	605	11

Continued

			n ind. planted		n ind. Survival		n ind. Biomass		n mean RGR height		n mean RGR plant proj. area		n mean RGR leaf length		n mean RGR no. of leaves	
no.	Species	Abbr.	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG
70	Rumex crispus	RumCri	4	3	3	3	3	3	18	11	18	13	14	11	14	9
71	Rumex obtusifolius	RumObt	16	3	10	3	11	3	79	15	79	15	75	15	75	14
72	Rumex thyrsiflorus	RumThy	12	3	8	3	8	3	56	13	56	11	56	13	56	13
73	Salvia pratensis	SalPra	26	3	9	1	9	1	77	9	77	11	75	11	75	11
74	Sanguisorba minor	SanMin	8	3	2	2	2	3	22	14	22	14	22	10	22	12
75	Saponaria officinalis	SapOff	6	3	4	3	4	3	26	15	26	15	26	15	26	15
76	Scabiosa columbaria	ScaCol	18	3	6	3	6	3	56	15	56	15	56	15	56	15
77	Scirpus sylvaticus	SciSyl	52	3	13	2	12	1	117	11	117	9	116	11	117	11
78	Sedum maximum	SedMax	12	3	2	3	2	3	27	15	27	15	26	15	26	15
79	Senecio jacobaea	SenJac	56	3	36	3	37	3	263	15	263	15	260	15	260	15
80	Silaum silaus	SilSil	2	3	2	3	2	3	12	10	12	8	12	8	12	6
81	Silene dioica	SilDio	4	3	2	3	2	3	20	13	20	15	20	15	18	15
82	Silene flos-cuculi	SilFlo	64	3	40	3	40	3	293	9	293	14	293	15	293	15
83	Silene latifolia	SilLat	66	3	26	2	26	2	232	14	232	14	222	14	222	14
84	Silene otites	SilOti	30	3	9	1	9	1	77	7	77	7	77	7	77	7
85	Silene vulgaris	SilVul	4	3	2	2	2	1	16	11	16	11	16	11	16	11
86	Symphytum officinale	SymOff	6	3	2	3	2	3	19	15	19	15	19	15	19	15
87	Thymus pulegioides	ThyPul	12	3	3	3	3	3	38	11	38	13	38	13	38	13
88	Tragopogon pratensis	TraPra	6	3	2	1	2	1	21	9	21	9	20	10	20	10
89	Trisetum flavescens	TriFla	50	3	29	3	29	3	209	11	209	15	209	15	209	15
90	Valeriana officinalis	ValOff	18	3	8	3	8	3	60	15	60	15	60	13	60	15
91	Veronica teucrium	VerTeu	4	3	2	2	2	2	11	11	11	13	11	13	11	13
92	Vicia cracca	VicCra	18	3	2	3	2	3	28	15	28	13	28	15	27	15
93	Vicia sepium	VicSep	4	3	4	3	4	3	22	15	22	15	22	15	22	15

Table S4.3 Species performance variables in the field and common garden experiment (CG). The following performance variables of all 93 species (species abbreviations are given in Table S4.1) are shown: Survival (percentage of number individuals that survived till end of experiment in relation to number of individuals planted at the start of the experiment), biomass at end of experiment was log-transformed, mean values of RGR of height, RGR of plant projection area, RGR of leaf length and RGR of number of leaves is the species RGR mean across all 6 time intervals in field and accordingly 5 in common garden and of all individuals of one species [cm cm $^{-1}$ week^{-1}] in field and common garden. Moreover, species scores of first (PC1) and second (PC2) axis are given for the two PCAs with all performance variables of field and common garden experiment respectively.

