Wissenschaftszentrum Weihenstephan
für Ernährung, Landnutzung und Umwelt

Lehrstuhl für Renaturierungsökologie

Drivers of plant diversity in grassland metacommunities: Integrating local and landscape-scale factors of taxonomic and functional community structure

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Vollständiger Abdruck der von der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften

genehmigten Dissertation.

Vorsitzender:	Univ.-Prof. Dr. Johannes Schnyder
Prüfer der Dissertation:	1. Univ.-Prof. Dr. Johannes Kollmann
	2. Univ.-Prof. Dr. Wolfgang W. Weisser
	3. Univ.-Prof. Dr. Carl Beierkuhnlein, Universität Bayreuth (nur schriftliche Begutachtung); Univ.-Prof. Dr. Anton Fischer (nur mündlicher Prüfer)

Die Dissertation wurde am 26.11.2015 bei der Technischen Universität München eingereicht und durch das Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt am 17.03.2016 angenommen.

für Mama, Papa und Steff

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Summary

Human land use is the leading driver of global losses in biodiversity. The transformation of natural ecosystems leads to widespread loss of primary habitats and divides formerly continuous landscapes into smaller and isolated fragments. Another significant characteristic of cultivated landscapes is that secondary ecosystems can re-establish after agricultural or silvicultural land use. Although their site conditions might be altered, such patches often exhibit sufficient habitat quality and thus can contribute to regional population persistence of at least some species. As a consequence, spatial dynamics of populations and communities in transformed landscapes are not only characterized by altered dispersal processes, but also by variable local interactions resulting from natural or human-induced variation in site conditions among habitat fragments.

The interaction of regional dispersal and variation in site conditions, as well as the conditions under which dispersal effectively regulates biodiversity in transformed landscapes are poorly understood. Therefore, the goals of this dissertation were (1) to improve the scientific understanding of how patterns of plant diversity are generated in transformed landscapes, and (2) to identify how environmental conditions drive the degree to which dispersal influences local and regional species co-existence. To accomplish these goals, the thesis combines experimental and observational investigations in historical calcareous grassland landscapes in southern Germany with modern analytical methods in three complementary studies.

The first study investigated how soil nutrient availability determines the importance of stochastic processes such as dispersal vs. niche-based selection for variation in plant species composition (i.e. beta diversity) among grasslands. For this purpose, a field experiment was established in which three levels of soil nutrient concentrations were manipulated; the successional dynamics of sown grassland communities were monitored over 3 years. Observed variation in species composition among replicate grasslands was then compared with expectations from null models. The resulting data revealed that compositional variation among oligotrophic grasslands hardly deviated from null expectations, whereas the deviation increased significantly with soil nutrient concentrations. These findings suggest that the effects of dispersal on landscape-scale biodiversity patterns decrease with increasing regional soil fertility.

The second study explored whether these experimental findings are transferable to real landscapes, and analyses the drivers of compositional variation among habitat fragments in transformed landscapes. Two historical calcareous grassland landscapes with contrasting regional soil fertility were compared. Using standardised methods in both landscapes, plant species composition, soil factors and – as measures of recent and past dispersal processes – contemporary and historical landscape context of multiple grassland fragments were studied. The leading drivers of species composition were identified using redundancy analysis, model selection and variation partitioning. Variation in species composition was driven by past dispersal processes in the landscape with lower regional soil fertility, whereas it was driven by variation in soil factors in the landscape with higher regional soil fertility. This confirms the experimental findings and emphasizes that regional soil nutrient concentrations are a critical environmental feature that determines the importance of dispersal vs. niche-based selection for biodiversity patterns in transformed landscapes.

Secondary habitat patches can potentially contribute to the persistence and regional dynamics of plant populations. Therefore, the third study focused on the limiting factors for utilizing this potential. Using mixed effects modelling in combination with an information theoretic approach and multi-model inference, this study dissected the principal drivers of species richness, the number of habitat specialists, and the functional trait composition of secondary grasslands. To improve the mechanistic understanding of operating ecological processes, the study used traits relevant for dispersal and interactions with local site conditions. The results showed that dispersal limitation of many habitat specialists during early stages of succession is not only the main driver of plant diversity in secondary grassland, but also strongly influences their functional trait composition. The positive effects of high immigration rates of specialist species even outweighed well-known negative effects of high soil nutrient concentrations on species numbers. Besides the dominant role of dispersal, there was also a significant influence of soil moisture that selected species according to their canopy height. This shows that dispersal and certain site factors interact in determining different aspects of plant community structure in secondary grasslands.

This PhD thesis demonstrates that combining complementary research approaches, large datasets and advanced analytical methods can produce novel insights into the drivers of plant diversity in human-transformed landscapes. In particular, the dissertation shows that dispersal can regulate biodiversity patterns under certain environmental conditions only, and reveals opportunities for and limits to directing successional trajectories in secondary grasslands. The results emphasize that conservation managers should actively assist dispersal and simultaneously reduce high soil nutrient concentrations. Successional trajectories in secondary grasslands can be manipulated using active species transfer measures during early stages of succession.

Zusammenfassung

Die anthropogene Transformation natürlicher oder traditionell genutzter Landschaften für eine intensive land- und forstwirtschaftliche Produktion ist weltweit der wichtigste Treiber des hohen Biodiversitätsverlusts im 20. und 21. Jahrhundert. Veränderte Landnutzung führt zu einem großflächigen Verlust von Lebensräumen vieler Arten und unterteilt ehemals zusammenhängende Habitate in kleinere und isolierte Fragmente. Ein wesentliches Merkmal solcher Landschaften ist aber auch, dass sekundäre Lebensräume nach zwischenzeitlicher Nutzung wieder verfügbar werden, die trotz dann veränderter standörtlicher Bedingungen eine ausreichende Habitatqualität aufweisen und dadurch zur regionalen Persistenz von Arten beitragen. Deshalb ist zu erwarten, dass die räumliche Dynamik von Populationen und Artengemeinschaften in transformierten Landschaften nicht nur durch veränderte Ausbreitungsprozesse charakterisiert ist, sondern auch durch unterschiedliche lokale Interaktionen als Folge natürlicher und vom Menschen induzierter standörtlicher Unterschiede zwischen Habitatfragmenten.

Dennoch sind die interagierenden Effekte regionaler Ausbreitungsprozesse und standörtlicher Unterschiede zwischen Habitatfragmenten sowie die Bedingungen, unter denen Ausbreitungsprozesse die Biodiversität transformierter Landschaften effektiv regulieren, bisher kaum erforscht. Die Ziele der Dissertation sind daher (1) das wissenschaftliche Verständnis darüber zu verbessern, wie pflanzliche Diversitätsmuster in transformierten Landschaften generiert werden, und (2) standörtliche Bedingungen zu identifizieren, unter denen Ausbreitungsprozesse die lokale und regionale Koexistenz von Arten entscheidend beeinflussen können. Die Arbeit kombiniert experimentelle Ansätze und Vegetationsuntersuchungen in transformierten ehemaligen Kalkmagerrasenlandschaften in Süddeutschland mit modernen Methoden der Datenanalyse in drei komplementären Studien.

Die erste Studie untersucht, ob Bodennährstoffgehalte beeinflussen, wie wichtig stochastische Prozesse, z.B. Ausbreitung, gegenüber nischenbasierter Selektion für Unterschiede in der Pflanzenartenzusammensetzung (Beta-Diversität) zwischen Grasländern sind. Dazu wurde ein Feldexperiment eingerichtet, in dem Bodennährstoffe in drei Stufen manipuliert wurden und die Vegetationsentwicklung angesäter Graslandgemeinschaften über 3 Jahre verfolgt wurde. Die Unterschiede in der Artenzusammensetzung zwischen den Replikaten jeder Nährstoffstufe wurden

dann mit Erwartungen eines Null-Modells verglichen. Es zeigte sich, dass floristische Unterschiede zwischen nährstoffarmen Grasländern kaum von den Erwartungen des Null-Models abwichen, während die Abweichung bei höheren Nährstoffgehalten signifikant zunahm, weil ähnliche Artenkombinationen selektiert wurden. Die Ergebnisse legen nahe, dass die Effektivität, mit der Ausbreitungsprozesse Biodiversitätsmuster in Landschaften regulieren, mit zunehmenden regionalen Bodennährstoffgehalten abnimmt.

Die zweite Studie untersucht, ob diese experimentellen Ergebnisse auf reale Landschaften übertragbar sind und welche Faktoren Unterschiede in der Artenzusammensetzung von Habitatfragmenten in transformierten Landschaften generieren. Dazu wurden in Südbayern zwei fragmentierte Kalkmagerrasenlandschaften mit unterschiedlichen regionalen Bodennährstoffgehalten verglichen. In beiden Landschaften wurden mit standardisierten Methoden Artenzusammensetzung, Bodeneigenschaften sowie, als Maß für die Bedeutung von rezenten und ehemaligen Ausbreitungsprozessen, aktueller und historischer Landschaftskontext von zahlreichen Graslandfragmenten erhoben. Die bestimmenden Faktoren der Artenzusammensetzung wurden mit Hilfe von Redundanzanalysen, Modellselektion und Varianzpartitionierung identifiziert. In der Landschaft mit allgemein niedrigen Bodennährstoffgehalten wurden Unterschiede in der Artenzusammensetzung ausschließlich durch ehemalige Ausbreitungsprozesse verursacht. In der Landschaft mit höheren Nährstoffgehalten hingegen wurde Beta-Diversität vor allem durch unterschiedliche Bodeneigenschaften hervorgerufen. Dies bestätigt die experimentellen Befunde und unterstreicht, dass regionale Bodennährstoffgehalte ein wichtiger Faktor sind, der die Bedeutung von Ausbreitungsprozessen gegenüber nischenbasierter Selektion für Biodiversitätsmuster in transformierten Landschaften steuert.

Sekundäre Habitate können potentiell zur Persistenz und regionalen Dynamik von Pflanzenpopulationen in transformierten Landschaften beitragen. Die dritte Studie fokussierte deshalb auf die limitierenden Faktoren für die Ausschöpfung dieses Potentials. Unter Verwendung gemischter Modelle und informationstheoretischer Multi-Modell-Inferenz wurden die wesentlichen Faktoren des Artenreichtums, der Anzahl an Habitatspezialisten sowie die Zusammensetzung verschiedener funktionaler Arteigenschaften (‚functional traits') untersucht. Um ein besseres Verständnis der Wirkungsmechanismen zu erzielen, kamen Pflanzeneigenschaften

zur Verwendung, die für Ausbreitung und die Interaktion von Pflanzen mit lokalen Standortbedingungen relevant sind. Die Ergebnisse zeigen, dass die Ausbreitungslimitierung zahlreicher Habitatspezialisten während früher Sukzessionsstadien nicht nur der wichtigste Faktor für den Artenreichtum sekundärer Grasländer ist, sondern auch deren funktionale Zusammensetzung wesentlich beeinflusst. Die positiven Effekte hoher Einwanderungsraten von Habitatspezialisten auf Artenzahlen überwogen sogar die bekannten negativen Effekte hoher Bodennährstoffgehalte. Neben der dominanten Rolle von Ausbreitungsprozessen wurde aber auch ein signifikanter Einfluss von Bodenfeuchteverhältnissen festgestellt, die Arten nach deren Wuchshöhe selektierten. Das zeigt, dass Ausbreitungsprozesse und bestimmte Standorteigenschaften interagieren, aber auf unterschiedliche Aspekte der Struktur von Pflanzengemeinschaften in sekundären Grasländern wirken.

Insgesamt zeigt die Dissertation, dass durch die Verwendung vielseitiger Forschungsmethoden und umfangreichen Datenmaterials neue Erkenntnisse über die Faktoren pflanzlicher Diversität in transformierten Landschaften möglich sind. Die Ergebnisse demonstrieren, dass Biodiversitätsmuster nur unter bestimmten standörtlichen Bedingungen durch Ausbreitungsprozesse reguliert werden und welche Möglichkeiten und Grenzen der Lenkung von Sukzessionsprozessen in sekundären Grasländern bestehen. Die Ergebnisse unterstreichen, dass Naturschutzpraktiker Ausbreitungsprozesse aktiv fördern und gleichzeitig hohe Nährstoffgehalte reduzieren sollten. Sukzessionsverläufe in sekundären Grasländern können durch Artentransfermaßnahmen während früher Sukzessionsstadien gesteuert werden.

Chapter 1

General introduction

1.1 BIODIVERSITY IN THE ANTHROPOCENE

In 2005, the *Science* journal celebrated its 125th anniversary. On this occasion, the editors initiated a global survey among scientists from all disciplines, with the aim to identify the leading research questions for the 21st century. Among the top 25 of these were questions like "*What is the universe made of?*" or "*How much can human life span be extended?"* Yet another one was

"What determines species diversity?"

It is two conflicting phenomena that make improving our knowledge of the determinants of species diversity a research priority for the coming decades: On one hand, the provision of goods and socio-economic benefits by natural and anthropogenic ecosystems, such as food and timber production, pest control, carbon sequestration or cultural services, is regulated and maintained by intact and diverse biota (Cardinale et al. 2012; Daniel et al. 2012; Gamfeldt et al. 2013; Isbell et al. 2015; Lefcheck et al. 2015). At the same time, human economic activities cause species extinction rates that are unusually high in the Earth's geological history (Barnosky et al. 2011; Pimm et al. 2014; Ceballos et al. 2015). Another thousands of plant and animal species are currently at risk (The IUCN Red List of Threatened Species Version 2015.3; www.iucnredlist.org, accessed 04 Nov 2015), and many of them will likely go extinct in the near future (Dullinger et al. 2013; Pimm et al. 2014).

The leading driver of this erosion of biodiversity is human land use (Sala et al. 2000; Millennium Ecosystem Assessment 2005). The modification of natural landscapes for agricultural production has led to widespread destruction of habitats and to the fragmentation of previously continuous habitat into smaller and more isolated fragments. Habitat fragmentation exposes small fragments to negative edge effects and constrains dispersal between them, with often negative consequences for population dynamics (Fahrig 2003; Hanski et al. 2013; Damschen et al. 2014; Haddad et al. 2015). In addition, the contrasting land-use intensities and histories of remaining fragments induce variable habitat qualities that select for different species combinations and numbers (Freschet et al. 2013; Allan et al. 2015; Newbold et al. 2015). As a consequence, population and community dynamics in human-transformed landscapes are not only characterized by altered regional dispersal processes, but also involve habitat patches with heterogeneous environmental conditions that alter local interactions of species with their biotic and abiotic environment (Hobbs et al. 2014; Mendenhall et al. 2014).

Mitigating the negative effects of anthropogenic global change on biodiversity requires immediate and effective conservation measures (Pimm et al. 2014; Ceballos et al. 2015), and these critically rely on a thorough scientific understanding of the response of species diversity to interacting anthropogenic drivers (Clark et al. 2001; Dawson et al. 2011). Yet, the simultaneous effects of regional dispersal processes and site-to-site variation in environmental conditions, as well as the conditions under which dispersal can effectively regulate diversity patterns at the landscape scale are poorly understood (Tscharntke et al. 2012). Thus, this dissertation was motivated by the pressing scientific challenge to better understand ecological dynamics in human-transformed landscapes. With the work presented here, I hope to contribute to a more synthetic view on the drivers of species diversity in the Anthropocene, which allows empirical findings to be aligned into a broader conceptual framework that provides guidance for conservation and habitat restoration.

1.2 STUDYING ECOLOGICAL DYNAMICS IN HUMAN-TRANSFORMED LANDSCAPES

Metacommunity dynamics

In this thesis, I adopt a metacommunity ecological perspective to explore the determinants of plant species diversity in fragmented and environmentally heterogeneous grasslands. The domain of the metacommunity concept is to explain why the composition and richness of communities varies from one locality to another (Leibold 2011). It does so by explicitly considering how dispersal among localities might interact with local environmental conditions to determine variation in community structure among localities. Therefore, this perspective integrates ecological processes that operate at different spatial scales, and is thus an extension of traditional approaches, which have mainly focused on either local factors or dispersal as drivers of community structure.

The definition of a metacommunity as a *"set of local communities that are linked by dispersal of multiple potentially interacting species"* (Leibold et al. 2004) reflects the view that community structure can be better understood in the light of regional dispersal processes. There are, however, different scenarios of how dispersal, local site conditions, and species' ecological characteristics might actually regulate community patterns. These can be conceptualised in four classes of metacommunity models, which differ in the importance they ascribe to dispersal, variation in local site factors, and species' characteristics as drivers of community assembly (Leibold et al. 2004; Leibold 2011).

First, *neutral metacommunity models* assume that species are ecologically equivalent and that variation in species richness and composition among communities results from random processes such as dispersal and demographic stochasticity (Hubbell 2001). The assumption of ecological equivalence implies that variation in community structure is related to spatial factors that influence the numbers and identities of immigrating species, but is not related to environmental differences.

By contrast, *models of environmental sorting* in metacommunities emphasize that species are ecologically not equivalent, and that their fitness in a given environment is a consequence of their functional characteristics. The prediction that follows is that environmental variation, rather than spatial factors, leads to deterministic, niche-based variation in species composition among localities. As such, the neutral and environmental sorting perspectives represent two radically different views of the world. In reality, however, both neutral stochastic and niche-based process operate simultaneously (Gravel et al. 2006; Adler et al. 2007; Vellend 2010), and instead of arguing for and against one or the other, it is more relevant to explore the conditions that determine the relative importance of these contrasting assembly mechanisms (e.g. Chase 2010; Myers et al. 2013; Vellend et al. 2014). I will investigate this issue in Chapters 2 and 3.

The third group of metacommunity models involves *mass effects*. The assumption is that species respond differentially to environmental conditions but high dispersal rates from source patches can prevent extirpations form sink habitats, in which there is a mismatch between environmental conditions and a species' optimal habitat requirements. This phenomenon might confound relationships of environmental conditions with community patterns (Leibold 2011). In Chapter 4, I will use plant functional traits as a surrogate of species' niches to show that mass effects exert significant influences on community patterns in regenerating grasslands.

Finally, *models of patch dynamics* ignore environmental differences among habitat patches. In such models, local extinctions can be stochastic or deterministic, and competition-colonisation or other trade-offs are necessary for local and regional co-existence (Leibold et al. 2004). I will not refer to this class of models in the course of the thesis, however, because trade-offs as co-existence mechanisms were not my focus here.

Using plant functional traits to infer community assembly mechanisms

As already indicated, I will also make use of plant functional traits to infer the ecological processes that generated the observed patterns of species diversity. A 'functional trait' is a *"morphological, physiological or phenological feature measurable at the individual level* (…) *which impacts fitness indirectly via its effects on growth, reproduction and survival"* (Violle et al. 2007), such as leaf characteristics indicative of resource economics, seed mass or plant height. The rationale of using such properties to infer community assembly mechanisms is based on the assumption that interspecific variation in functional traits reflects contrasting strategies to maximize fitness in a given environment (Grime 1977; Westoby 1998; Westoby et al. 2002). Hence, according to environmental sorting models of metacommunity dynamics, the functional trait composition of communities should vary systematically along environmental gradients (McGill et al. 2006; Westoby & Wright 2006), whereas there should be no such variation if community assembly is neutral with respect to trait differences (e.g. Kraft et al. 2008). Alternatively, when mass effects operate, trait-environment relationships will be confounded, and instead, the functional composition of local communities will resemble that of nearby source habitats. Because the focus is on species' ecological characteristics rather than taxonomic identity, one additional advantage of trait-based approaches is that they allow for generalizable conclusions that can be transferred to other biogeographic regions, what goes beyond statements based on purely taxonomic approaches (McGill et al. 2006).