	Survival		Biomass		RGR height		RGR plant proj. area		RGR leaf length		RGR number of leaves		PC1 scores		PC2 scores	
Spec ID	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG	Field	CG
AchMil	78.26	100.00	0.057	1.757	0.005	0.136	0.033	0.129	0.015	0.044	0.012	0.146	-0.461	-0.390	0.259	0.000
AgrEup	50.00	100.00	-0.611	1.178	0.011	0.086	0.017	0.154	0.013	0.060	0.011	0.055	-0.198	0.231	-0.275	-0.215
AllVin	18.75	100.00	-0.335	0.505	0.054	0.061	-0.008	0.113	-0.001	0.013	-0.023	-0.018	0.074	0.886	-1.023	0.494
AloPra	16.67	100.00	-0.484	2.030	0.005	0.062	0.004	0.150	0.012	0.073	-0.018	0.087	0.170	-0.150	-0.661	-0.105
AntOdo	82.14	100.00	0.124	1.819	-0.011	0.001	0.016	0.123	0.017	0.061	0.017	0.106	-0.342	0.027	0.545	0.461
ArrEla	32.61	100.00	0.611	2.112	-0.014	0.068	0.018	0.117	-0.003	0.046	0.011	0.102	-0.163	-0.191	0.560	0.357
ArtVul	41.67	100.00	1.266	2.430	-0.007	0.147	0.007	0.199	-0.024	0.037	0.033	0.204	-0.287	-1.085	1.261	-0.331
AstGly	33.33	100.00	1.131	1.532	0.038	0.038	0.104	0.256	0.016	0.070	0.031	0.128	-1.347	-0.356	0.114	-0.625
BetOff	42.86	100.00	-0.484	1.210	0.004	0.141	0.030	0.180	0.005	0.068	-0.001	0.114	-0.105	-0.176	-0.250	-0.651
BraPin	66.67	100.00	-0.174	1.770	-0.003	0.042	0.002	0.125	0.001	0.011	-0.001	0.125	0.029	-0.159	0.218	0.750
BriMed	61.67	100.00	0.037	1.783	-0.002	0.041	0.027	0.170	0.013	0.079	0.011	0.134	-0.336	-0.246	0.210	-0.160
BroEre	66.67	100.00	0.189	1.927	-0.009	0.020	0.026	0.130	0.012	0.040	0.013	0.106	-0.338	-0.088	0.429	0.541
CamRot	75.00	100.00	-0.838	1.042	0.003	0.109	-0.028	0.168	-0.009	0.010	-0.043	0.106	0.665	-0.047	-0.358	0.103
CarFla	25.00	66.67	-0.735	1.118	0.015	0.052	0.045	0.145	0.023	0.071	0.005	0.093	-0.344	0.435	-0.741	-0.263
CenJac	59.52	100.00	0.336	2.019	-0.003	0.151	0.034	0.193	0.012	0.027	0.009	0.169	-0.411	-0.792	0.329	-0.275
CenNig	50.00	100.00	0.272	1.862	-0.012	0.130	0.029	0.148	0.006	0.016	0.017	0.175	-0.319	-0.608	0.471	0.200
CenSca	50.00	66.67	-0.704	1.523	0.002	0.072	0.016	0.124	0.006	0.053	-0.006	0.020	0.055	0.571	-0.309	-0.099
CicInt	40.00	66.67	0.138	2.043	0.013	0.133	0.027	0.231	0.015	0.052	0.002	0.172	-0.354	-0.620	-0.177	-0.867
CirAca	50.00	100.00	-0.239	1.453	0.022	0.103	0.023	0.160	0.019	0.070	-0.009	0.073	-0.254	0.020	-0.500	-0.389
CynCri	75.00	100.00	0.345	1.385	0.003	0.075	0.010	0.080	-0.001	0.023	0.008	0.087	-0.224	0.208	0.520	0.707
DiaCar	36.11	100.00	-0.617	0.789	-0.015	0.088	0.004	0.079	0.002	0.021	-0.001	0.077	0.211	0.449	-0.097	0.612
DipFul	21.43	100.00	0.620	2.119	0.013	0.105	0.003	0.130	0.006	0.047	0.001	0.054	-0.191	-0.105	-0.008	0.047

Continued

	Survival		Biomass		RGR height		RGR plant proj. area		RGR leaf length		RGR number of leaves		PC1 scores		PC2 scores	
FesAru	50.00	100.00	-0.837	1.601	-0.004	0.075	0.011	0.159	0.002	0.040	0.008	0.121	0.060	-0.198	-0.117	0.098
FesGue	100.00	100.00	0.172	1.559	0.011	0.030	0.009	0.063	0.010	0.027	0.014	0.149	-0.389	0.025	0.493	1.048
FesOvi	71.43	100.00	0.172	1.757	0.004	0.022	0.008	0.053	0.008	0.012	0.011	0.153	-0.257	-0.036	0.349	1.309
FesPra	77.27	100.00	0.395	2.076	0.016	0.067	0.045	0.146	0.028	0.034	0.010	0.120	-0.735	-0.336	0.114	0.298
FesRub	78.57	100.00	-0.394	1.646	-0.023	0.034	-0.010	0.135	-0.011	0.037	0.003	0.144	0.276	-0.172	0.596	0.488
FilUlm	60.00	100.00	-0.944	1.541	0.031	0.116	0.045	0.148	0.041	0.068	0.005	0.046	-0.584	0.097	-0.931	-0.375
GalMol	16.67	100.00	-0.206	2.123	0.036	0.124	0.059	0.177	0.040	0.018	0.020	0.268	-0.859	-1.141	-0.841	0.136
GalPum	50.00	100.00	0.465	2.102	0.023	0.094	0.064	0.194	0.003	0.006	0.051	0.277	-0.978	-1.166	0.510	0.288
GerPra	100.00	100.00	-0.431	1.729	0.030	0.114	0.007	0.171	0.017	0.073	-0.009	0.098	-0.243	-0.231	-0.261	-0.492
GerPyr	50.00	33.33	-0.385	1.277	-0.056	0.089	-0.071	0.143	-0.124	0.041	-0.013	0.061	1.780	0.643	1.792	-0.360
GerSyl	100.00	100.00	-0.567	1.778	0.013	0.109	0.035	0.183	0.021	0.078	-0.006	0.101	-0.351	-0.278	-0.187	-0.584
GeuRiv	66.67	100.00	-0.430	1.505	0.005	0.070	0.027	0.121	0.010	0.055	0.014	0.071	-0.291	0.157	0.051	0.160
GeuUrb	83.33	100.00	-0.555	2.017	0.009	0.090	0.007	0.102	0.011	0.039	-0.013	0.083	-0.004	-0.090	-0.189	0.387
HelNum	33.33	33.33	-1.469	0.976	0.015	0.045	-0.030	0.176	-0.021	0.037	-0.033	0.136	0.829	0.454	-0.838	-0.278
HelPub	50.00	100.00	-0.171	1.992	-0.009	0.008	0.021	0.114	0.015	0.037	0.001	0.109	-0.146	-0.063	-0.004	0.733
HiePil	50.00	66.67	-0.440	0.639	-0.009	0.008	0.000	0.192	-0.004	0.002	-0.007	0.201	0.226	0.083	0.029	0.357
HolLan	82.93	100.00	0.365	2.332	-0.013	0.080	0.016	0.149	0.001	0.071	0.011	0.106	-0.234	-0.370	0.769	-0.118
HypPer	64.29	100.00	-0.271	1.970	0.010	0.104	-0.003	0.122	0.002	0.024	0.002	0.142	-0.020	-0.398	0.028	0.386
HypRad	100.00	33.33	-0.221	0.862	0.019	0.121	0.035	0.146	0.016	0.042	-0.007	0.061	-0.405	0.735	-0.067	-0.569
KnaArv	50.00	100.00	-0.271	2.054	-0.006	0.116	-0.012	0.153	0.000	0.051	-0.002	0.091	0.190	-0.305	0.100	-0.168
KoePyr	100.00	100.00	-0.498	1.668	0.015	0.062	0.010	0.086	0.011	0.025	-0.014	0.112	-0.085	0.010	-0.123	0.743
LatPra	30.00	100.00	-0.573	1.775	-0.018	0.066	0.015	0.137	-0.014	0.024	-0.049	0.125	0.617	-0.220	-0.423	0.442
LeoAut	50.00	33.33	-0.199	1.265	0.005	0.142	0.007	0.150	0.006	0.044	-0.004	0.068	-0.026	0.508	-0.102	-0.672
LeoHis	50.00	66.67	-0.232	1.231	-0.002	0.083	0.033	0.134	0.015	0.043	0.023	0.098	-0.408	0.319	0.111	-0.065
LeuVul	50.00	33.33	-0.076	0.022	-0.044	0.106	-0.006	0.113	-0.005	0.026	-0.007	0.034	0.390	1.258	0.581	-0.221
LolPer	42.86	100.00	0.126	1.878	-0.008	0.079	-0.008	0.089	-0.001	0.013	-0.007	0.150	0.159	-0.270	0.189	0.822
LotCor	55.56	100.00	0.437	1.502	0.004	0.119	0.024	0.165	0.002	0.043	0.001	0.126	-0.266	-0.277	0.300	-0.185