Landscape history and diversity patterns in fragmented landscapes

A further significant component of understanding diversity patterns in human-transformed landscapes is to acknowledge the role of landscape history. In their now classic paper, Lindborg and Eriksson (2004) showed that species richness of fragmented grasslands better reflected habitat connectivity 50 to 100 years ago rather than present-day connectivity. This was the first study to demonstrate that present-day richness patterns can still reflect past dispersal rates. A large body of empirical work followed to show that such historical contingency in the richness and composition of fragmented habitats is the rule rather than the exception (e.g. Helm et al. 2006; Lindborg 2007; Krauss et al. 2010; Purschke et al. 2012; Bommarco et al. 2014; Kimberley et al. 2014). Together, these studies emphasize that historical landscape configurations have to be accounted for in order to correctly estimate the importance of regional processes for diversity patterns in human-transformed landscapes.

1.3 OBJECTIVES AND OUTLINE OF THE THESIS

In order to derive improved predictions of diversity patterns in human-transformed landscapes, it is necessary to evaluate the roles of local site factors as well as past and present dispersal processes relative to each other. Knowing their relative contributions to observed community patterns is crucial not only for fundamental science but also for implementing effective conservation measures (Bengtsson 2010). However, most existing studies focussed on local or regional factors in isolation although this might lead to wrong conclusion (Chang et al. 2013). In addition, comparative studies that examined how environmental features (e.g. regional productivity) dictate the degree to which metacommunity dynamics are driven by dispersal relative to local factors are rare. As a consequence, we currently lack a robust synthetic framework for understanding the determinants of plant species diversity in human-transformed landscapes.

Therefore, the main objectives of this dissertation were (1) to improve the scientific understanding of how plant diversity patterns in human-transformed landscapes are generated, and (2) to stimulate theoretical developments about when and how environmental conditions should influence the magnitude by which dispersal can effectively promote local and regional co-existence. To accomplish these goals, I combined experimental and observational investigations in calcareous grassland metacommunities with advanced analytical tools in three complementary studies that are reported in Chapters 2–4. Chapter 5 synthesizes their main findings and discusses implications for science and conservation practice.

Resource availability and niche-based vs. stochastic community assembly – Study I

The first study of this thesis reports on a 3-year field experiment that explored the effects of soil resource supply on the importance of niche-based vs. stochastic processes for variation in species composition among grassland plots (Figure 1). For this purpose, I manipulated three levels of soil nutrient concentrations in sown grassland communities and monitored species composition over three consecutive growing seasons. The observed spatial turnover in species composition among replicates of each treatment was then compared with expectations from null models of beta diversity, and the magnitude of the deviation from null expectations was compared among resource treatments.

Drivers of beta diversity in grassland metacommunities – Study II

To examine whether my experimental findings were consistent with assembly processes in real grassland metacommunities, the second study compares the roles of past and present dispersal relative to environmental conditions as drivers of beta diversity among two human-transformed grassland landscapes with contrasting regional soil fertility. To better understand how these factors generated variation in species composition, I quantitatively decomposed beta diversity into its turnover and nestedness components, and then disentangled their respective drivers using distance-based redundancy analysis and variation partitioning for each study area separately. To correctly evaluate the importance of local site factors as well as past and present landscape-scale dispersal processes for beta diversity, I compiled an extensive dataset covering species composition, soil data, and past and present landscape context of 34 grasslands (see Figure 2).

Plant diversity and functional traits in secondary grasslands – Study III

The third study uses mixed effects modelling and multi-model inference to assess local and regional drivers of species richness and functional trait composition of secondary grasslands. This study takes advantage of the large and functionally distinct species pools of primary calcareous grasslands (see below), the known functional relevance of selected plant traits, and the detailed landscape and soil data of the second study, to evaluate the potential role of mass effects, trait-based environmental sorting, and trait-neutral, dispersal-driven assembly.

1.4 STUDY SYSTEM AND AREAS

Calcareous grassland as a model system

In this thesis, I focus on Central European calcareous grasslands, which are a suitable model system to investigate local and regional drivers of diversity patterns in human-transformed landscapes. Like other semi-natural grasslands in Europe, calcareous grasslands are the result of centuries or even millennia of low-intensity livestock grazing or hay-making, and are therefore anthropogenic ecosystems (Ellenberg & Leuschner 2010). Already starting in the Neolithic, livestock grazing of forests gradually reduced the natural forest cover and led to increasingly open pastures. In several regions, vast open pastoral landscapes covered by calcareous grassland expanded especially in the 15th century and persisted until the early 20th century. During that time, the grassland landscapes were maintained and connected with others by transhumant sheep flocks (Poschlod & WallisDeVries 2002), which efficiently dispersed diaspores of many plant species within and across regions (Fischer et al. 1996). Owing to socio-economic changes in the late 19th century, and the large-scale production of synthetic fertilisers, sheepherding became increasingly uneconomic, so that massive transformations of the grassland landscapes into intensively used agricultural systems, forest plantations, or abandoned land took place at that time (Poschlod & WallisDeVries 2002). Remaining fragments of the ancient calcareous grassland landscapes are often small and isolated and are managed by nature conservation using annual mowing or grazing and no application of fertiliser.

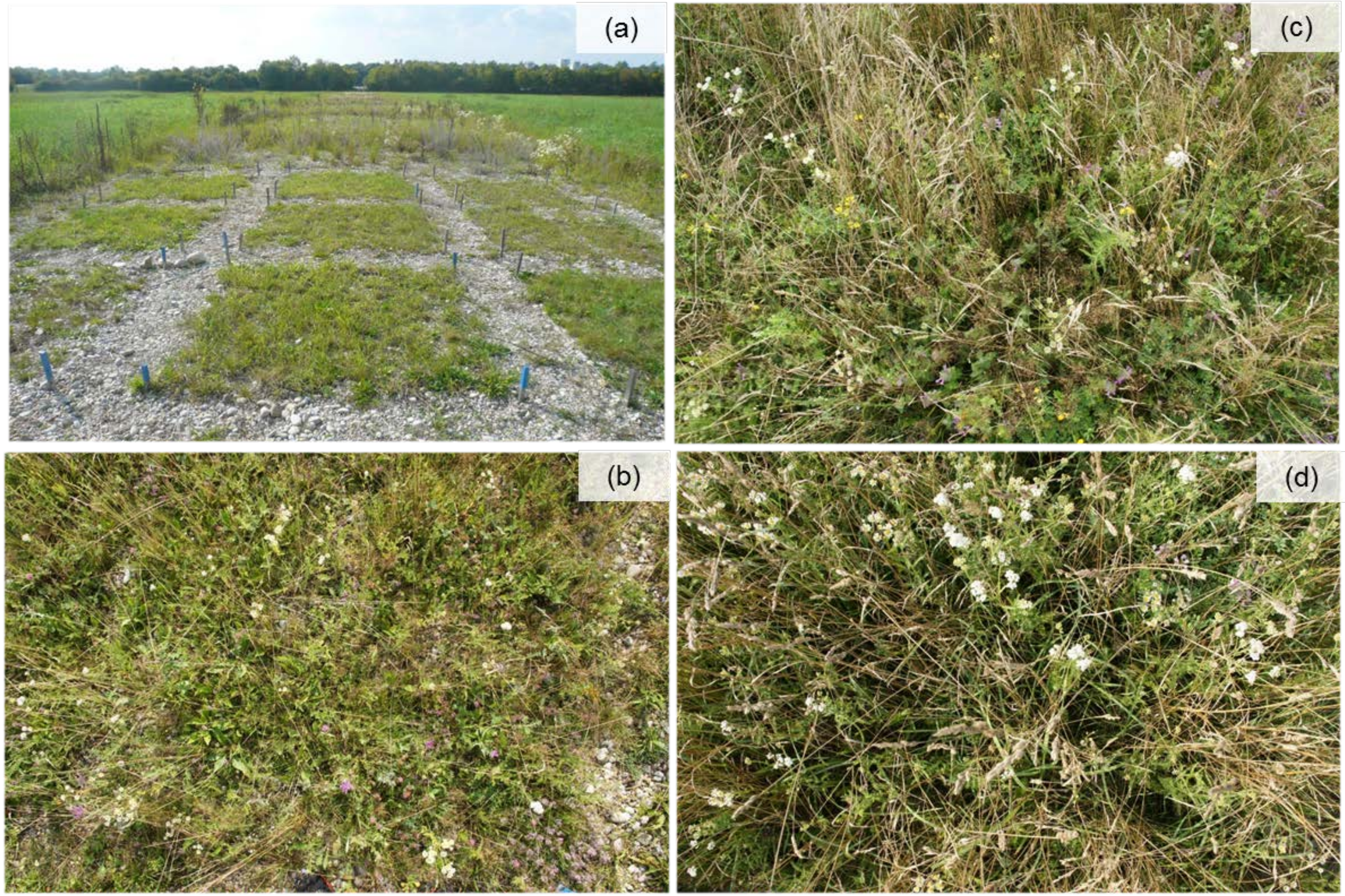


Figure 1 | Grassland communities sown in an experiment that investigated the effect of soil resource availability on the importance of niche-based vs. stochastic community assembly (Chapter 2). Picture (a) shows mown grassland communities of one replicate block in the second year of the experiment (Photo credit: Johannes Kollmann). The remaining pictures were taken in the second year of the experiment before mowing and show experimental plots with (b) no, (c) moderate and (d) high soil resource availability.

Figure 2 | Aspect of three calcareous grasslands in southern Germany. Picture (a) shows the 'Königsbrunner Heide', a species-rich primary grassland in the Lech River Valley. Picture (b) shows the 'Kissinger Bahngruben', a species-rich secondary grassland in the Lech River Valley that originated in 1840 after gravel extraction. Picture (c) shows a moderately species-rich secondary grassland in the nature reserve 'Mallertshofer Holz mit Heiden' in the Munich Gravel Plain.

If well-preserved, calcareous grasslands contain a rich and characteristic flora and fauna of otherwise rare species (Veen et al. 2009). Indeed, at spatial scales <100 m^2, this vegetation type holds world records in vascular plant species richness that even exceed those of tropical rain forests (Wilson et al. 2012). Because of their unique and diverse flora and fauna on one hand, and the immense habitat loss on the other hand, calcareous grassland are in the focus of nature conservation and habitat restoration efforts across Europe (e.g. Pywell et al. 2002; Kiehl & Pfadenhauer 2007; Helsen et al. 2012; Conradi et al. 2015).

For simplicity, I refer to those grasslands that were part of the historical grassland landscape as 'primary' grasslands, although I emphasize again that they are in fact anthropogenic habitats. Those grasslands that had a discontinuity of semi-natural grassland cover and are recovering through natural processes are referred to as 'secondary' grasslands (cf. Corlett 1994; Chazdon et al. 2009). Such discontinuities of semi-natural grassland cover typically result from abandonment or different interim land use such as intensified agriculture, forestry, or gravel extraction. I also include patches in this category that originated after a major disturbance (e.g. flood, deforestation) in places that were not part of the historically continuous grassland landscape. The unifying feature of all these secondary grasslands is that – in comparison to primary grasslands – they have a shorter continuity of semi-natural grassland management. As a consequence, their successional trajectories were influenced by the colonisation from the adjacent landscapes, but the composition of these landscapes has changed over time.

The co-existence of primary and secondary habitat patches is a characteristic feature of most human-transformed landscapes (Chazdon et al. 2009; Hobbs et al. 2014; Kueffer & Kaiser-Bunbury 2014). Secondary patches can provide suitable site conditions for species of the historically continuous landscapes and can thus contribute to regional persistence of populations (Jackson & Sax 2010; Piqueray et al. 2011; Mendenhall et al. 2014). As a consequence, metacommunity dynamics in human-transformed landscapes involve both primary and secondary habitat patches. Because of interactive effects of natural and human-induced variation in local site conditions, the variable land-use histories, and the contrasting contemporary and past landscape contexts of the patches, disentangling local and regional drivers of diversity patterns in such landscapes is challenging. However, the availability of detailed historical information makes ancient calcareous grassland landscapes a particularly suitable model system for this purpose. Because of the high species diversity of calcareous grassland, there is a long tradition of documentation among natural scientists and conservationists. In addition, detailed historical maps from various time periods exist, including maps of the pre-transformed landscapes. This makes the reconstruction of patch continuities and historical landscape contexts possible and allows for robust evaluations of the importance of regional relative to local processes for diversity patterns, which might be transferable to other regions with less well-documented history.

Grasslands on calcareous gravel in southern Germany

The study was conducted in two geographically separated, human-transformed ancient grassland landscapes in southern Germany, the Lech River Valley (LRV) (Figure 3) and the Munich Gravel Plain (MGP) (Figure 4). The climate is temperate and humid, with a mean annual temperature of ca. 8.5 °C and an annual precipitation of ca. 835 mm (1981–2010; www.dwd.de, accessed 25 Feb 2015). In both study areas, the investigated grasslands are distributed across a similar geographic extent of 22 km, and are located between 491–561 m and 469–520 m a.s.l. in the LRV and MGP, respectively. The underlying bedrock is calcareous gravel consisting mainly of dolomite and limestone clasts. With one exception, the investigated grasslands in the MGP study area are located on fluvio-glacial gravel from the late Pleistocene (Freudenberger 1996), whereas grasslands of the LRV study area are located on younger fluvial gravel deposited during various periods of the Holocene until the early 19th century (Gesslein 2013). The natural pedogenesis has led to carbonate-rich, nutrient-poor and relatively shallow leptosols in most places but thicker alluvial soils that were deposited during flood events can be found occasionally in some grasslands close to rivers (Fetzer et al. 1986). Although pastoral use of the natural forest vegetation began in the Neolithic (LRV) and Bronze Age (MGP), leading to first open woodlands in some areas (Kollmannsberger 1973; von den Driesch 2001), extensive deforestation as a consequence of increasing human populations started already around 1400 BP and led to vast open grassland landscapes (Pfeuffer 2010). These were mainly used as pastures and persisted for centuries (as can be reconstructed from historical maps and reports, e.g. Kollmannsberger 1973; Müller 1990; Pfadenhauer et al. 2000; Pfeuffer 2010) until a drastic agricultural transformation of the landscape started in the first decades of the 20th century (Kollmannsberger 1973;

Pfeuffer 2010). Today, primary and secondary grasslands are managed by nature conservation using annual mowing or, in larger grasslands, grazing by sheep herds including few goats. There are also some efforts to recreate calcareous grasslands which attempt to re-connect and to increase the habitat amount of existing fragments using hay transfer (e.g. Kiehl & Pfadenhauer 2007). Such grasslands were not included in this study, because it is impossible to discern which species colonised such sites on their own accord or, alternatively, to discern whether absent species are missing because they were not included in the hay or because they failed to establish.

Figure 3 | Distribution of semi-natural calcareous grasslands in the Lech River Valley study area in southern Germany. Grasslands that were investigated in Chapters 3 and 4 are mapped in dark grey. Shown are primary and secondary calcareous grasslands that include at least one of the indicator species *Bromus erectus* Huds. and *Brachypodium rupestre* (Host.) Roem. & Schult., and have <60 % woody cover. The grassland distribution is based on data of the 'Habitat Mapping' of the Bavarian Environmental Office (LfU), and was amended based on own field observations and interpretation of aerial photographs. Oliver Zachow (unpubl. M.Sc. thesis) prepared the 'Habitat Mapping' data.

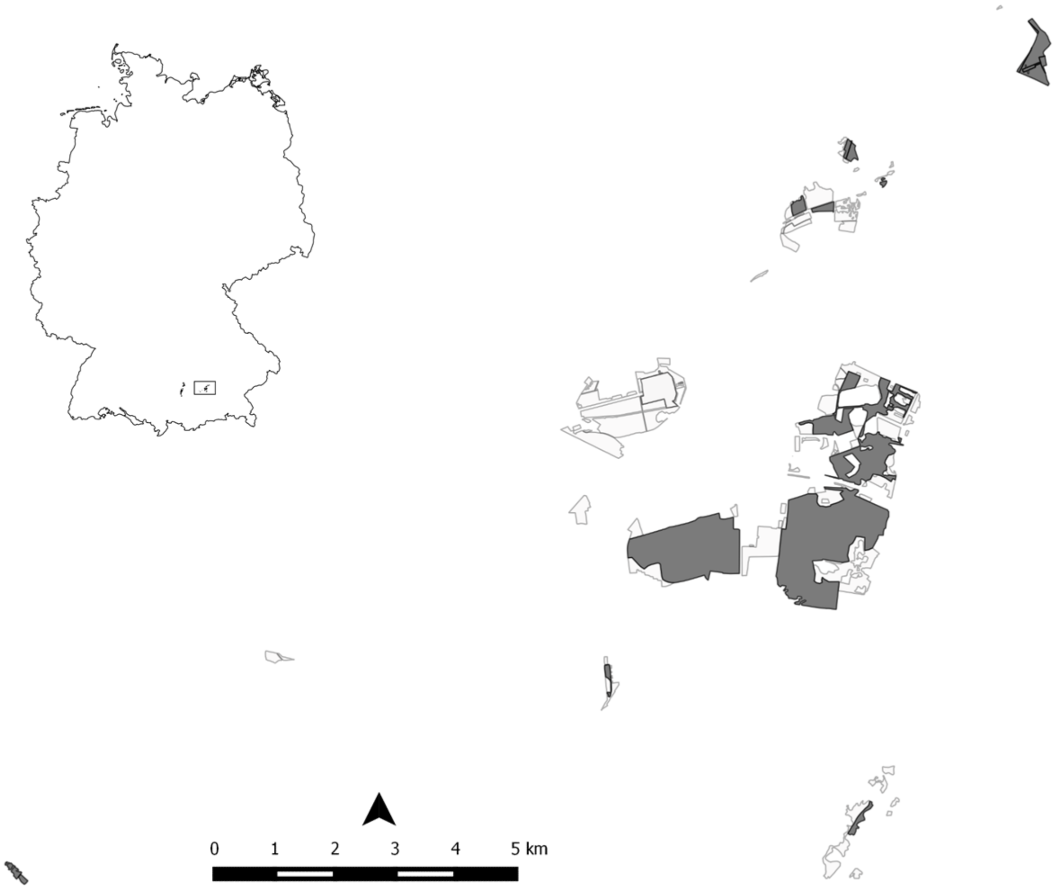


Figure 4 | Distribution of semi-natural calcareous grasslands in the Munich Gravel Plain study area in southern Germany. Grasslands that were investigated in Chapters 3 and 4 are mapped in dark grey. Shown are primary and secondary calcareous grasslands that include at least one of the indicator species *Bromus erectus* Huds. and *Brachypodium rupestre* (Host.) Roem. & Schult., and have <60 % woody cover. The grassland distribution is based on data of the 'Habitat Mapping' of the Bavarian Environmental Office (LfU), and was amended based on own field observations and interpretation of aerial photographs. Oliver Zachow (unpubl. M.Sc. thesis) prepared the 'Habitat Mapping' data.