Continued

	Survival		Biomass		RGR height		RGR plant proj. area		RGR leaf length		RGR number of leaves		PC1 scores		PC2 scores	
LuzCam	61.54	100.00	-0.142	1.281	-0.016	0.019	0.008	0.088	0.007	0.032	-0.007	0.098	0.059	0.292	0.184	0.826
MedFal	50.00	100.00	0.010	2.038	-0.027	0.090	-0.009	0.214	-0.009	0.005	-0.018	0.206	0.404	-0.907	0.361	0.119
MedLup	8.33	33.33	-0.947	-0.420	-0.032	0.066	-0.018	0.166	-0.028	-0.025	-0.030	0.096	0.965	1.066	-0.227	0.133
MedXva	83.33	100.00	0.589	2.629	0.011	0.076	0.041	0.202	0.001	-0.015	0.022	0.225	-0.634	-1.168	0.686	0.508
OriVul	60.00	100.00	-0.637	1.938	0.002	0.127	-0.007	0.133	-0.002	0.022	-0.016	0.117	0.288	-0.360	-0.202	0.197
PasSat	26.92	33.33	-0.354	1.201	-0.004	0.115	0.004	0.153	-0.013	0.092	0.006	0.089	0.179	0.537	0.058	-1.003
PhlPhl	40.00	100.00	-0.198	1.441	0.005	0.029	0.002	0.121	-0.004	0.045	-0.031	0.102	0.293	0.123	-0.341	0.460
PicHie	35.00	66.67	-0.233	1.985	0.014	0.158	0.010	0.190	0.002	0.058	0.004	0.138	-0.091	-0.400	-0.198	-0.815
PimMaj	66.67	66.67	-0.900	1.205	0.015	0.041	0.013	0.148	0.016	0.064	-0.011	0.047	-0.030	0.590	-0.556	-0.204
PimSax	25.00	66.67	-0.419	1.067	0.053	0.193	0.049	0.187	0.036	0.079	0.005	0.068	-0.727	0.189	-1.160	-1.294
PlaLan	70.00	66.67	0.441	1.386	-0.016	0.119	0.014	0.094	0.000	0.038	0.016	0.097	-0.216	0.294	0.807	0.079
PlaMed	66.67	100.00	-0.206	1.235	0.017	0.129	0.042	0.097	0.025	0.036	0.005	0.065	-0.529	0.218	-0.259	0.190
PoaAng	25.00	100.00	-1.602	1.083	-0.057	-0.018	0.026	0.124	-0.005	0.068	0.032	0.031	0.314	0.646	0.256	0.360
PoaPra	75.00	100.00	-0.784	1.408	-0.026	-0.010	-0.018	0.141	-0.003	0.073	-0.026	0.059	0.589	0.354	0.077	0.210
PotArg	39.19	100.00	-0.392	1.499	0.001	0.102	0.004	0.161	0.003	0.022	-0.001	0.156	0.067	-0.372	-0.150	0.146
PruVul	67.86	100.00	0.484	1.315	0.002	0.114	0.025	0.158	0.006	0.030	0.007	0.121	-0.370	-0.173	0.435	-0.017
PseSpi	50.00	100.00	-0.385	1.268	-0.002	0.076	0.007	0.140	-0.003	0.032	0.001	0.093	0.071	0.076	0.041	0.229
RanAcr	60.53	100.00	-0.275	1.304	0.003	0.072	-0.002	0.171	0.013	0.066	-0.013	0.049	0.056	0.198	-0.185	-0.297
RanRep	65.79	100.00	-0.014	1.763	-0.011	0.081	0.014	0.254	-0.010	0.056	-0.003	0.139	0.049	-0.577	0.428	-0.659
RumAce	76.23	100.00	-0.622	1.271	-0.038	-0.022	-0.009	0.194	-0.002	0.073	-0.025	0.108	0.542	0.096	0.276	-0.033
RumCri	75.00	100.00	0.289	1.481	-0.012	0.134	0.030	0.113	-0.024	0.049	-0.003	0.120	-0.018	-0.133	0.761	0.012
RumObt	62.50	100.00	-1.270	2.170	-0.036	0.136	-0.054	0.160	-0.022	0.045	-0.027	0.045	1.120	-0.227	0.110	-0.273
RumThy	66.67	100.00	-0.485	1.854	-0.007	0.209	-0.014	0.231	-0.007	0.075	-0.030	0.122	0.468	-0.702	-0.073	-1.291
SalPra	34.62	33.33	-0.347	1.229	-0.013	0.032	0.011	0.101	0.004	0.052	0.002	0.035	0.073	0.992	-0.002	0.045
SanMin	25.00	66.67	-0.232	1.210	-0.001	0.091	-0.013	0.106	0.004	0.007	-0.016	0.095	0.289	0.363	-0.311	0.408
SapOff	66.67	100.00	-1.027	1.901	-0.006	0.082	-0.015	0.158	-0.012	0.040	-0.020	0.142	0.541	-0.406	-0.164	0.103
ScaCol	33.33	100.00	0.113	1.578	0.027	0.135	0.023	0.183	0.016	0.062	0.003	0.097	-0.389	-0.252	-0.383	-0.578

Continued

	Survival		Biomass		RGR height		RGR plant proj. area		RGR leaf length		RGR number of leaves		PC1 scores		PC2 scores	
SciSyl	25.00	66.67	1.055	0.086	0.016	0.070	0.062	0.197	0.036	0.091	0.011	0.030	-0.940	0.927	-0.098	-1.003
SedMax	16.67	100.00	-2.222	0.192	-0.042	0.049	-0.034	0.170	-0.018	0.037	-0.052	0.033	1.443	0.701	-0.893	-0.020
SenJac	64.29	100.00	0.154	2.223	0.029	0.158	0.024	0.182	0.013	0.063	0.011	0.139	-0.505	-0.697	-0.043	-0.596
SilSil	100.00	100.00	-0.985	1.213	0.010	0.086	0.015	0.206	0.008	0.066	-0.006	0.097	-0.039	-0.077	-0.169	-0.554
SilDio	50.00	100.00	-0.308	1.465	-0.034	0.077	0.002	0.101	0.005	0.046	-0.005	0.024	0.244	0.388	0.278	0.289
SilFlo	62.50	100.00	-0.184	1.442	-0.050	-0.008	0.003	0.086	0.000	0.015	-0.002	0.049	0.293	0.466	0.679	1.092
SilLat	39.39	66.67	-0.020	1.656	-0.021	0.100	-0.009	0.183	-0.016	0.015	-0.015	0.124	0.430	-0.134	0.315	-0.136
SilOti	30.00	33.33	-0.648	0.460	0.006	0.129	0.011	0.162	0.010	0.031	-0.009	0.062	0.071	0.818	-0.544	-0.624
SilVul	50.00	66.67	-0.698	0.558	0.015	0.075	-0.019	0.165	-0.019	0.001	-0.057	0.092	0.732	0.491	-0.670	0.113
SymOff	33.33	100.00	-0.425	2.332	-0.039	0.071	-0.040	0.200	-0.025	0.070	-0.012	0.119	0.847	-0.539	0.445	-0.375
ThyPul	25.00	100.00	-1.232	1.192	-0.001	0.051	-0.012	0.149	-0.007	0.040	-0.020	0.155	0.575	-0.110	-0.670	0.269
TraPra	33.33	33.33	-0.378	0.385	-0.009	0.045	0.002	0.141	0.007	0.065	-0.005	0.084	0.142	1.000	-0.166	-0.414
TriFla	58.00	100.00	-0.114	1.313	-0.008	0.067	0.021	0.162	0.003	0.049	0.011	0.092	-0.163	0.041	0.293	-0.023
ValOff	44.44	100.00	-0.526	1.901	0.014	0.136	-0.002	0.123	0.011	0.042	-0.014	0.106	0.093	-0.273	-0.512	0.020
VerTeu	50.00	66.67	-0.754	1.406	0.054	0.062	0.051	0.165	0.007	0.027	-0.008	0.096	-0.429	0.199	-0.970	0.000
VicCra	11.11	100.00	-1.328	1.142	-0.008	0.055	-0.030	0.122	-0.002	0.046	-0.010	0.121	0.664	0.112	-0.646	0.324
VicSep	100.00	100.00	0.260	1.966	0.004	0.056	0.041	0.159	0.008	0.041	0.020	0.099	-0.601	-0.218	0.655	0.177

Table S4.4: Spearman correlation coefficients for performance variables (biomass, survival, RGR of height, plant projection area, leaf length and number of leaves) between observations on mean species values in the field and the common garden experiment.