Chapter 2

Resource availability determines the importance of niche-based vs. stochastic community assembly in grasslands

Abstract – *Niche-based and stochastic processes can operate simultaneously to generate spatial and temporal variation in species composition. Yet, the conditions under which ecological dynamics are dominated by niche-based vs. stochastic processes are poorly understood. Using a field experiment in temperate grassland and null models of beta diversity, this study investigates the effects of soil resource supply on the relative importance of niche-based vs. stochastic dynamics for variation in species composition among sites. Individual seed mixtures with 25 species were sown and then stochastic and deterministic niche-based assembly processes were allowed to happen. We found that compositional variation among grassland plots with low resource supply was driven by stochastic immigration and extinctions. By contrast, nutrient enrichment reduced the importance of stochasticity and imposed a deterministic environmental filter that homogenised communities through the selection of few species with greater competitive ability for light. This demonstrates that soil resource availability is a critical environmental feature that dictates the degree to which terrestrial plant communities are controlled by niche-based selection vs. stochastic assembly processes. Our study shows further that alternative states of eutrophic grasslands emerge from initial stochastic variation in the composition of a particular functional group of species that can become dominant at high resource supply. Potential mechanisms underlying the shift from stochastic to niche-driven dynamics along soil resource gradients are discussed.*

Keywords: *Beta diversity; Environmental filtering; Eutrophication; Metacommunity; Neutral theory; Null models; Spatial ecology; Succession*

2.1 INTRODUCTION

A central goal in ecology is to understand the mechanisms underlying diversity patterns in space and time. Niche-based models of community assembly assume that contrasting functional characteristics of species and competitive interactions determine variation in species composition along environmental gradients (Keddy 1992; Götzenberger et al. 2012; HilleRisLambers et al. 2012). By contrast, neutral models of community assembly emphasize the roles of random processes such as demographic stochasticity and dispersal for spatial and temporal variation among communities ('ecological drift'; Hubbell 2001). While the past decade has seen much debate about which perspective more accurately describes natural systems (Rosindell et al. 2012), consensus is emerging that both niche and stochastic processes operate during community assembly (Adler et al. 2007; Cadotte 2007; Vellend et al. 2014). Thus, the research focus has now shifted towards identifying the conditions under which ecological dynamics of a system are driven more by niche-based vs. stochastic processes (Fisher & Mehta 2014; Dini-Andreote et al. 2015) and to place communities along a niche-to-stochasticity gradient (Chase & Myers 2011; Logue et al. 2011; Vellend et al. 2014). Comparative studies investigating the effects of natural or anthropogenic factors on the relative importance of these assembly processes in a study system can thus fundamentally increase the scientific understanding of the mechanisms that create and maintain biodiversity patterns (e.g. Chase 2007, 2010; Myers et al. 2013).

The use of null models of beta diversity has recently been proposed to dissect the relative importance of niche-based vs. stochastic drivers of variation in species composition (Chase et al. 2011; Chase & Myers 2011). In this approach, observed beta diversity between communities is compared to a null expectation of beta diversity calculated from randomly assembled communities. The magnitude of the deviation between observed and expected beta diversity ('beta deviation') is then used to infer whether niche-based or stochastic processes generated the observed variation in species composition. Beta deviations can then be compared across experimental treatments or environmental gradients to evaluate whether a factor of interest alters the importance of the two dissimilar community assembly processes (Chase & Myers 2011).

Although there is ample evidence that soil nutrient concentrations determine variation in alpha diversity of grasslands (e.g. Stevens et al. 2004; Crawley et al. 2005;

Harpole & Tilman 2007; Ceulemans et al. 2014), little is known about whether contrasting soil resource concentrations also induce dissimilar mechanisms of community assembly. For example, community assembly in resource-poor sites might be deterministic because stressful environments select for similar species combinations (Chase 2007, 2010; Guo et al. 2014). Alternatively, if low resource levels reduce population carrying capacities, this could increase the importance of demographic and environmental stochasticity relative to deterministic niche-based interactions, such that local community composition is more a result of stochastic extinctions and differential immigration (Fisher & Mehta 2014). Likewise, it is unclear whether resource-rich sites consistently select for similar combinations of competitive species, especially since authors often found divergent compositional trajectories after nutrient enrichment (Chalcraft et al. 2008; Houseman et al. 2008), indicating that extinctions after nutrient enrichment might not necessarily be deterministic with respect to species identities.

This study reports on a 3-year field experiment, which was explicitly designed to test whether the importance of niche-based vs. stochastic community assembly processes in temperate grasslands changes along a soil resource gradient. For this purpose, we manipulated three levels of resource availability and compared observed turnover in grassland species composition with expectations from null models. Upon observing that one particular functional group dominated grassland plots with high resource supply, we also tested whether stochastic variation in the initial composition of this group led to divergent alternative states after nutrient enrichment. This would create a priority effect, where the arrival order in a site strongly influences which species can be found later (von Gillhaussen et al. 2014; Fukami 2015).

2.2 METHODS

Study site

The experiment was established within a large fenced grassland north of Munich, Germany, in early April 2013. The climate in the region is temperate and humid with a mean annual rainfall of 834 mm and a mean annual temperature of 8.7 °C (1981–2010; www.dwd.de, accessed 25 February 2015). The grassland was subdivided by 9 m broad, east-west running calcareous gravel roads which were artificially deposited by extracting gravel from nearby pits. We used one of these gravel roads for our experiment as resource-poor initial conditions were required to create realistic soil fertility levels with our treatments. The gravel road had no soil layer and only a sparse, species-poor vegetation, consisting mainly of mosses and tussock grasses. In October 2012, a systemic herbicide was applied to the areas on the gravel road where the experiment was to be set up later, and these were rotary tilled in late November 2012 in order to completely remove the existing vegetation. In early April 2013, one day before sowing the plant species, the sites were harrowed and then raked to make them as homogeneous as possible. Plots were established and received their experimental resource addition treatments on the same day.

Experimental design

The experiment consisted of three 8×8-m replicate blocks, each with nine 2×2-m plots arranged in a rectangular grid with 0.5 m spacing between plots, resulting in a total number of 27 plots. The small distance between plots was chosen to minimize dispersal limitation. We manipulated three levels of soil resource availability, each with nine replicates equally distributed among blocks. The resource levels were randomly assigned to the 2×2-m plots and consisted of no, moderate (50 kg N ha^{-1} a^{-1}), or high (100 kg N ha^{-1} a^{-1}) fertilisation. Nutrients were added annually prior to the start of the growing season and consisted to two thirds of a fertiliser that released nutrients over a period of 5-6 months to ensure continuous nutrient supply (11-11-18 N-P-K; Osmocote Exact Standard High K 5-6M, Everris), and to one third of a short-term fertiliser (12-12-17 N-P-K; Complex, Linzer Agro Trade) to ensure that treatment levels were fully differentiated right from the beginning of the growing season. The high fertilisation level corresponds to the empirically derived amount of annual N removal in grasslands with moderate management intensity in this region, which is then compensated by fertilisation (Wendland et al. 2012). Thus, the manipulated range of soil resource levels realistically resembled that of semi-natural grasslands in the study region, which were the focus of this and related studies (Chapters 3–4).

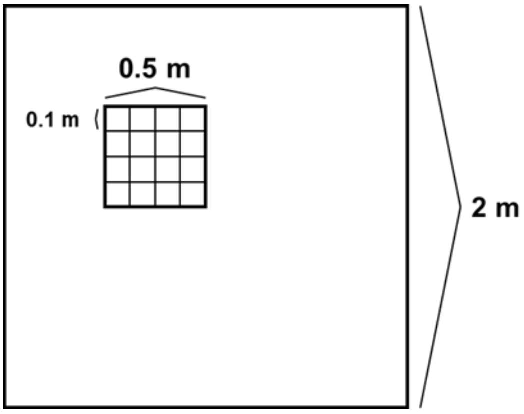


Figure 5 | Depiction of the sampling strategy in the experiment. Within each of the 27 2×2-m plots, one 0.5×0.5-m permanent subplot was established, that was further subdivided into 25 0.1×0.1-m squares, in which presence/absence of plant species was recorded.

The experimental species pool consisted of 54 species (Table S1) that occurred with ≥10% frequency in the sampling quadrats of a vegetation survey of semi-natural grasslands in the region (Chapters 3 and 4, as per field season 2012) and were also available from a supplier of wild local seed (J. Krimmer, Pulling). Tree, shrub and (hemi-)parasitic species were not included because they did not fit the purpose of the study. Preliminary tests confirmed that there were no functional trait differences to species that were found in the survey but not included in the experiment, indicating that the species used in the experiment represented the regional grassland species pool well. All seeds were harvested in 2012 from populations that were propagated for a maximum of 6 years under common garden conditions comparable to our field site and stem from wild local populations. Therefore, we reduced confounding maternal effects and used fresh seed material from locally adapted sources.

Each of the 27 2×2-m plots received a different seed mix of 25 plant species that, for each plot separately, was randomly drawn from the experimental species pool, but had to contain seven graminoid species, three legumes, and 15 non-legume forbs. Different communities were sown to increase the generality of experimental results, and to allow for potential priority effects to manifest. The total number of 25 species and the ratio of the three life forms were based on mean values of species densities in sampling quadrats of the survey mentioned above. Sowing density was 12 g seeds (0.48 g per species) per plot, based on the long-term experience of a restoration practitioner and seed supplier, and aimed to resemble vegetation cover of semi-natural grasslands as best as possible within the course of the experiment, and to enable interactions among plant individuals. By sowing an equal seed mass per species, more seeds from small-seeded species were sown and vice versa, resembling the trade-off between seed size and seed number in comparable grassland ecosystems (Jakobsson & Eriksson 2000). The plots were mown once during the course of the experiment in early August 2014.

In each plot, a randomly placed 0.5×0.5-m permanent plot was marked and surveyed in June and July 2013, 2014 and 2015 using a sampling frame that was subdivided into 25 0.1×0.1-m squares, in which the presence/absence of a species was recorded (Figure 5). To allow for comparisons at a larger scale, we also recorded species occurring outside the permanent plot but within the inner 1.9×1.9-m of each 2×2-m plot. These species were assigned an abundance of 1 and subsequently, abundances of all species were multiplied by 16 to extrapolate abundances measured at the scale of 0.25-m^2 permanent plots (although this overestimates abundances of rare species). For the determination of biomass productivity, standing biomass was harvested at the peak of the growing season in the final year of the experiment and dried until constant weight prior to measurements.

Analysis of beta diversity

To compare whether grassland communities became more similar or dissimilar along the soil resource gradient, reflecting changing community assembly processes, we quantified their dissimilarity using the incidence-based Jaccard's index. However, as with most metrics of beta diversity, this index can increase with decreasing alpha diversity of the communities compared, simply for probabilistic reasons (Chase et al. 2011). Therefore, a null model approach is necessary to discern whether the observed beta diversity resulted from processes other than random sampling effects. Hence, we also calculated a modified Raup-Crick dissimilarity among grassland plots for each census separately (Chase et al. 2011). This metric compares the observed number of shared species to the distribution of the expected number of shared species between a pair of sites. For any pair, this null-expectation of shared species was generated by randomly sampling species from the pool 999 times, while keeping constant the observed alpha diversities of the sites. The sampling probability of a species was based on the proportion of plots across all treatments occupied by this species (Chase et al. 2011). The resulting dissimilarity metric ranges between 0 and 1 and represents the probability that two sampling units share more species than expected by random chance given their alpha diversity (Anderson et al. 2011). To test for significant differences in community assembly processes, Raup-Crick dissimilarities among replicate plots of each treatment were compared among treatments using permutational distance-based tests for homogeneity of multivariate dispersions (PERMDISP; Anderson 2006; Anderson et al. 2006; Chase 2010). Finally, Raup-Crick dissimilarities were rescaled to range between -1 and 1, enabling us to discern more easily whether local communities were more dissimilar (approaching 1), as dissimilar (approaching 0), or less dissimilar (approaching -1) than expected by random chance (Chase et al. 2011). As such, large deviations from zero are a signature of niche-based assembly processes: Positive deviations can be interpreted as spatial aggregation, resulting for instance from competitive interactions, whereas negative deviations indicate environmental filtering of similar species combinations. By contrast, values close to zero indicate that an external driver (e.g. resource availability) generated turnover among communities by altering local extinctions and colonisations in a stochastic, non-selective way (Chase & Myers 2011).

All calculations were performed at the 0.5×0.5-m and the 2×2-m sampling scale and were carried out using R (R Core Team 2014). Though less significant, results for the 2×2-m sampling scale were similar and are presented in the Supporting Information (Figures S3–S6).

Upon observing that grasses dominated experimental plots with high resource supply, we also performed these analyses for grasses separately to test whether stochastic variation in the initial composition of this group led to divergent alternative states after nutrient enrichment.

2.3 RESULTS

Contrasting biomass productivity among the experimental treatments indicated that the resource manipulation successfully generated biologically meaningful differences in resource limitation (Figure 1; Figure S1). Average alpha diversity of grassland plots was similar and high in the first year at all resource levels, and decreased towards the end of the experiment (Figure 6a). However, there were marked differences in species loss rates among treatments. While local-scale species loss was smaller at low and moderate resource supply, alpha diversity decreased markedly at high resource supply until the final year of the experiment. This resulted in significantly lower local richness at high resource supply compared to both other treatments (ANOVA high vs. low supply: $F_{1,16} = 49.87$, $P < 0.001$; ANOVA high vs. moderate: $F_{1,16} = 25$, $P < 0.001$), which did not differ in alpha diversity in the final year (ANOVA low vs. moderate: $F_{1,16} = 3.67$, $P > 0.05$). There was a concomitant increase in grass relative abundance (Figure 6b), and a reduction of gamma diversity in the high resource treatment of ca. 20% compared to both other treatments. Moreover, the pool of species that could persist at high resource supply was a nested subset of species that could persist at low and moderate resource levels. Taken together, this indicates that high resource levels impose environmental filtering on community assembly, whereas environmental filtering appears less important at low and moderate soil fertility.

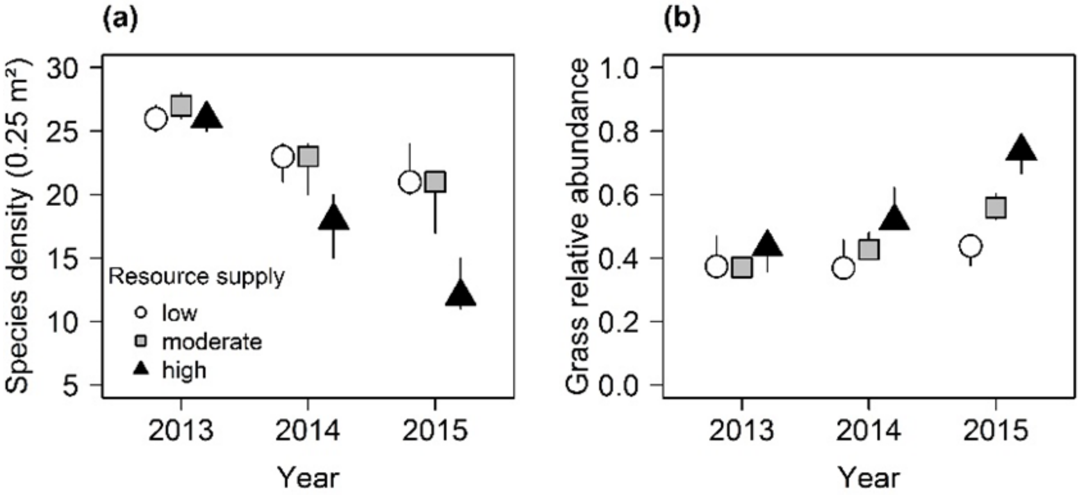


Figure 6 | Effects of soil resource supply on temporal dynamics of (a) species density and (b) grass relative abundance in experimental grasslands. Symbols are median values, bars are upper and lower quartiles.

However, this does not yet unambiguously imply that contrasting levels of soil fertility imposed contrasting community assembly processes in the grassland plots. This is because patterns of alpha diversity and species composition could be either stochastic or deterministic at both low and high resource supply, depending on whether resource availability alters extinctions and colonisations without respect to species identities or in a selective manner (Chase & Myers 2011). Indeed, although non-significant, beta diversity tended to be higher among high-resource grasslands plots, and this effect increased throughout the course of the experiment (Figure 7a). This would suggest that the species composition of grasslands in this treatment was stochastic rather than driven by a deterministic environmental filter that selected for similar species combinations. However, an opposing picture emerged once we controlled for the probabilistic sampling effect that leads to high beta diversity values when alpha diversity is low. Using Raup-Crick dissimilarity, we found that, in the final year of the experiment, replicates of high-resource grasslands shared substantially more species than expected by random chance (approaching -1) relative to replicates of low-resource grasslands (Figure 7b) (PERMDISP high vs. low: permutational Welsh's t = 2.55, $P < 0.03$), with replicates of moderately resource-rich grasslands showing intermediate deviations from the null expectation (PERMDISP low vs. moderate: t = 0.9, $P > 0.05$; moderate vs. high: t =1.23 , $P > 0.05$). Importantly, replicates of low-resource grasslands shared almost exactly as many species as expected by random chance (approaching 0) (Figure 7b).

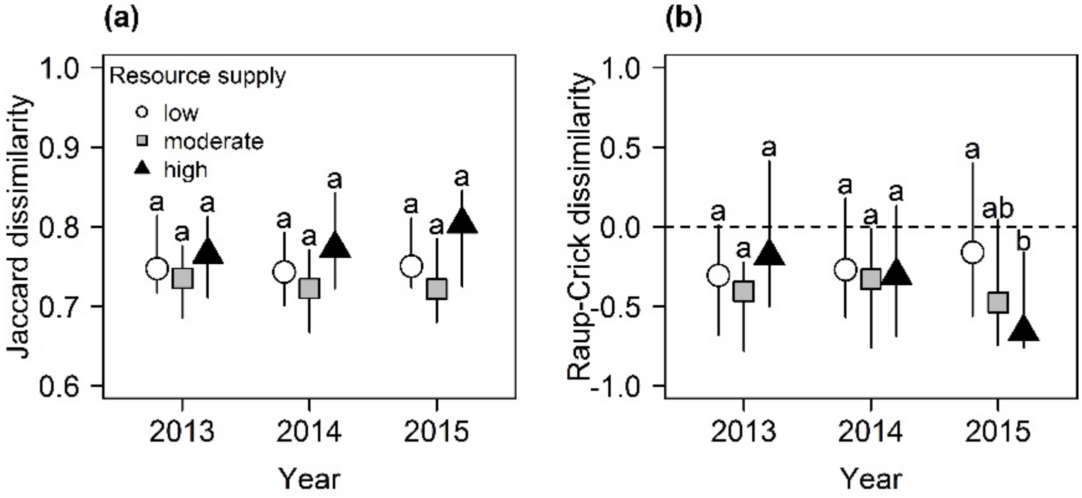


Figure 7 | Temporal change in beta diversity among grassland plots within contrasting resource treatments. Beta diversity was measured as (a) raw turnover in species composition using Jaccard's dissimilarity or (b) using a modified Raup-Crick dissimilarity metric, indicating the degree to which the observed number of shared species between communities deviates from a null-expectation. Different letters indicate significant differences ($P < 0.05$) in beta diversity among treatments within years, based on permutational distance-based tests for homogeneity of multivariate dispersions (Anderson 2006). In (b), these differences were assessed before Raup-Crick dissimilarities were rescaled to range between -1 and 1. Note the opposing temporal trends of Raup-Crick dissimilarity in low vs. high resource treatments in (b).

Interestingly, low and high resource treatments also showed opposing temporal trends in the degree to which assembly was driven by niche-based vs. stochastic processes (Figure 7b). Although raw temporal turnover (i.e. the average Jaccard's dissimilarity of communities in each plot from year to year) was small at low relative to high resource supply (0.32 ± 0.02 vs. 0.45 ± 0.02, mean ± SE; ANOVA: $F_{1,16} = 21.67$, $P < 0.001$), the Raup-Crick dissimilarities of low-resource replicates increasingly approached 0 during succession, indicating that the observed temporal turnover resulted from ecological drift. Alternatively, grassland communities at high resource supply appeared to be a result of stochastic assembly in the first year, but then transitioned to a system dominated by selection. The grasslands at moderate resource supply were intermediate regarding temporal turnover (0.36 ± 0.01, mean ± SE; ANOVA low vs. moderate: $F_{1,16} = 4.23$, $P > 0.05$; moderate vs. high: $F_{1,16} = 13.1$, $P < 0.01$), and their Raup-Crick dissimilarities showed a slight unimodal relationship with time (Figure 7b). Considering the similar high alpha diversity as in low resource grasslands, but the increasing grass abundance (Figure 6), this suggest that temporal turnover in this treatment was driven by a slow replacement of competitively inferior species by immigrating strongly competitive species and dominant grasses.

When grass species composition was analysed separately, we found similar and close-to-zero Raup-Crick dissimilarities in all resource treatments and censuses (Figure 8). Likewise, raw temporal turnover in grass composition was not affected by resource supply (ANOVA: $F_{2,24} = 0.29$, $P > 0.05$) and was low in all treatments (average Jaccard's dissimilarities <0.27). In addition, there were no temporal trends in plot-scale grass species richness (measured as the difference between first and last census) in any of the resource treatments (mean difference in all treatments between 0–1; ANOVA: $F_{2,24} = 0.34$, $P > 0.05$). This shows that – in contrast to the overall species composition – the initially sown grass communities were temporarily quite stable across all treatments and not affected by the environmental filter imposed by high resource supply. Hence, the divergent alternative community states among replicates of the species-poor high-resource plots seen in Figure 7a resulted mainly from the initial stochastic variation in the composition of this functional group (i.e. a priority effect resulting from the random compilation of seed mixtures), which persisted until the end of the experiment.

2.4 DISCUSSION

Although it is well-known that resource enrichment reduces grassland diversity at local scales (e.g. Gough et al. 2000; Stevens et al. 2004; Crawley et al. 2005; Harpole & Tilman 2007), it is unclear whether different community assembly processes operate at contrasting levels of resource supply. Here, we show that soil resource availability determines the importance of niche-based vs. stochastic assembly processes in grasslands. The species composition of unproductive grassland communities at low resource supply hardly differed from what would be expected by random sampling from the species pool, indicating that stochastic community assembly generated the observed variation in species composition. By contrast, productive grasslands at high resource supply shared substantially more species than expected by chance from their low species richness, indicating that deterministic, niche-based selection was the main driver of community assembly in this habitat.

The contrasting importance of stochasticity among resource levels is consistent with observations from real grassland metacommunities, seed addition experiments and theoretical work. For instance, Conradi et al. (unpubl.; see Chapter 3) compared beta diversity of grassland metacommunities among regions with contrasting soil fertility and found that dispersal limitation was the single driver of compositional differentiation at low regional soil fertility, whereas species turnover in the more fertile region was principally driven by environmental sorting. Likewise, experiments often find declining effects of seed addition on community structure at higher soil resource levels (Foster 2001; Myers & Harms 2009), indicating declining importance of stochasticity.

However, what are the mechanisms allowing for stochastic processes being effective drivers of species composition at low but not at high resource supply? – Recent theoretical work suggests that communities can transition between a neutral and a niche-driven phase, depending on the degree of environmental stress they are exposed to (Fisher & Mehta 2014). When environmental stress is high, such as might occur when soil resources are limiting, carrying capacities of most populations are reduced, thus increasing the significance for stochastic demographic variation, and immigration relative to competitive interactions with deterministic outcomes (Fisher & Mehta 2014). A second important mechanism was that the realized pool of species able to persist in the highly competitive environment of resource-rich sites was a nested subset of the total pool of species encountered in the experiment (see also

Chase 2010). Hence, the apparent strong environmental filtering of similar species combinations in this habitat might simply result from characteristics of regional grassland species pools that contain only few species with traits conferring competitive advantage at higher soil fertility (cf. Zobel 1997; Pärtel 2002; Laliberté et al. 2014; Zobel 2015). The resource-rich grassland plots selected for few tall-statured species, but not for species with aquisitative leaf traits or a particular seed mass (Figure S2), lending support to the notion that competition for light is the principal environmental filter after grassland eutrophication (Hautier et al. 2009; Borer et al. 2014).

Interestingly, however, the separate analysis focusing solely on the grasses, which were the dominating group on high-resource plots, revealed that the grass communities initially sown were temporarily relatively stable in terms of richness and composition. Moreover, variation in grass species composition reflected stochastic assembly in all years (Figure 8), indicating that the grass fraction of the communities still resembled the stochastic variation among the initially sown seed mixtures. Thus, the environmental filter imposed by high resource supply seen in Figure 7b was deterministic in the sense that it selected for the whole functional group of grasses without respect to grass species identity, but filtered out most forb species.

Earlier studies reported increasing divergence of communities following nutrient enrichment when beta diversity was estimated as raw spatial turnover (Chalcraft et al. 2008; Houseman et al. 2008). Indeed, when compositional dissimilarity was quantified using Jaccard's dissimilarity, our communities also appeared more dissimilar at high resource supply (Figure 7a), but this pattern turned into the opposite once we controlled for the probabilistic increase of beta diversity when alpha diversity is low (Figure 7b). Combining this finding with results from the grass-only analysis provides a more differentiated understanding on the effects of nutrient enrichment on community trajectories. Together they show that, when overall species composition is considered, nutrient enrichment does homogenise communities to levels substantially below what would be expected by chance from the richness and composition of the regional species pool (Figure 7b). Although more homogenous than expected by chance, such alternative states dominated by few competitive species can emerge from stochastic variation in the initial composition of those species that are selected during eutrophication, at least in the case of grasses.

To show that these alternative states are stable, however, subsequent seed addition experiments would be required, but existing experimental evidence suggest that this is likely (Ejrnæs et al. 2006; Chase 2010; Kardol et al. 2013; von Gillhaussen et al. 2014).

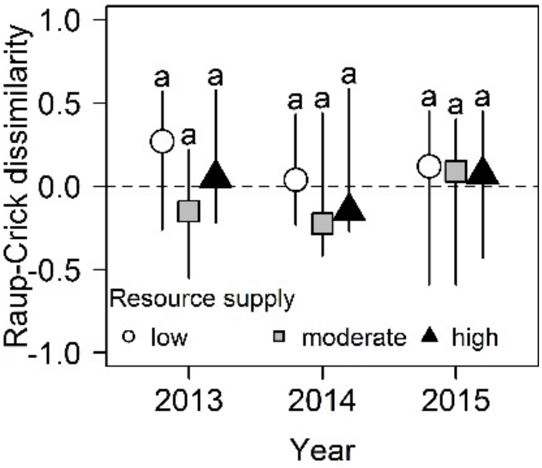


Figure 8 | Temporal change in grass species beta diversity among replicate plots at contrasting levels of soil resource supply. Beta diversity was measured using a modified Raup-Crick dissimilarity metric, indicating the degree to which the observed number of shared grass species between communities deviates from a null-expectation. Common letters indicate non-significant differences ($P > 0.05$) in beta diversity among treatments within years, based on permutational distance-based tests for homogeneity of multivariate dispersions (Anderson 2006). Note that grass species composition reflects stochastic assembly across treatments and years, contrasting overall species composition (Figure 7b).

2.5 CONCLUSIONS

Increasing nutrient inputs to terrestrial ecosystems through agricultural intensification and atmospheric deposition have led to an erosion of biodiversity (Vitousek et al. 1997; Gough et al. 2000; Stevens et al. 2004; Crawley et al. 2005; Wassen et al. 2005; Clark & Tilman 2008), and scenarios of future biodiversity loss predict that this continues to be among the most important threats (Sala et al. 2000). Therefore, successful conservation efforts critically rely on the scientific understanding of the ecological mechanisms that generate biodiversity patterns along soil resource gradients. As a novel contribution, this study revealed that fundamentally different assembly processes operate at low vs. high soil resource availability. The decreasing importance of stochastic processes at higher resource levels might impose constraints to conservation and ecological restoration efforts that often aim to increase dispersal rates among habitats. In such situations, accompanying measures such as increasing disturbances and lowering soil nutrient concentrations might be necessary to conserve species diversity.

SUPPORTING INFORMATION

Table S1 | List of plant species sown in the experiment. Nomenclature follows Wisskirchen and Haeupler (1998).

Non-legume forbs (n=32)		Legumes (n=9)		Graminoids (n=13)	
Family	Species	Family	Species	Family	Species
Anthericaceae	*Anthericum ramosum*	Fabaceae	*Anthyllis vulneraria*	Cyperaceae	*Carex flacca*
Apiaceae	*Peucedanum oreoselinum*		*Dorycnium germanicum*	Juncaceae	*Luzula campestris*
	Pimpinella saxifrage		*Genista tinctoria*	Poaceae	*Agrostis capillaris*
Asteraceae	*Achillea millefolium*		*Hippocrepis comosa*		*Brachypodium pinnatum*
	Buphthalmum salicifolium		*Lotus corniculatus*		*Briza media*
	Centaurea jacea		*Medicago lupulina*		*Bromus erectus*
	Centaurea scabiosa		*Securigera varia*		*Dactylis glomerata*
	Hieracium pilosella		*Trifolium pratense*		*Festuca ovina*
	Leontodon hispidus		*Vicia cracca*		*Festuca rubra*
	Leontodon incanus				*Helictotrichon pratense*
Campanulaceae	*Campanula rapunculoides*				*Helictotrichon pubescens*
	Campanula rotundifolia				*Koeleria pyramidata*
Cistaceae	*Helianthemum nummularium*				*Poa angustifolia*
Globulariceae	*Globularia cordifolia*				
Lamiaceae	*Betonica officinalis*				
	Clinopodium vulgare				
	Prunella grandiflora				
	Prunella vulgaris				
	Teucrium montanum				
	Thymus praecox				
	Thymus pulegioides				
Linaceae	*Linum perenne*				
Plantaginaceae	*Plantago lanceolata*				
	Plantago media				
Rosaceae	*Agrimonia eupatoria*				
	Filipendula vulgaris				
	Potentilla tabernaemontani				
	Sanguisorba minor				
Rubiaceae	*Asperula cynanchica*				
	Galium album				
	Galium verum				
Scrophulariaceae	*Veronica chamaedrys*				

Figure S1 | Differences in biomass productivity among the manipulated levels of resource supply. Different letters indicate significant differences in biomass productivity (P < 0.05). P-values are from permutation t-tests with 999 permutations and corrected for multiple comparisons following (Benjamini & Hochberg 1995).

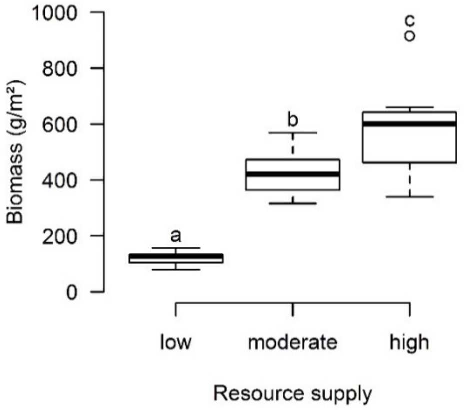
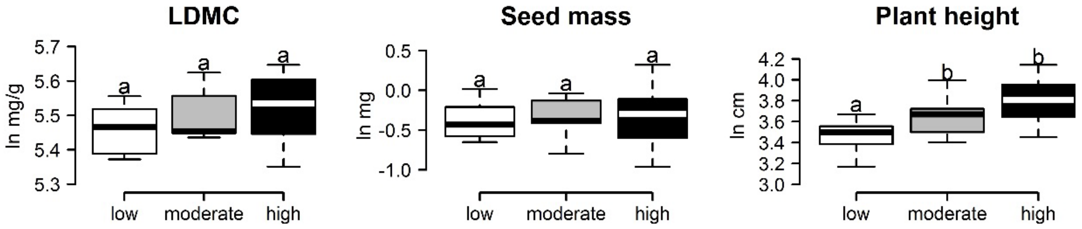


Figure S2 | Community weighted mean (CWM) trait values in grassland plots (0.25 m^2) of contrasting resource supply. Different letters indicate significant differences (P < 0.05) among resource treatments, evaluated using permutation t-tests with 9999 permutations. LDMC = leaf dry matter content.



Trait values are from databases (Jäger 2007; Kleyer et al. 2008; Hintze et al. 2013). Maximum (seed mass, height) or minimum (LDMC) values were used for calculations, after trait values from experiments and unrealistically high or low values had been removed. Values were ln-transformed to reduce outliers prior to the calculation of CWMs. Database values conserve species rankings based on field-measured trait values well (Kazakou et al. 2014), and interspecific rather than intraspecific trait variation was found to explain much larger amounts of total trait variation in an experiment using some of the species found in our study, with similar site conditions and located close (~2.5 km) to our field site (Andrade et al. 2014). Additionally, comparing self-measured seed mass values of the sown species with values extracted from databases, we found a very high correlation of r = 0.95. As LDMC values for *Oenothera biennis* agg. and *Thymus pulegioides* were not available from databases, we used values from the closely related, morphologically and ecologically similar species *Oenothera erythrosepala* and *Thymus serpyllum*, respectively.

Figure S3 | Effects of soil resource supply on temporal dynamics of (a) species density and (b) grass relative abundance in experimental grasslands plots (4 m^2). Symbols are median values, bars are upper and lower quartiles.

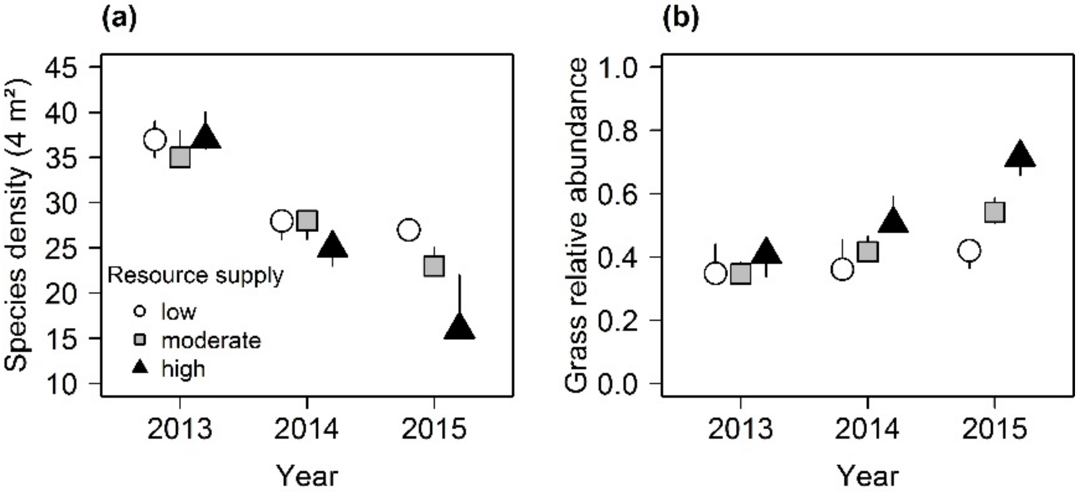


Figure S4 | Temporal change in beta diversity among grassland plots (4 m^2) within contrasting resource treatments. Beta diversity was measured as (a) raw turnover in species composition using Jaccard's dissimilarity or (b) using a modified Raup-Crick dissimilarity metric, indicating the degree to which the observed number of shared species between communities deviates from a null-expectation. Different letters indicate significant differences ($P < 0.05$) in beta diversity among treatments within years, based on permutational distance-based tests for homogeneity of multivariate dispersions (Anderson 2006). In (b), these differences were assessed before Raup-Crick dissimilarities were rescaled to range between -1 and 1. Note the opposing temporal trends of Raup-Crick dissimilarity in low vs. high resource treatments in (b).

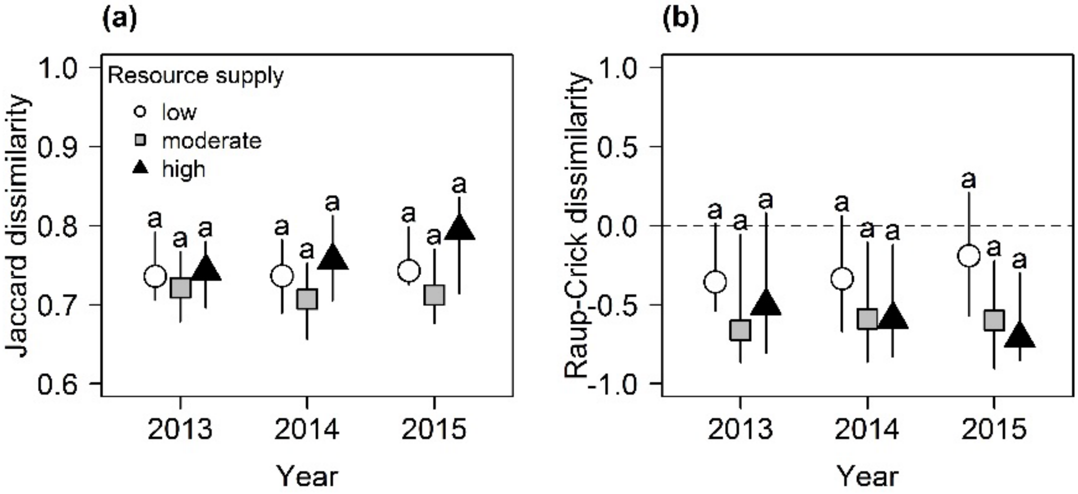


Figure S5 | Temporal change in grass species beta diversity among replicate plots (4 m^2) at contrasting levels of soil resource supply. Beta diversity was measured using a modified Raup-Crick dissimilarity metric, indicating the degree to which the observed number of shared grass species between communities deviates from a null-expectation. Common letters indicate non-significant differences (P > 0.05) in beta diversity among treatments within years, based on permutational distance-based tests for homogeneity of multivariate dispersions (Anderson 2006).