	Spearman's rank correlation rho	p-value
Biomass	0.4225	0.0000
Survival	0.3149	0.0021
RGR height	0.2765	0.0075
RGR plant projection area	0.1179	0.2597
RGR leaf length	0.3166	0.0021
RGR number of leaves	0.2145	0.0392

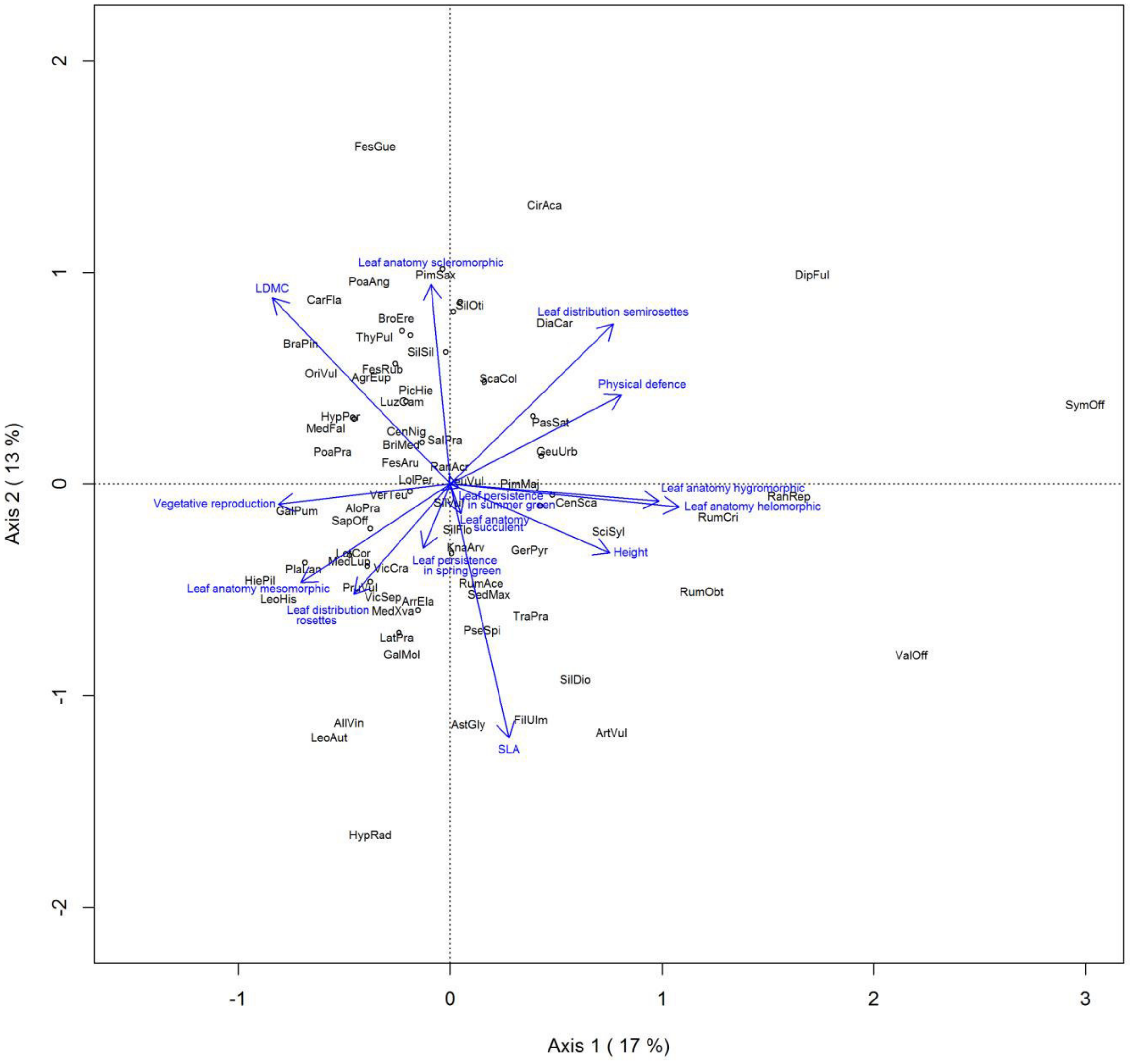

Figure S4.1 Principal component analysis (PCA) based on 14 traits (SLA, LDMC, height, leaf anatomy (succulent, scleromorphic, mesomorphic, hygromorphic and helomorphic), leaf persistence (in spring green and in summer green), leaf distribution (rosettes and semirosettes), physical defense and vegetative reproduction) and all 93 species (for abbrevations of species names see supporting information Table S4.2).