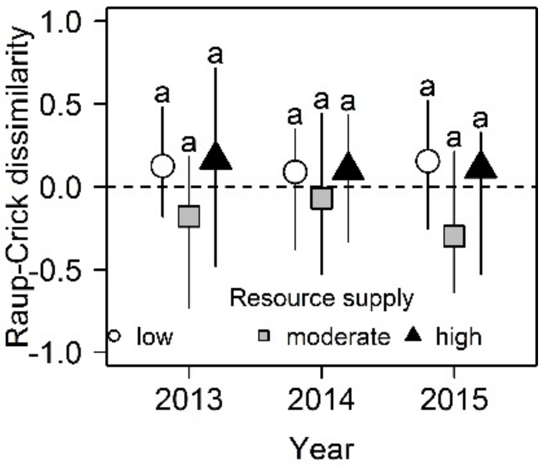
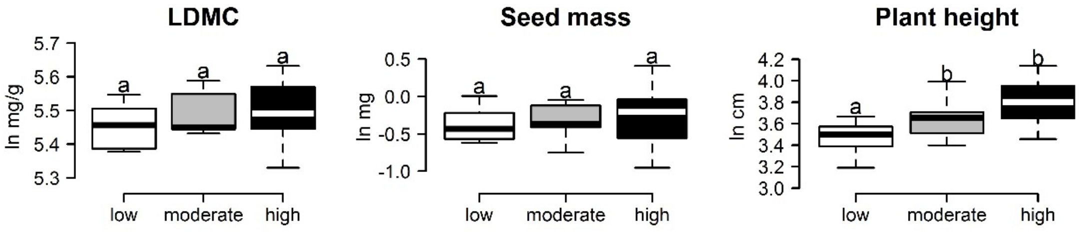


Figure S6 | Community weighted mean (CWM) trait values in grassland plots (4 m^2) of contrasting resource supply. Different letters indicate significant differences ($P < 0.05$) among resource treatments, evaluated using permutation t-tests with 9999 permutations. LDMC = leaf dry matter content.



Trait values are from databases (Jäger 2007; Kleyer et al. 2008; Hintze et al. 2013). Maximum (seed mass, height) or minimum (LDMC) values were used for calculations, after trait values from experiments and unrealistically high or low values had been removed. Values were ln-transformed to reduce outliers prior to the calculation of CWMs. Database values conserve species rankings based on field-measured trait values well (Kazakou et al. 2014), and interspecific rather than intraspecific trait variation was found to explain much larger amounts of total trait variation in an experiment using some of the species found in our study, with similar site conditions and located close (~2.5 km) to our field site (Andrade et al. 2014). Additionally, comparing self-measured seed mass values of the sown species with values extracted from databases, we found a very high correlation of $r = 0.95$. As LDMC values for *Oenothera biennis* agg. and *Thymus pulegioides* were not available from databases, we used values from the closely related, morphologically and ecologically similar species *Oenothera erythrosepala* and *Thymus serpyllum*, respectively.

Chapter 3

Drivers of beta diversity in human-transformed landscapes: the key role of regional soil fertility for community assembly processes

Abstract - *Recognizing that beta diversity is derived from two opposing phenomena, spatial turnover and nestedness, allows a more refined evaluation of how alternative assembly mechanisms might control regional diversity patterns. This study evaluates how environmental sorting as well as past and present dispersal processes regulated spatial turnover and nestedness in fragmented grassland landscapes, and whether their relative importance varied among landscapes with contrasting regional soil productivity. The results show that historical dispersal limitation was the only determinant of nestedness-driven dissimilarity, irrespective of regional productivity. By contrast, spatial turnover was driven by opposing mechanisms in productive* vs. *marginal landscapes. When regional soil productivity was below an empirical threshold of resource limitation, spatial turnover was generated by neutral historical dispersal processes. Beyond this threshold of resource limitation, species turnover was deterministic and increased with increasing differences in resource supply. The findings are consistent with theoretical considerations and empirical evidence from small-scale experiments.*

Keywords: *Calcareous grasslands; Dispersal; Environmental filtering; Habitat fragmentation; Metacommunity; Nestedness; Neutral theory; Spatial ecology*

3.1 INTRODUCTION

Understanding what causes site-to-site variation in species composition ('beta diversity') is one of the oldest and most central challenges in plant community ecology (Jaccard 1912; Whittaker 1960; Anderson et al. 2011). Patterns of beta diversity are sensitive to a range of external drivers, including environmental variation (Tuomisto et al. 2003; Chase 2010), dispersal limitation (Hubbell 2001; Cadotte 2006), and historical factors at different temporal scales (Dexter et al. 2012; Purschke et al. 2012). Disentangling their relative importance can therefore generate significant insights into the local and regional controls over community assembly (Cottenie 2005; Myers et al. 2013).

Inference of ecological processes from patterns of beta diversity has been limited by the fact that identical values of beta diversity can derive from two different components: (i) spatial turnover of species (i.e. the replacement of species from site to site), and (ii) nestedness (i.e. the species composition of one site is a strict subset of another site) (Harrison et al. 1992; Legendre 2014). This limits inference from beta diversity in two important ways: First, it remains unknown which of the two components contributes more to compositional dissimilarity among communities. Second, external drivers might influence either spatial turnover or nestedness, or both but with different effect sizes. A better understanding of how ecological or anthropogenic drivers control the two components of beta diversity would thus substantially advance community assembly models. Recently, methods have been developed that additively partition popular indices of compositional dissimilarity into their turnover and nestedness components (Baselga 2010, 2012). These can then separately be modelled as a function of environmental, spatial or historical variables to shed more light on the mechanisms that generate spatial variation in community composition (e.g. Svenning et al. 2011).

Here, we use this approach to investigate community assembly mechanisms in two landscapes of fragmented calcareous grasslands with contrasting regional soil productivity. Specifically, we explored the role of local environmental conditions, as well as present and historical dispersal processes as drivers of community assembly, and whether their relative importance varies among landscapes with contrasting regional soil productivity. In Europe, grassland landscapes expanded markedly in the bronze age and during the medieval period as a consequence of pastoral land use (Poschlod & WallisDeVries 2002). Land-use change during the early 20th century led to strong habitat loss and fragmentation of the grassland landscapes. Today, few historically old grassland patches remain within nature reserves, which often contain the most unique and species-rich communities (Wilson et al. 2012; Dengler et al. 2014). Together with younger grasslands recovering from interim agricultural land use, they form environmentally heterogeneous metacommunities with variable present and historical connectivity.

Based on metacommunity theory (Leibold et al. 2004), which provides a conceptual framework for the interpretation of beta diversity patterns (Cottenie 2005; Chase & Myers 2011; Myers et al. 2013), and the specific empirical evidence for historical drivers of community structure in fragmented landscapes, we evaluated the following hypotheses about how beta diversity and its components are generated:

1) *Environmental sorting*: Differences in local community structure are determined by interspecific differences in resource requirements and physiological tolerance limits that confine species to certain sections of environmental gradients. Hence, beta diversity is explained by environmental variation (Chase & Myers 2011). In human-transformed landscapes, environmental sorting might be an important driver of community structure because habitat patches often differ in soil properties due to contrasting land-use histories (Verheyen et al. 1999; Freschet et al. 2013). In the environmental sorting scenario, environmental variation can produce nestedness when soil gradients reach into marginal habitats where only a subset of species can survive. Alternatively, high resource availability may lead to competitive displacement of many species by a subset of few competitive species (Chapter 2; Harpole & Tilman 2007). It can also produce spatial turnover when different species replace each other along environmental gradients. When environmental sorting is important, nestedness might also result from variation in soil spatial heterogeneity because of the contrasting numbers of niches provided (Tilman 1982; Adler et al. 2013).
2) *Dispersal-driven assembly*: Differences in local community structure result from dispersal limitation (Hubbell 2001). Hence, beta diversity is related to variation in landscape spatial configuration and factors that influence colonization probabilities such as patch size (McArthur & Wilson 1967), habitat connectivity (Hanski 1998), or edge effects (Tscharntke et al. 2012).

Dispersal assembly can result in nestedness when some species are dispersal-limited and others do not compensate for their absence (e.g. Chapter 4). In human-transformed landscapes, this might result from the limited capability of the species-poor, intensively used agricultural matrix to provide colonists. If dispersal limited species are replaced by others, dispersal assembly will result in spatial turnover.

3) *Historical contingency*: A special case of dispersal assembly in which variation in local community structure is explained by past dispersal processes (Fukami 2015). Previous investigations of alpha and beta diversity in fragmented landscapes showed diversity patterns reflect past rather than present habitat connectivity (Lindborg & Eriksson 2004; Helm et al. 2006; Purschke et al. 2012). Hence, in this scenario, beta diversity is related to variation in historical landscape configuration. Mechanisms leading to nestedness and turnover are similar to the dispersal-driven assembly scenario, with the exception that the dispersal processes happened in the past and are no longer occurring in the contemporary landscape.

4) *Contrasting assembly mechanisms in regions with productive* vs. *marginal soils*: Seed addition experiments in grasslands showed that effects of dispersal on community structure declined with increasing soil fertility (Foster 2001; Myers & Harms 2009). Likewise, there is experimental evidence that stochastic processes such as dispersal can effectively generate patterns of beta diversity in metacommunities with low, but not with high productivity (Chapter 2). We thus hypothesized that this pattern would also manifest at the landscape level, so that (historical) dispersal assembly should be more important for beta diversity in landscapes with low soil fertility as compared to landscapes with higher soil resource supply, where environmental sorting should be the main driver of community assembly.

3.2 METHODS

Study system and areas

To disentangle the drivers of beta diversity in human-transformed landscapes, we studied plant species composition, abiotic site conditions, and current and historical landscape context of 34 calcareous grasslands in two geographically separated study areas, the Lech River Valley (LRV) and the Munich Gravel Plain (MGP) in southern Germany (48°15' N, 10°54' E and 48°15' N, 11°37' E, respectively) (see maps in Figure 3–4). The climate is temperate and humid with a mean annual rainfall of ca. 835 mm and a mean annual temperature of ca. 8.5 °C in both study areas (1981–2010; www.dwd.de, accessed 25 Feb 2015). As a consequence of medieval pastoral land use, both study areas were covered almost entirely by species-rich calcareous grasslands for several centuries until the beginning of the 20th century, when a transformation of the grassland landscapes into intensively used agri- and silvicultural systems led to widespread habitat loss and fragmentation (Pfadenhauer et al. 2000; Pfeuffer 2010). Fertility of calcareous grassland soils was lower in the MGP study area, where soils were significantly coarser and have lower P, NH_4^+ and base cation concentrations than LRV soils (Figure S7; see methods of soil analysis below). In addition, total N and K concentration were also slightly lower in the MGP study area, though these differences were not significant. The differences in soil P are especially important, because P is the main limiting nutrient in calcareous grasslands (Jeffrey & Pigott 1973; Willems et al. 1993; Carroll et al. 2003). With one exception, the grasslands in the MGP study area were located on older fluvial sediments from the late Pleistocene, whereas grasslands of the LRV study area were located on younger fluvial sediments deposited during various periods of the Holocene until the early 19th century (Freudenberger 1996). Thus, the lower regional soil fertility in the LRV might result from longer soil weathering and/or from longer-lasting pastoral land-use that has depleted soil resources.

Vegetation sampling

We focused on sites that contained the indicator species of nutrient-poor calcareous grasslands, i.e. *Bromus erectus* Huds. and *Brachypodium rupestre* (Host.) Roem. & Schult. (Oberdorfer 2001), and those that have never received any translocated species, e.g. in the context of grassland restoration. This information was derived from management plans and interviews with conservation officers, shepherds and farmers. Single grassland patches were delineated by their unique management regime (mowing or grazing), site history (e.g. continuity of no fertilization, previous land-use), or by their spatial separation from other habitats. Finally, 18 grasslands were selected in the LRV, and 16 in the MGP study area. In both areas, the selected grasslands were distributed across a similar geographic area with pairwise distances ranging between 0–22 km (median = 6.7 and 5.5 km in the LRV and MGP, respectively) and elevations between 491–561 m and 469–520 m a.s.l. in LRV and MGP, respectively.

Floristic surveys were conducted in the years 2012 and 2013 between June and August in both study areas, using Wisskirchen and Haeupler (1998) as taxonomic reference. The species composition of each grassland was sampled in multiple arbitrarily located 1-m^2 plots for so long until no additional species were encountered during the inspection of three consecutive plots, resulting in 262 sampling plots in total (3–15 plots per grassland). This sampling strategy minimized undersampling bias in beta diversity calculations and accounts for site-specific species-area relationships.

Explanatory variables

To evaluate our hypotheses about environmental controls over beta diversity patterns, we measured soil nutrient (N, P, K) concentrations, pH, base concentrations (Ca^{2+}, Mg^{2+}), as well as soil texture and depth at each vegetation sampling plot, and used the median values across the plots of each grassland in subsequent analyses. Additionally, we noted whether a plot was located in a relic floodplain channel with temporally higher soil moisture and used this information as binary variable. Soil spatial heterogeneity of each grassland was then calculated based on plot-level measurements, and information about its current management (mowing or grazing) was gathered from land managers (see Supporting Information for details about soil analyses and calculations). Except spatial heterogeneity and moisture, soil variables were then subject to Principal Components Analysis (PCA) in order to reduce their dimensionality, with separate PCAs for each study area. The nominal variable soil texture was converted into an ordinal scale with higher values for large grain sizes and then treated as a metric variable in the PCA. Variables were transformed to reduce outliers when necessary, and all variables were scaled to unit variance to give them equal weights in the PCA. The first three principal components (PC) accounted for 81% (LRV) and 88% (MGP) of the total environmental variation (Table 1) and hence the grassland scores on these PCs were used as explanatory environmental variables along with soil heterogeneity and management in subsequent analyses.

Table 1 | Pearson correlation of environmental variables with principal component (PC) scores of grassland patches of the Lech River Valley (LRV) and Munich Gravel Plain (MGP) in southern Germany. Percentage values below PCs are their explained variance.

	LRV			**MGP**		
	PC1 (45%)	**PC2 (22%)**	**PC3 (14%)**	**PC1 (56%)**	**PC2 (21%)**	**PC3 (11%)**
Soil depth	0.86	-0.03	-0.32	-0.27	0.86	-0.36
Soil texture	-0.70	-0.01	0.43	-0.59	-0.57	-0.38
pH	0.49	0.75	0.17	0.88	-0.18	0.23
Ca^{2+}	0.28	0.91	-0.02	0.88	0.26	0.22
Mg^{2+}	-0.62	0.02	0.45	0.78	-0.52	-0.14
P	-0.45	0.40	-0.75	0.74	0.50	0.03
K	-0.76	0.31	0.08	0.82	-0.43	-0.09
N	-0.92	-0.17	-0.18	0.73	-0.27	-0.55
NO_3^-	-0.70	-0.15	-0.54	0.61	0.41	-0.58
NH_4^+	-0.66	0.67	0.06	0.92	0.17	0.21

To examine influences of current dispersal processes on beta diversity, we measured grassland patch area, and the connectivity of each patch as the amount of semi-natural grassland in radii of 100, 300, and 500 m around each grassland, using data of the 'Habitat Mapping' of the Bavarian Environmental Office (LfU; www.lfu.bayern.de, accessed 6 Feb 2015). Historical and younger grasslands, but not grasslands that have been recently restored with species translocations, were considered for this purpose. In addition, the spatial distance in the contemporary landscape to the next historical grassland (DIST.OLD.CONTEMP) (see definition for historical grassland below) that could provide colonists of the characteristic calcareous grassland species pool was also calculated. The perimeter-area ratio of each patch was calculated to describe the importance of edge effects, specifically the potential for spill-over of species from surrounding habitats (Tscharntke et al. 2012). To quantify the spatial structure of survey grassland locations at multiple scales, we obtained spatial eigenvectors from principal coordinates of neighbour matrices (PCNM; Borcard & Legendre 2002; Borcard et al. 2004) which were computed for each study area separately based on an edge-to-edge distance matrix of the investigated grasslands. Only eigenvectors with positive spatial correlation were retained, yielding one eigenvector for LRV and three eigenvectors for MGP (Figure 9).

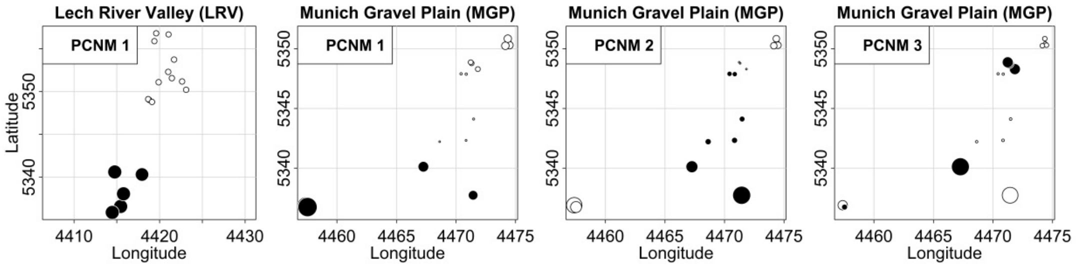


Figure 9 | Map of principal coordinates of neighbour matrices (PCNM) eigenvectors with positive spatial correlation. The geographical location of each investigated grassland patch is indicated by a circle. Increasing circle size indicates increasing positive (black) or increasing negative (white) eigenvector values. Grid cells are 5 km × 5 km large.

Finally, to estimate the importance of historical dispersal processes for current patterns of beta diversity, we collected information on the age of each grassland patch and its historical connectivity. Patch age was measured as the time period of unfertilized land use or, if there was no indication that the site has ever been fertilized, as the year of its origin. This information was compiled from interviews with land managers, management plans, and from historical, geomorphological and geological maps and literature. Grasslands that were already depicted on historical land cover maps from 1809–1858, and for which no indication of different interim land use was at hand, qualified as ‘historically old’ grasslands. They were ascribed an origin in the year 1500 because this was the time for which the earliest reliable sources of vast open grassland landscapes in our study areas were available (report of Michel de Montaigne from 1580 cited in Pfeuffer 2010).

Patch age might influence beta diversity because patches with a long continuity were more likely to have been colonized by species of pristine nutrient-poor calcareous habitats, i.e. unfertilized grasslands, dry forests and woodlands, which dominated the pre-transformed landscape, whereas the identity (and eventually the numbers) of colonizing species should have changed over time as the relative amount of novel habitat types (e.g. fertilized grasslands, managed forests, arable fields, urban area) in the study areas increased. Historical connectivity (DIST.OLD.ORIG) of a grassland was measured as the distance to historically old grasslands (origin 1500), which could have served as a source pool of characteristic calcareous grassland flora, at the time in which the grassland was created. For this purpose, historical maps from relevant time periods were analysed (see details in Supporting Information). Variances of environmental, spatial, and historical variables were similar among the two study areas except for DIST.OLD.CONTEMP, soil pH, and P concentration (greater variance in MGP), and NH_4^+ concentration (greater variance in LRV) (see Figure S8).

Data analysis

Beta diversity was measured using Sørensen dissimilarity (β_{sor}), which can be decomposed into its additive components spatial turnover and nestedness (β_{nes}) as described in Baselga (2010). The spatial turnover component (β_{sim}) quantifies compositional changes resulting from the substitution of species from site to site and is invariant to richness gradients. Nestedness-driven dissimilarity (β_{nes}) is the fraction of β_{sor} that is not attributable to β_{sim} ($\beta_{sor} - \beta_{sim}$; Baselga 2010, 2012) and reflects dissimilarity owing to the loss of species from site to site in a nested pattern. Other frameworks for decomposing beta diversity exist (Podani & Schmera 2011; Carvalho et al. 2012) but their replacement component has been shown to be not independent of species richness differences (Baselga & Leprieur 2015). To characterise the total amount of floristic heterogeneity in the two study areas, and the degree to which this was driven by spatial turnover and nestedness, we also calculated multiple-site dissimilarity measures (β_{SOR}, β_{SIM}, β_{NES}; Baselga 2013).

Distance based redundancy analysis (db-RDA) with forward selection of explanatory variables, and variation partitioning was then used to identify the main drivers of species turnover and nestedness in each study area separately. Highly correlated numerical variables (Pearson $|r| > 0.7$; Dormann et al. 2013) were removed to account for collinearity within each study area and set of explanatory variables separately. Forward selection was only conducted if the full model, that included all variables of the respective variable set, was statistically significant ($P \leq 0.05$) (Blanchet et al. 2008), and was stopped when no additional variable was significant. Variation partitioning (Peres-Neto et al. 2006) was then used to quantify the variation in beta diversity components explained by pure and joint variation in the forward-selected environmental, spatial and historical factors. The significance of pure fractions explained by the selected environmental, spatial or historical variables was evaluated using partial db-RDA that controlled for variation in variables of the respective other variable sets.

To explore whether habitat specialist and generalist species showed opposing trends along major gradients of floristic variation within study areas, we performed separate

Non-metric Multidimensional Scaling (NMDS) ordinations based on β_{sor}. The ordination results were then plotted with grassland symbol sizes scaled to specialist and generalist species richness patterns, respectively. Because NMDS ordination condenses the main axes of compositional variation into a low dimensional space whilst preserving the relationships among sampling sites well (Legendre & Legendre 2012), this approach can help identify which species are involved in spatial turnover and thus facilitates data interpretation. Classification as habitat specialists followed Conradi et al. (2015). Briefly, these were characteristic species (sensu Oberdorfer 2001) of European dry grasslands, thermophilous fringe communities, calcareous and steppe Pine forests, thermophilous Oak forests, natural alpine limestone habitats, calcareous grasslands with fluctuating soil moisture, and dry outcrops, all of which are typical elements of well-preserved calcareous grasslands in southern Germany (Ellenberg & Leuschner 2010).

All calculations were carried out in R using mainly the 'vegan' (Oksanen et al. 2014) and 'betapart' (Baselga & Orme 2012) packages.

3.3 RESULTS

Main gradients of compositional variation

The NMDS ordinations with two dimensions were appropriate to represent the multivariate relationships among grasslands, as indicated by the high linear fit between ordination distances and pairwise β_{sor} of $R^2 = 0.95$ for both study areas. Hence, the major axes of compositional variation were well-captured by the two ordination axes shown in Figure 10. Inspection of symbol sizes indicated that opposing trends of habitat specialist and generalist species underlay compositional variation among grasslands. In both study areas, there was a clear trend of specialist species richness along the first NMDS axis (Figure 10a, b), and this was especially pronounced in the MGP study area. The numbers of generalist species showed opposing trends along this axis (Figure 10c, d), although this was less clear in the LRV study area. The different symbol sizes in Figure 10 also reveal that the loss of habitat specialists was not fully compensated by increasing generalist numbers.

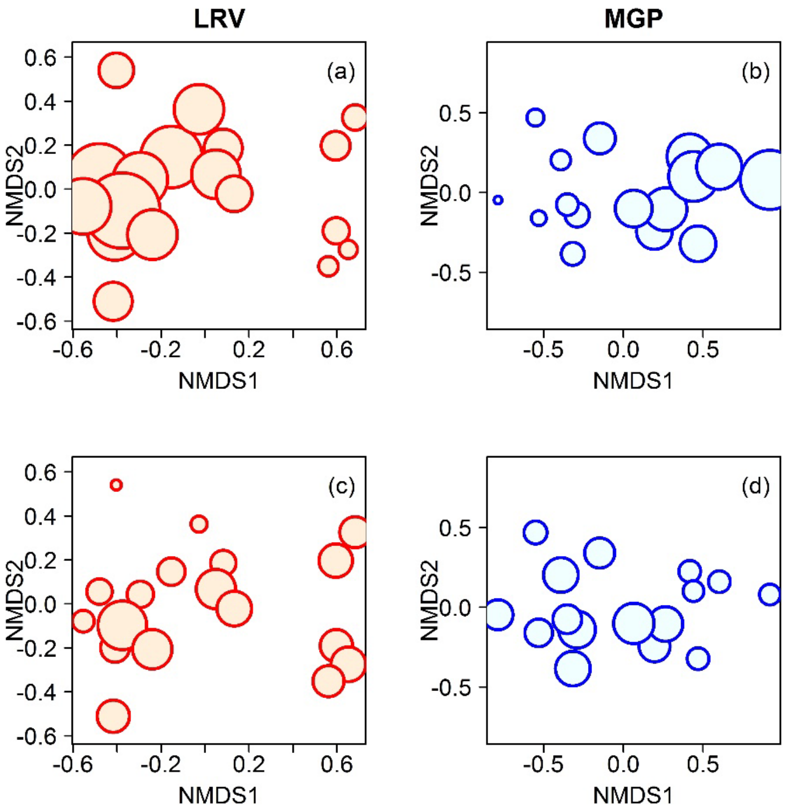


Figure 10 | Non-metric Multidimensional Scaling (NMDS) ordinations of plant species composition of fragmented semi-natural grasslands in the Lech River Valley (LRV) and the Munich Gravel Plain (MGP) in southern Germany. Point size was scaled to the number of habitat specialist (a, b) and generalist (c, d) species, showing that opposing trends of these groups underlie compositional variation among grasslands. The NMDS ordinations were based on Sørensen dissimilarities (β_{sor}) and used two dimensions (stress: LRV = 0.10, MGP = 0.10).

Drivers of beta diversity

Overall variation in species composition among semi-natural grasslands (LRV: β_{SOR} = 0.84; MGP: β_{SOR} = 0.82) resulted mainly from spatial turnover (LRV: β_{SIM} = 0.80; MGP: β_{SIM} = 0.78) rather than nestedness (LRV: β_{NES} = 0.05; MGP: β_{NES} = 0.05). In both study areas, nestedness was only explained by the distance to the next old grassland in the historical landscape (Figure 11). By contrast, turnover was driven by environmental factors in the more fertile region (LRV), but not in the unproductive region (MGP), where – again – past dispersal processes were the main factor.

In the LRV study area, nestedness-driven dissimilarity (β_{nes}) in species composition resulted from variation in historical connectivity among grasslands (DIST.OLD.ORIG; i.e. distance to old grassland at time of origin), explaining a significant fraction of 8.9% (P = 0.007; see Figure 11). Historical factors (patch age) were also related to turnover-driven dissimilarity (β_{sim}) in grassland composition in the LRV study area. However, this effect, as well as the influence of perimeter-area ratios, could not be disentangled from covariation with environmental variables. Only the selected environmental variables (consisting of PC3, management type, and soil spatial heterogeneity) explained a significant pure fraction of 9.2% (P = 0.003) of spatial turnover (β_{sim}). Of these, only PC3, representing a gradient of soil P concentration, was significant (6.9%; P = 0.008) when the effect of all other selected variables, including spatial and historical ones, was controlled for.

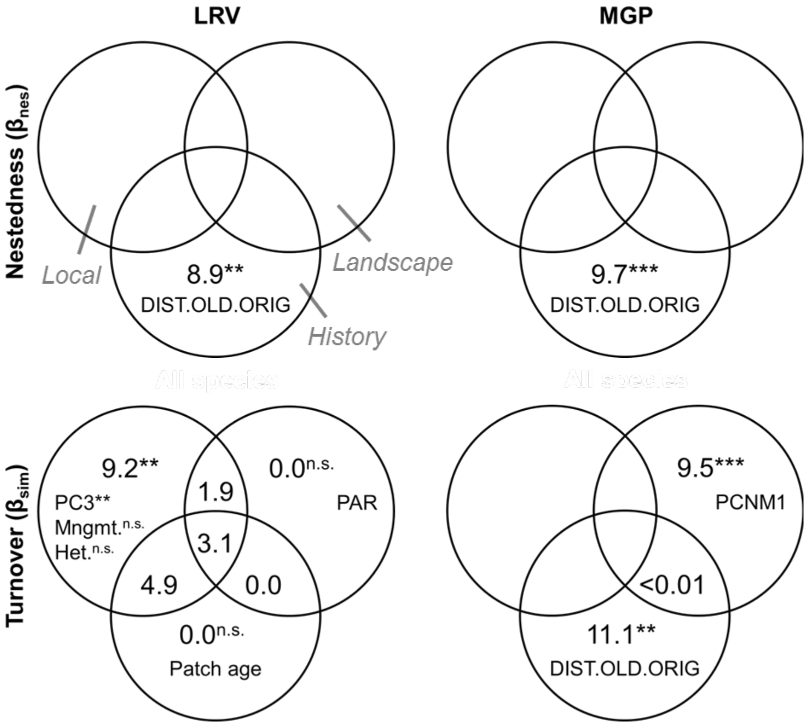


Figure 11 | Results of the variation partitioning. Shown are pure and joint contributions (in %) of the three explanatory variable sets to nestedness- and turnover-driven dissimilarity in species composition of semi-natural grasslands in two study areas in southern Germany, the Lech River Valley (LRV) and the Munich Gravel Plain (MGP). Local, environment; Landscape, contemporary landscape; History, historical landscape. Variables obtained from forward-selection are presented in the circles in the order by which they were selected. DIST.OLD.ORIG, distance to old grassland at time of origin. Het, soil spatial heterogeneity; Mngmt, management regime (mowing/grazing); PAR, perimeter-area ratio. Significance of individual pure fractions of predictor sets was evaluated using permutation tests. When multiple variables of the same predictor set were selected, the significance of their individual fractions was evaluated while controlling for the effects of all other selected variables, including those from other predictor sets. ***, $P \leq 0.001$; **, $P \leq 0.01$; *, $P \leq 0.05$; n.s., non-signifcant.

In the MGP study area, historical connectivity was also an important determinant of variation in species composition of present-day grassland communities (Figure 11). Again, DIST.OLD.ORIG was the only variable that explained a significant fraction of nestedness-driven dissimilarity (9.7%; P = 0.001). As hypothesized, variation in historical dispersal processes (DIST.OLD.ORIG) was also strongly related to spatial turnover (β_{sim}) among grasslands in the MGP study area (9.5%, P = 0.001), where regional soil fertility was low. Here, species turnover was also related to a large-scale spatial gradient (PCNM1; see Figure 9) (9.5%; P = 0.001). Local environmental conditions had no effect on either beta diversity component in this study area.

3.4 DISCUSSION

Species pools and dispersal limitation as drivers of nestedness

Variation in historical connectivity to old grasslands (DIST.OLD.ORIG) was the only variable that produced nestedness-driven dissimilarity of grasslands in both study areas. This means that grasslands with low historical connectivity were only a nested subset of historically well-connected grasslands. This pattern is likely to have resulted from two important characteristics of old calcareous grassland species pools. First, these pools are characterized by very high species numbers (Wilson et al. 2012; Dengler et al. 2014) and, second, many of these species have low dispersal abilities and are dispersal-limited even at short spatial distances (Verkaar et al. 1983; Hutchings & Booth 1996; Diacon-Bolli et al. 2013; see also Chapter 3). Hence, the number of species from this pool ('habitat specialists') likely to colonize a grassland decreases with decreasing (historical) connectivity. Considering habitat specialists only, this would result in grasslands with low connectivity being a nested subset of grasslands with high connectivity. However, the overall contribution of nestedness to beta diversity was only about 6% in both study areas, indicating that other species compensated for the absence of most dispersal limited specialist species, thus increasing spatial turnover (β_{sim}) rather than nestedness (β_{nes}). Inspection of Figure 10 suggests that increasing numbers of generalists compensated for the absence of many habitat specialists, especially in the MGP study area. That this was not a complete replacement of specialists, however, probably reflects the generally lower species numbers in intensively used agricultural landscapes (Allan et al. 2015;

Newbold et al. 2015) from which immigrating species could be recruited in the absence of historically old grassland.

Importantly, the distance to old-grassland source pools was only an important predictor when it was measured for past landscape configurations, whereas contemporary distance to source pools (DIST.OLD.CONTEMP) or the current amount of semi-natural grasslands (old and young) in the selected buffer radii was not related to beta diversity. This is in agreement with previous studies finding variation in specialist richness (Krauss et al. 2010), total species richness (Lindborg & Eriksson 2004), and species composition (Purschke et al. 2012) to be linked to historical rather than contemporary landscape configurations. Such historical contingencies emphasize the importance of priority effects for compositional variation in fragmented landscapes, where propagule arrival order can lead to stable alternative states in vegetation of single patches over long time frames (e.g. Fukami et al. 2005; Martin & Wilsey 2014; Fukami 2015). However, vegetation patterns that are contingent on historical landscape connectivity can also indicate a time-delayed response of plant species to habitat loss and fragmentation, what might result in future extinctions if patch or population sizes are too small (Tilman et al. 1994; Helm et al. 2006; Kuussaari et al. 2009).

Context-dependent drivers of spatial turnover

Variation in historical connectivity to old-grassland species pools was also an important determinant of turnover-driven dissimilarity of grasslands in the MGP study area (Figure 11). Figure 10 suggests that habitat specialists were increasingly replaced by generalist species as the distance to old grasslands in the historical landscape increased. In addition, there was also a large independent spatial component influencing the identity of species encountered in the grasslands. The variable selected (PCNM1) modelled variation in species identities at the largest spatial scale (Figure 9), and could reflect unmeasured spatially structured environmental or historical factors, or, alternatively, dispersal limitation of certain species confined to the parts of the MGP study area that it discriminated. Considering the comprehensive range of measured environmental variables, however, it seems more likely that the spatial gradient is indeed related to dispersal limitation of certain species, though this might have unknown historical reasons. In summary, there was little evidence for environmental conditions driving species turnover in this study area. Instead, species turnover was related to past and present landscape configurations, indicating that a dispersal-driven assembly has generated beta diversity patterns (Chase & Myers 2011) in our study area with marginal habitat conditions.

By contrast, species turnover was mostly driven by environmental sorting in the LRV study area (Figure 11), where grassland soils were more productive (see Figure S7). The only variable with a significant pure effect on turnover was PC3, which mainly represented a gradient of soil P concentration (Figure 11). Soil P is a key limiting factor to plant growth (Elser et al. 2007; Laliberté et al. 2015), and even slight P-enrichment can have dramatic negative effects on species richness of European grasslands (Ceulemans et al. 2014). Higher soil P concentrations confer greater fitness to competitive species, confining those with conservative resource economics – such as many calcareous grassland specialists (see Chapter 4) – to habitat patches with low P availability (Wassen et al. 2005; Ceulemans et al. 2011; Fujita et al. 2014). Therefore, competitive displacement of habitat specialists by competitive generalists under high soil P concentrations emerged as the main mechanism underlying turnover-driven dissimilarity in the LRV study area. Other variables were related to spatial turnover in this study area, too, but their effects could not be disentangled and where insignificant when the effects of other variables were controlled for. For instance, old grasslands may have been colonized by different species than younger patches because the type of ecosystems in surrounding landscapes has changed over time, resulting in patch age being related to turnover. Likewise, contrasting management regimes such as grazing *vs*. mowing are well-known to select for different traits and species combinations in calcareous grassland (Kahmen et al. 2002), and hence, might also contribute to turnover.

Metacommunity dynamics in landscapes with productive vs. marginal soils

As hypothesized, turnover-driven dissimilarity resulted from environmental sorting in the study area with more productive soils (LRV), whereas (historical) dispersal processes determined turnover patterns in the study area with marginal soil conditions (MGP). Dispersal-driven assembly of terrestrial plant communities on marginal soils is consistent with findings from community assembly experiments

(Chapter 2) and seed addition experiments, where effects of seed dispersal on community structure were high on unproductive soils but declined at high soil fertility (Foster 2001; Myers & Harms 2009). This can be understood in the light of niche theory, which suggests that multiple fitness trade-offs in environments with multiple limiting resources prevent competitive displacement (Harpole & Tilman 2007; Allesina & Levine 2011; Eskelinen & Harrison 2015), and hence, community differentiation of grasslands on marginal soils should be driven by demographic stochasticity and regional dispersal processes below certain thresholds of resource supply. Indeed, previous studies have shown that thresholds of P-availability below which high species numbers in semi-natural grasslands are stabilized do exist (Janssens et al. 1998; Gilbert et al. 2009).

In the LRV study area, soil P-availability was significantly higher (Figure S7) and here, soil P-availability emerged as the main driver of species turnover. Results of a pan-European study by Ceulemans et al. (2014) showed that species richness of calcareous grasslands declined beyond values of ca. 25 mg P kg^{-1} until species-loss rates levelled-off at concentrations of 105 mg P kg^{-1}. This coincides with the median soil P concentration in LRV grasslands of 25 mg P kg^{-1} compared to only three values >15 mg P kg^{-1} in MGP soils. Our results from LRV show that this species loss is accompanied by a change in species identities, thus resulting in high turnover among grasslands with contrasting soil P concentrations when overall regional P supply is close to or beyond thresholds of P limitation. Our finding of contrasting roles of dispersal vs. niche-based environmental sorting in unproductive vs. productive regions is also in agreement with theoretical models that predict transitions from niche to neutral phases beyond system-specific thresholds of environmental stress, where the importance of environmental and/or demographic stochasticity for community dynamics outweigh niche-based competitive interactions (Fisher & Mehta 2014).

3.5 CONCLUSION

The present study provides empirical evidence for the relative contributions of local environmental conditions, contemporary landscape spatial configuration, and historical landscape context for beta diversity in fragmented grasslands. To our knowledge, this is the first attempt to link these contrasting variable sets to spatial turnover and nestedness components of beta diversity in fragmented landscapes. Investigating the drivers of beta diversity components in two fragmented grassland landscapes, we found that dispersal limitation of the large source species pools of calcareous grasslands was a general determinant of nestedness-driven dissimilarity. Contrasting assembly mechanisms led to spatial turnover, depending on regional soil productivity. When regional soil fertility was below an empirical ecosystem-specific threshold of resource (P) limitation, species turnover was generated by neutral dispersal processes, consistent with theoretical predictions. By contrast, beyond this threshold of resource (P) limitation, species turnover was deterministic and increased with increasing differences in resource supply. Our findings are thus not only novel contributions to a better understanding of how site-to-site variation in species composition is generated in environmentally heterogeneous metacommunities with variable land-use history. They also demonstrate that empirical evaluations of metacommunity dynamics should consider species pool characteristics (thresholds of P-limitation in this case) that mediate the magnitude to which neutral dispersal vs. deterministic processes can dictate community assembly.

SUPPORTING INFORMATION

Study system and areas

The investigated grasslands are located on fluvial terraces of different age consisting of carbonate-rich gravel that was deposited during various periods from the late Pleistocene to the early 19th century by the Lech (LRV) and Isar (MGP) rivers (Feldmann 1994; Gesslein 2013). The soils are mainly carbonate-rich, nutrient-poor to moderately rich, relatively shallow leptosols, but thicker alluvial soils that were deposited during flood events can be found occasionally in some grasslands close to the rivers (Fetzer et al. 1986). Although pastoral use of the natural forest vegetation began in the Neolithic (LRV) and Bronze Age (MGP), leading to first open woodlands in some areas (Kollmannsberger 1973; von den Driesch 2001), extensive deforestation as a consequence of increasing human populations started around 1400 BP (Pfeuffer 2010) and led to vast open grassland landscapes that were mainly used as pastures and persisted for centuries (as can be reconstructed from historical maps and reports, e.g. Kollmannsberger 1973; Müller 1990; Pfadenhauer et al. 2000; Pfeuffer 2010) until a drastic agricultural transformation of the landscape started in the first decades of the 20th century (Kollmannsberger 1973; Pfeuffer 2010).

Vegetation sampling

Previous to surveying a grassland, several sampling plot locations were arbitrarily selected on aerial photographs, but had to represent the grassland spatially well (i.e. no clustering), and had to be at least 5 m apart from other plots, and 2 m from patch edges, soil disturbances (e.g. molehills), trees, scrubs and hiking trails (Conradi et al. 2015). Parts of grasslands that had been abandoned were excluded from sampling and subtracted from calculations of patch area (see below).

In each grassland, vascular plant species composition was then sampled in 1-m^2 plots at the previously defined locations in the arbitrary order with which they were selected on the aerial photographs, with additional revisiting of plots sampled earlier in the field season to check for later emerging species. The survey of a grassland was finished when no new species were detected during the inspection of three consecutive plots. Therefore, the number of sampling plots differed among grassland patches (n = 3–15), but this sampling strategy captures their species diversity and average community structure independent of variation in species density. In total, 262 plots were sampled and their spatial coordinates were noted, so that the plots could be revisited for soil sampling. Phanerophyte species were excluded from the analysis since they were encountered as seedlings only.

Environmental variables

In all plots soil sampling was conducted during 17 consecutive days with relatively stable weather conditions at the beginning of the growing season in early April 2014. The short sampling period minimized temporal variation in soil chemistry, and the date of sampling ensured that analysis results reflected the actual soil fertility and not only the residual nutrient contents after plant nutrient uptake (Hoffmann 1991; McTaggart & Smith 1993). As the inaccuracy of our GPS was 2 m, and the topography at the proposed original plot locations was homogeneous, we randomly drilled several topsoil (0–10 cm) samples within a radius of 2 m around the plots with an auger (2 cm diameter), to obtain one composite sample per plot. Subsequently, soil depth was measured by coring 3–5 times until the auger reached a stony layer, and calculating the median depth of the resulting boreholes. The samples were stored in cooling boxes and brought to the lab on the same day, where they were stored at -25 °C until analysis.

Following Hoffmann (1991), the soil samples were analysed for pH in $CaCl_2$, and total plant available P and K using CAL-extraction from oven-dried (40 °C) soils; 17 samples, in which the P concentration was below the detection limit of 3 mg kg^{-1}, were given a P concentration of 1 mg kg^{-1}. Total N was determined by combustion and gas chromatography using a vario EL elemental analyzer (Elementar Analysensysteme, Hanau, Germany). Concentrations of NO_3^-, NH_4^+, Ca^{2+} and Mg^{2+} were determined by ion chromatography using a Dionex AS-DV Autosampler (Thermo Fisher Scientific, Braunschweig, Germany). Concentrations of NO_3^- and NH_4^+ below the detection limits (0.08 mg l^{-1} and 0.06 mg l^{-1}, respectively) were given a concentration of 0 mg l^{-1}. To obtain a soil solution for ion chromatography, 10 g moist (thawing) fine soil were suspended in 100 ml distilled water in an Erlenmeyer flask, which was agitated for 60 min on a horizontal shaker (170 rotations min^{-1}), and then left for sedimentation for 45 min, after which the supernatant suspension was extracted from each sample. This suspension was centrifuged for 15 min with 5000 rotations min^{-1}. The resulting supernatant solution was extracted and used for ion chromatography, and the measured ion concentrations were then related to soil dry weight. Soil texture was determined by hand by trained persons (Bioanalytik Weihenstephan, Freising, Germany) and treated as an ordinal variable with six levels in the data analysis, with large values indicating more permeable soil types.

Relic flood channels up to 1.5 m below soil surface can be found in some grasslands of the LRV study area. Because such areas have greater soil moisture during periods of high ground water table, we noted whether a sampling plot was located in such a relic channel and included this information as a binary variable ‘moisture’. Information about the management of a patch (mowing or grazing) was compiled from interviews with land owners and nature conservation authorities.

As the data analysis focused on the compositional differentiation among whole patches, we calculated the median of each variable measured at the plot-scale across all plots of the respective patch. Within-patch spatial heterogeneity in soil properties was calculated as multivariate dispersion (Anderson et al. 2006) based on Gower’s dissimilarity using plot-level data on N, P, K, NO_3^-, NH_4^+, Ca^{2+}, Mg^{2+}, pH, soil texture, soil depth, and moisture.

Spatial data

The area of each investigated grassland patch was calculated based on the criteria for site selection mentioned in the main text. Abandoned and forested areas were subtracted from total patch area. As a measure of connectivity, we calculated the habitat amount in radii of 100, 300 and 500 m, respectively, around the surveyed grasslands based on data of the ‘Habitat Mapping’ of the Bavarian Environmental Office (LfU; www.lfu.bayern.de, accessed 6 Feb 2015). Of the ‘Habitat Mapping’, only patches that had <60% woody cover and contained at least one of the two indicator species of low productive, calcareous grasslands (*Bromus erectus, Brachypodium rupestre*) qualified as suitable habitat. This included historically old and younger grasslands, but not grasslands that have recently been restored with hay transfer. The habitat mapping data was corrected or amended based on own knowledge and visual interpretation of aerial photographs when necessary.

Quantification of patch historical connectivity

Historical connectivity (DIST.OLD.ORIG) of a grassland was measured as the spatial distance to the nearest old (with origin in year 1500) grassland (including open woodland pastures) which could had served as a potential source of characteristic species of the pre-transformed landscape, in the year of origin of the focal grassland. We used data of the 'Habitat Mapping' mentioned above in combination with historical land cover maps from 1809–1858 (1:25,000) to identify historically old grassland patches in the contemporary landscape. Again, of the 'Habitat Mapping', only patches that had <60% woody cover, contained at least one of the two indicator species of low productive, calcareous grasslands (*Bromus erectus, Brachypodium rupestre*), were already plotted as grasslands on the historical maps, and for which no indication of abandonment or different interim land-use was present, qualified as historically old source patches. Based on historical reports of continuous open grassland landscapes (Pfeuffer 2010), surveyed historically old grasslands (origin in 1500) were ascribed DIST.OLD.ORIG values of zero, indicating high historical connectivity. Historical land cover maps (1809–1858) were used to infer the historical connectivity of patches that originated between 1840 and 1910, and modern land cover maps from 1959 until present (1:25,000) as well as current aerial photographs were used to infer the historical connectivity of patches that originated more recently.

Table S2 | Variables measured to investigate environmental, spatial and historical controls over beta diversity in human-transformed ancient grassland landscapes.

Variable	Scale	Unit/Levels
Environmental variables		
Total N	metric	[g kg^{-1}]
Total P	metric	[mg kg^{-1}]
Total K	metric	[mg kg^{-1}]
NH_4^+	metric	[mg l^{-1}]
NO_3^-	metric	[mg l^{-1}]
Ca^+	metric	[mg l^{-1}]
Mg^+	metric	[mg l^{-1}]
pH	logarithmic	[$-\log_{10}(H^+)$]
Soil texture*	ordinal	[1–6]
Soil depth	metric	[cm]
Moisture**	categorical	[moist, normal]
Management	categorical	[mowing, grazing]
Soil spatial heterogeneity	metric	-
Spatial variables		
Patch area	metric	[m^2]
Perimeter-area ratio	ratio	-
Habitat amount within 100 m	metric	[m^2]
Habitat amount within 300 m	metric	[m^2]
Habitat amount within 500 m	metric	[m^2]
PCNM eigenvectors	metric	-
Distance to historical grassland in contemporary landscape	metric	[m]
Historical variables		
Patch continuity	metric	[yr]
Distance to historical grassland at time of origin	metric	[m]

*Soil type levels: 1, silty loam; 2, humic; silty loam; 3, sandy loam; 4, humic; strongly loamy sand; 5, strongly loamy sand; 6, weakly loamy sand.
**Used for the calculation of soil spatial heterogeneity only.

Figure S7 | Differences in soil conditions among calcareous grasslands in the Lech River Valley (LRV) and the Munich Gravel Plain (MGP) in south Germany. *P*-values are from permutation t-tests using 9999 permutations. The ordinal variable soil texture (large values indicate coarser soils) was treated as a numeric variable for this analysis.

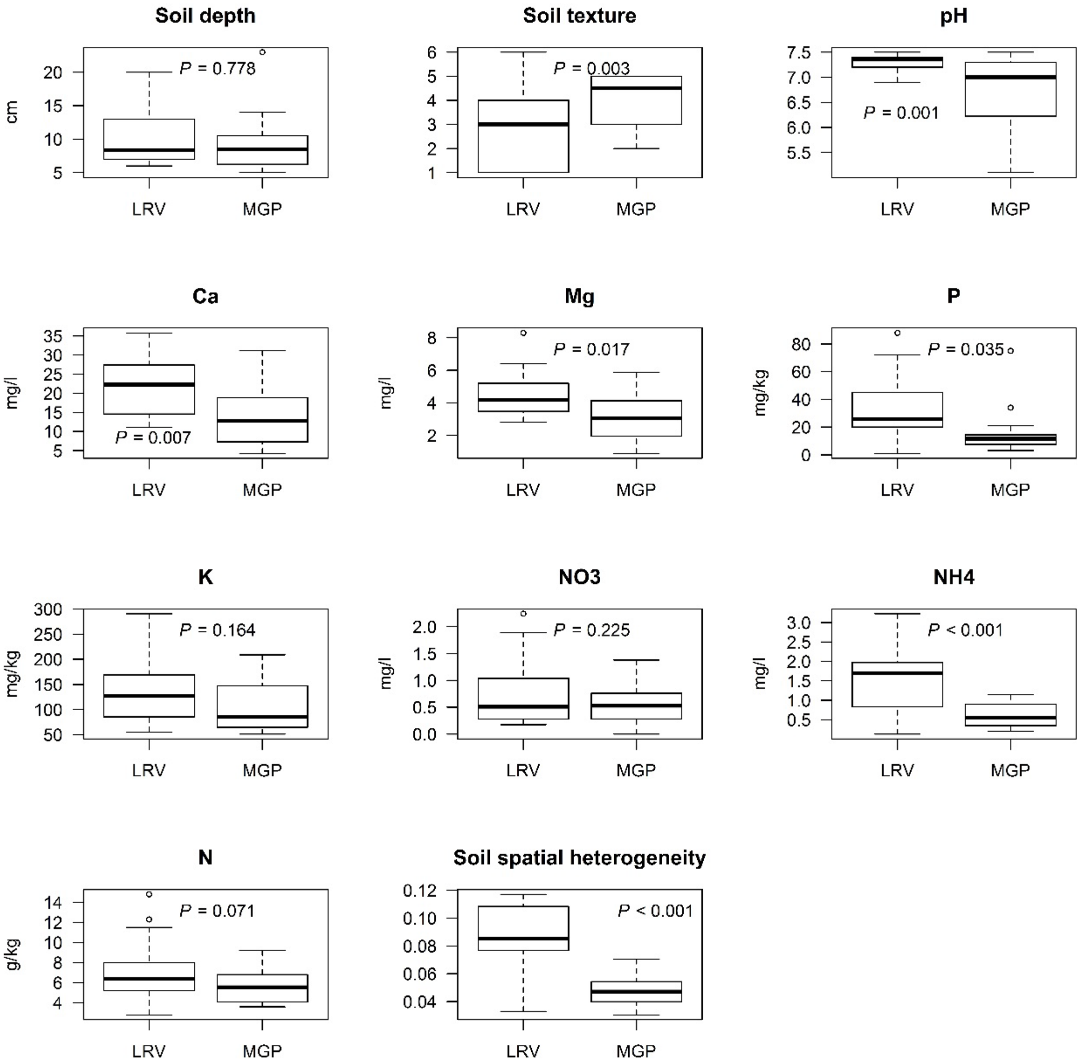
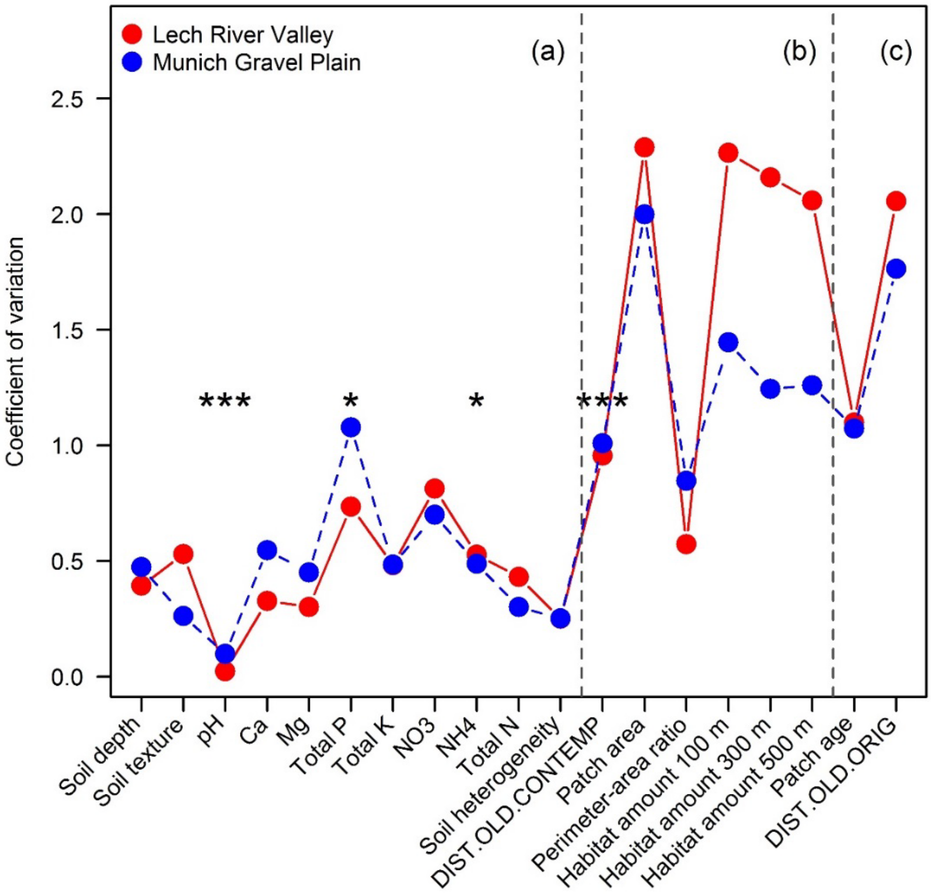


Figure S8 | Variance of each (a) environmental, (b) spatial, and (c) historical variable within, and differences in variances among the two study areas. The PCNM eigenvectors were excluded from this analysis. A Fligner-Killeen test was used to evaluate significance of differences in variances among study areas with *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$. Differences in the proportions of mown *vs.* grazed grassland patches (not shown) among study areas were not significant ($P = 1$) based on Fisher's Exact Test.



Chapter 4

Species pools, mass effects and environmental sorting interact to determine plant diversity and functional trait composition in secondary grasslands

Abstract – *Successional trajectories of secondary habitats are regulated by local environmental factors and dispersal processes that influence the number and identities of immigrating species. However, systematic investigations of how local and regional processes combine to determine different aspects of taxonomic and functional community structure in secondary habitats are rare. Using detailed information on environmental factors, as well as past and present landscape configurations, this study investigated local and regional drivers of plant community structure in secondary grasslands. A special focus was on the role of species pool characteristics of primary grasslands which might serve as sources for the colonization of secondary patches. We found that most aspects of species diversity and functional composition were driven by immigration from primary grasslands during early stages of succession. Such species pool influences were even more important than long gradients of soil factors, spatial characteristics of contemporary landscapes, and patch age. High immigration rates confounded well-known relationships between soil nutrient concentrations and species diversity or resource-economic traits, suggesting that mass effects are an important assembly mechanism. However, we also found an important role of soil texture that selected species according to their canopy height irrespective of species pool associations. The results illustrate that multiple assembly mechanisms operate simultaneously to determine different aspects of plant community structure.*

Keywords: *Calcareous grasslands; Community assembly; Historical contingency; Landscape ecology; Novel ecosystems; Metacommunity; Multi-model inference*

3.1 INTRODUCTION

Land use and its increasing intensification have resulted in widespread losses of natural ecosystems and associated biodiversity at regional and global scales (Sala et al. 2000; Foley et al. 2005; Karp et al. 2012; Allan et al. 2015; Newbold et al. 2015), and more effective strategies for conservation are required to mitigate the looming next mass extinction (Barnosky et al. 2011; Ceballos et al. 2015). Protection of (near)natural habitat patches has highest priority for the maintenance of species diversity (Gibson et al. 2011; Veldman et al. 2015). However, there are continued extinctions even from intact and protected areas as a consequence of small fragment size, missing habitat connectivity, and biological invasions (Fischer & Stöcklin 1997; Gibson et al. 2013). Extinction debts (Kuussaari et al. 2009; Krauss et al. 2010; Dullinger et al. 2013), and the need for many species to track climate change (Urban 2015) have led to increasing awareness of the significance of restored or novel habitats in contemporary and future landscapes (Hobbs et al. 2014; Kueffer & Kaiser-Bunbury 2014). As a consequence, understanding the factors that determine community assembly and the potential for species conservation in man-made habitats has become a research priority (Barlow et al. 2007; Chazdon et al. 2009; Mendenhall et al. 2014). However, this remains a challenge, because of variable land-use histories that have produced variation in local site conditions, as well as the often contrasting spatial configurations, and the contrasting history of land use in the surrounding landscape that might have influenced the numbers and identities of immigrating species in secondary habitat patches (Chapter 3). The metacommunity framework considers how regional dispersal processes and local environmental conditions might interact to determine local community structure (Leibold et al. 2004), and thus provides a relevant conceptual background for studying drivers of plant community structure in secondary habitats. According to this framework, three alternative assembly scenarios might regulate variation in taxonomic and functional community structure among secondary habitat patches with variable environmental conditions in human-transformed landscapes.

First, environmental sorting might be an important determinant of variation in community structure (Leibold et al. 2004), because of interspecific variation in life-history strategies, resource economics and physiological tolerance limits to soil factors (Westoby et al. 2002; Reich 2014). In this scenario, plant species occurrences are determined by traits related to resource acquisition and use, and hence, community-level composition of relevant traits should change along soil gradients (e.g. Spasojevic & Suding 2012; Fortunel et al. 2014; Jager et al. 2015). Environmental sorting can be important even in fragmented landscapes where species might not always track their environmental optimum due to dispersal limitation (Dupré & Ehrlén 2002; Kimberley et al. 2014). Moreover, environmental sorting should also lead to higher species numbers if soil spatial heterogeneity is high (Questad & Foster 2008; Adler et al. 2013), but in homogenous, resource-rich habitats with few trade-off opportunities it might reduce diversity of species and traits (Harpole & Tilman 2007).

Second, patterns of species diversity and functional composition of secondary habitats might also be moderated by the influences of spatial landscape configuration on dispersal processes (Hubbell 2001; Tscharntke et al. 2012). For instance, small patch size and low connectivity can act as dispersal filters as they strongly decrease colonization probabilities of species with ineffective dispersal strategies (Kolb & Diekmann 2005; Lindborg 2007; Schleicher et al. 2011). In addition, the lower propagule pressure on such patches can result in smaller species numbers (McArthur & Wilson 1967), which may be offset, however, by increased spill-over from adjacent habitats when perimeter-area ratios are high (Cook et al. 2002).

Third, mass effects, where high immigration rates from source species pools can lead to population persistence despite non-optimal environmental conditions, can strongly influence local community structure (Shmida & Wilson 1985; Leibold et al. 2004). Primary habitat patches often have large and functionally distinct species pools (Gibson et al. 2011). If they serve as sources for the colonisation of secondary patches, in a mass effects scenario, variation in species diversity and functional composition among recipient secondary patches mainly reflects immigration rates from primary source pools and is unrelated to environmental gradients (Kirmer et al. 2008; Cornell & Harrison 2014; Laliberté et al. 2014; Zobel 2015). In this context, it is important to note that community structure of later-successional stages is often contingent on arrival order during early stages of succession (Fukami et al. 2005; Ejrnæs et al. 2006; Helsen et al. 2012; Kardol et al. 2013; Fukami 2015). Therefore, to correctly evaluate the importance of mass effects of source species pools for community structure of secondary habitats, it seems necessary to also consider landscape spatial configurations at the time secondary habitat originated.

European landscapes formerly covered by semi-natural calcareous grasslands are suitable model systems to test the relative roles of these alternative mechanisms:

Vast calcareous grassland landscapes resulting mainly from medieval pastoral land use persisted for centuries in several parts of Europe until profound landscape transformations started in the early 20th century, during which most of the nutrient-poor grassland became fallow land or was converted into fertilized agricultural grasslands, arable fields, plantation forests, or urban area (Poschlod & WallisDeVries 2002). The few remnants of historically old calcareous grasslands have a distinct species pool characterized by an outstanding species richness (Wilson et al. 2012), and a large and unique set of species otherwise rare in contemporary landscapes (Ellenberg & Leuschner 2010), which is reflected by the high conservation status of such grasslands (Veen et al. 2009) and allows testing local, regional, and species pool effects on community structure of secondary grasslands.

Here we take advantage of the well-documented land-use history of semi-natural grassland patches and their surrounding landscape, and detailed soil and spatial data in two study areas in southern Germany from Chapter 3 to empirically test the relative importance of alternative mechanisms of community assembly in secondary grasslands in human-transformed landscapes. We focus on secondary grasslands, defined here as patches which have had a discontinuity of semi-natural vegetation and are recovering through natural processes (Corlett 1994; Chazdon et al. 2009), or patches that originated after a major disturbance in places that were not part of the historically continuous grassland landscape (e.g. in forest) but are also naturally recovering and managed as semi-natural grasslands after the disturbance event by annual mowing or grazing and no application of fertilizer. In summary, we tested the following hypotheses:

1) Environmental factors drive variation in plant community structure of secondary grasslands: Species diversity is high in resource-poor sites and when soil spatial heterogeneity is high. The composition of functional traits related to interactions with local site conditions varies systematically along environmental gradients.
2) Contemporary landscape spatial configuration drives variation in plant community structure of secondary grasslands: Species diversity is highest in large, well-connected grasslands with high perimeter-area ratios. The composition of functional traits related to dispersal should vary systematically along spatial gradients.

3) Characteristics of source species pools drive variation in plant community structure of secondary grasslands via mass effects: Species diversity and functional trait composition reflect the distance to historically old grasslands that have large and functionally distinct species pools. This confounds diversity- and trait-environment relationships.

3.2 METHODS

Study areas and vegetation sampling

The study was conducted in two former grassland landscapes in Bavaria, south Germany, the Lech River Valley (LRV; 48°15’ N, 10°54’ E) and the Munich Gravel Plain (MGP; 48°15’ N, 11°37’ E) (see maps in Figures 3–4). Both have a temperate and humid climate, mean annual rainfall of ca. 835 mm, and a mean annual temperature of ca. 8.5 °C (1981–2010; www.dwd.de, accessed 25 Feb 2015). Profound landscape transformations starting in the early 20th century led to widespread habitat losses and fragmentation of former continuous semi-natural calcareous grasslands (Müller 1990; Pfadenhauer et al. 2000). The semi-natural grassland patches present today include old historical and young secondary grasslands, the latter originating from the time period 1840–1998.

Twenty-four (13 in LRV, 11 in MGP) secondary semi-natural grasslands were selected for this study because they had a traceable land-use history. Their species composition was sampled in 2012 and 2013 in multiple, randomly selected 1-m^2 plots for so long until no additional species were encountered during the inspection of three consecutive plots. Sampling plots were at least 2 m away from patch borders and hiking trails to reduce edge effects and disturbance from visitor trampling (Conradi et al. 2015).

Soil data

All plots were revisited for soil sampling in spring 2014 and soils where analysed for soil depth and texture, pH, total N, P and K, as well as for NH_4^+, NO_3^-, Ca^{2+} and Mg^{2+}. We also recorded whether a plot was located in a relic floodplain channel with slightly higher soil moisture due to a periodically elevated groundwater table. Soil spatial heterogeneity of each grassland was calculated as multivariate dispersion

(Anderson et al. 2006) based on Gower's dissimilarity using plot-level data of the soil variables mentioned. The soils covered a considerable range of physico-chemical characteristics because of natural environmental variation and the variable land-use history of the secondary grasslands, ranging from intensive agricultural use to gravel extraction. For instance, concentrations of N, P, and K ranged between 2.8–12.3 g kg^{-1}, 1–88 mg kg^{-1}, and 55–274 mg kg^{-1}, respectively.

Table 2 | Pearson correlation of principal component (PC) scores of secondary grassland patches with environmental variables. Percentage values below PCs are their explained variance.

	PC1 (45%)	**PC2 (25%)**
Soil depth [cm]	0.83	-0.42
Soil texture	-0.28	0.84
pH	-0.41	-0.66
Mg [mg l^{-1}]	-0.86	-0.12
P [mg kg^{-1}]	-0.16	-0.64
K [mg kg^{-1}]	-0.88	-0.08
N [mg kg^{-1}]	-0.81	-0.05

Soil variables except spatial heterogeneity and moisture were subject to Principal Components Analysis (PCA) in order to reduce the number of explanatory soil variables for modelling. For this purpose, the nominal variable soil texture was converted into an ordinal scale with higher values for large grain sizes and then treated as a metric variable in the PCA. Variables causally related to others (Ca^{2+}, NH_4^+, NO_3^-) were excluded from the analyses and the remaining variables were transformed to reduce outliers when necessary and were then scaled to unit variance to give them equal weights in the PCA. The first two principal components (PC) accounted for 70% of the total environmental variation, and hence the grassland scores on these PCs were used as explanatory environmental variables along with soil heterogeneity in subsequent analyses.

Past and present landscape context, species pools and historical contingency

We used data of the 'Habitat Mapping' of the Bavarian Environmental Office (LfU; www.lfu.bayern.de, accessed 6 Feb 2015) in combination with historical land cover maps of the pre-transformed landscapes from the 19th century to identify historically old grassland remnants. Only patches that were already mapped as grassland on the historical maps and for which no indication of different interim land use was present (based on local literature and interviews with land managers) qualified as 'old'. For the remaining secondary patches we reconstructed their year of origin (i.e. the year in which secondary succession and semi-natural grassland management started after intensive agricultural use or disturbance) from interviews with land managers, management plans, and from historical, geomorphological and geological maps and literature. Patch ages (as of 2014) ranged between 174 and 16 years.

This information was used to calculate a measure of species pool influences: the spatial distance to the nearest historically old grassland (DIST.POOL) that could provide colonists of the species pool of the pre-transformed landscape. Because some secondary grasslands were formerly close to historically old grasslands but are now isolated, we measured this distance on land cover maps from the approximate time of origin of each focal secondary grassland to avoid confounding historical contingencies. This approach reflects that the species composition in later-successional stages is usually contingent on arrival order during early stages of succession (Fukami et al. 2005; Ejrnæs et al. 2006; Helsen et al. 2012; Kardol et al. 2013; Fukami 2015), and is also supported by the observation that immigration rates level off after one or two decades of succession in this system even when source pools are nearby (Kiehl & Pfadenhauer 2007). Preliminary analyses showed that when the distance to historically old source grassland was measured for the time in which a secondary patch emerged rather than in the present landscape, it explained much more of the variation in taxonomic and functional community structure (Table S3).

To test the hypotheses about contemporary landscape configuration for secondary grassland community structure, we calculated patch area and perimeter-area ratio, a measure of spill-over potential from adjacent habitats (Tscharntke et al. 2012), as well as the amount of suitable habitat in radii of 100, 300, and 500 m around each grassland as a measure of connectivity in QGIS (QGIS Development Team 2014). Only semi-natural grasslands (old and secondary) and open woodlands (<60% woody cover) with the indicator species *Bromus erectus* Huds. and *Brachypodium rupestre* (Host.) Roem. & Schult. (Oberdorfer 2001) were considered suitable habitat. This information was obtained from the 'Habitat Mapping' data mentioned above (see also Chapter 3).

Functional traits, commonness and habitat specialism

Information about selected plant functional traits was compiled from databases and the literature (mainly Klotz et al. 2002; Jäger 2007; Kleyer et al. 2008; Hintze et al. 2013) using median values when multiple data entries were available for a species. In four cases, single trait values were taken from morphologically and ecologically similar species of the same genus that were not present in our samples to improve statistical inference of missing trait values (see below). Database values conserve species rankings based on field-measured trait values well (Kazakou et al. 2014), mainly because interspecific trait variability is most often larger than intraspecific variation, as has also been demonstrated in our study areas by Andrade et al. (2014). We focused on six uncorrelated traits (maximum Spearman's rank correlation coefficient $|\rho| = 0.52$) capturing variation in dispersal, resource use and life-history strategies (Westoby et al. 2002; Laughlin 2014): canopy height, specific leaf area (SLA), length of the flowering period, seedbank persistence (Bekker et al. 1998), diaspore attachment potential to sheep wool (Römermann et al. 2005), and wind dispersal ability (releasing height × terminal velocity^{-1}). Both height and terminal velocity were found to significantly influence wind dispersal over long distances in open landscapes (Heydel et al. 2014) and were thus combined to one measure of wind dispersal ability.

To test our hypotheses about the role of species pool influences for variation in community structure among secondary grasslands, we obtained species' commonness in the regional flora of Bavaria (www.bayernflora.de; accessed 01 Sep 2015), measured as the number of occurrences in 5.5 km × 5.5 km quadrants. Additionally, we classified species characteristic of European dry grasslands (phytosciological class Festuco-Brometea; Oberdorfer 2001) as well as of thermophilous fringe communities (Trifolio-Geranietea), calcareous Pine forests (Erico-Pinetea), steppe Pine forests (Pyrolo-Pinetum), thermophilous Oak forests (Potentillo-Quercion petraeae), natural alpine limestone habitats, calcareous grasslands with fluctuating soil moisture (Cirsio tuberosi-Molinietum arundinaceae), and dry outcrops (Sedo-Scleranthetea) as habitat specialists (see also Kiehl & Pfadenhauer 2007; Conradi et al. 2015). Such species are typical elements of historically old and well-preserved calcareous grasslands in southern Germany (Oberdorfer 2001; Ellenberg & Leuschner 2010).

Preparatory data analysis

Species richness, the number of habitat specialist species, and the average commonness of the species were calculated for each grassland. To further elucidate the ecological mechanisms that have led to divergent species diversity patterns, community mean trait values and the functional diversity of individual traits were computed for each grassland, giving equal weights to the species encountered. Community mean trait values provide information about the trait values conferring fitness or patch occupancy under the particular environmental conditions and landscape context of the focal grassland patch. Functional diversity was measured as Functional Dispersion (FDis), the average distance of each species to the community centroid in functional trait space (Laliberté & Legendre 2010). A small FDis is observed when species in a community have similar trait values, indicating strong selection operating on this trait (e.g. Conradi et al. 2015). Trait values were transformed to improve normality prior to the calculation of community mean trait values and FDis.

Indices of functional community structure and the conclusions about ecological processes drawn from them strongly depend on the degree of completeness of the trait data (Pakeman 2014). We therefore inferred missing trait values using the 'missForest' algorithm from the eponymous R package (Stekhoven & Buehlmann 2012; Stekhoven 2013) and improved the imputation by taking the phylogenetic relatedness among species into account, as recommended by Penone et al. (2014). We also included 27 additional species in the imputation that were found in old grasslands surveyed with the same vegetation sampling strategy only (Chapter 3). Phylogenetic information was included by computing phylogenetic eigenvectors (PEV; Diniz-Filho et al. 1998) from a cophenetic distance matrix derived from a pruned dated ultrametric phylogeny of the European flora (Durka & Michalski 2012), and using the first eleven PEVs, accounting for ca. 81% of the total phylogenetic variation, as additional predictor variables in the imputation (Penone et al. 2014). Phylogenetic eigenvectors are the eigenvectors of a Principal Coordinates Analysis (PCoA) on a phylogenetic distance matrix and express the total variation contained in it at different scales. The first PEVs represent divergences close to the root of the phylogeny whereas PEVs of higher order represent divergences closer to the tips of the phylogeny (Diniz-Filho et al. 2012). To further improve the imputation of missing values in our focal traits we used a much broader set of traits covering multiple aspects of plant-strategy variation for the imputation (see Table S4). Missing values for diaspore attachment potential and wind dispersal ability were calculated from imputed trait values.

To examine whether species considered elements of the old-grassland species pool (habitat specialists) were functionally different from and less common than non-specialists, we tested for differences in the six plant traits and commonness between specialists and non-specialists using permutation t-tests.

Statistical modelling

Linear mixed effects modelling (LMM) was used in combination with an information theoretic approach and multi-model inference (Burnham & Anderson 2002; Grueber et al. 2011) to dissect the leading drivers of plant diversity and functional community structure of secondary grasslands. Prior to modelling, explanatory variables where transformed to reduce outliers when necessary and each variable was centered and divided by its standard deviation in order to give parameter estimates on a comparable scale (Gelman 2008; Schielzeth 2010). We took the following approach to account for collinearity among explanatory variables: For each variable of variable pairs with $|\rho| > 0.7$ (Dormann et al. 2013), univariate LMMs with a random intercept for study area were built to model each response variable (i.e. species diversity measures, community mean trait values and FDis) and the Akaike Information Criterion adjusted for small sample size (AIC_C) was calculated. Only the variable of the correlated variable pair yielding higher AIC_C values for the majority of modelled response variables was retained, effectively reducing all pairwise correlations to $|\rho| < 0.5$.

For each species diversity measure and index of functional community structure, a global LMM with a random intercept for each study area and the retained explanatory variables as fixed effects was built using restricted maximum-likelihood estimation in the ‘nlmer’ package (Pinheiro et al. 2014) in R (R Core Team 2014). We then fitted all possible submodels nested in the global model and ranked them by their AIC_C. All models within 2 AIC_C of the most parsimonious model were considered as receiving substantial empirical support (Burnham & Anderson 2002) and were thus included in a ‘confidence set’ of models, which was used to calculate model-averaged effect sizes of the explanatory variables, their 95% confidence intervals, and relative importance.

Model-averaged effect sizes and their variances were calculated across all models in the confidence set, with their estimates being set to zero in those model where the variable was absent ('zero method'; Burnham & Anderson 2002; Grueber et al. 2011). If there was more than one model in the confidence set, 95% confidence intervals of the model-averaged effect sizes were computed as described in Burnham and Anderson (2002) using a revised formula for the variance estimator (Burnham & Anderson 2004). Otherwise, standard 95% confidence intervals for the effect sizes were obtained. Confidence intervals not including zero indicate that the explanatory variable significantly affects the response (cf. Grueber et al. 2011). The relative importance of a variable was calculated by summing the Akaike weights, i.e. the probability that the model is the best of all models in the set considered, of all models in the confidence set in which the variable occurred (Burnham & Anderson 2002). Finally, we obtained conditional $R^2_{\mathrm{GLMM}(c)}$ (i.e. variance explained by both fixed and random factors) of each model in the confidence set as described in Nakagawa and Schielzeth (2013). Multi-model inference was performed using the R package 'MuMIn' (Barton 2015).

To check for spatial autocorrelation we inspected variograms of the residuals of the most parsimonious model. Additionally, we re-fitted this model with several alternative spatial correlation structures applied to observations within the same study area and compared $\mathrm{AIC_C}$ values of models with and without these structures (Zuur et al. 2009). Both approaches consistently indicated that there was no spatial autocorrelation. LMMs were used because residuals of the respective most parsimonious model were approximately normally distributed and had constant spread.

3.3 RESULTS

Trait differences between habitat specialists and non-specialists

In all functional traits investigated, species considered elements of the old-grassland species pool ('habitat specialists') had functional trait values that were significantly ($\alpha = 0.05$) lower than those of 'non-specialist' species (Figure 12). This confirms that the species pools of old grasslands are functionally distinct, what is the basis for detecting mass effects as drivers of the functional community structure of secondary grasslands. Habitat specialist species were also significantly ($P < 0.001$) less common in the regional flora than non-specialists (Figure S9).

Variable pre-selection

We found high correlations between the three connectivity measures ($\rho \geq 0.83$), and between patch area and perimeter-area ratio ($\rho = -0.85$). To reduce collinearity effects, connectivity based on habitat amount in 100 and 500 m, and patch area were removed from the analysis based on $\mathrm{AIC_C}$ comparisons of the univariate models. Thus, the global model for the 15 response variables included the first two principal components of the soil PCA, soil spatial heterogeneity, connectivity based on habitat amount in a 300 m radius (square-root transformed), perimeter-area ratio (square-root transformed), patch age, and DIST.POOL ($\log_{10}$-transformed) (see Table 3).

Explained variation in taxonomic and functional community structure

The models included in the confidence sets for species richness, habitat specialist richness, and average commonness, as well as those for community mean trait values explained considerable amounts of variation in these variables (Table 3). This indicates that the most important sources of variation in taxonomic and functional community structure were captured by our dataset. The Functional Dispersion of trait values in secondary semi-natural grasslands, however, showed no systematic variation along gradients described by the explanatory variables, as in all but one case the empty model (random intercept only) was the only one included in the confidence set. The only exception was seedbank persistence where DIST.POOL was included in the second-best model (by means of $\mathrm{AIC_C}$).

Relative variable importance

Table 3 shows the relative importance of each explanatory variable for each index of taxonomic and functional community structure, indicating how likely each explanatory variable was to be included in the best-performing model of all models in the set. DIST.POOL was the variable with the highest number of important responses (relative importance > 0.5). All measures of taxonomic community structure and all but one mean trait value were best explained when DIST.POOL, i.e. the distance to historically old grassland patches providing propagules of the characteristic species pool of pre-transformed landscapes, was included in the model. The second component of the soil PCA, reflecting mainly variation in soil texture (Table 2), was also important in many cases, although not for total and habitat specialist species richness. Soil heterogeneity was important for predictions of taxonomic but not functional community structure. The remaining soil and landscape variables were not likely to be included in the best performing model in most cases.

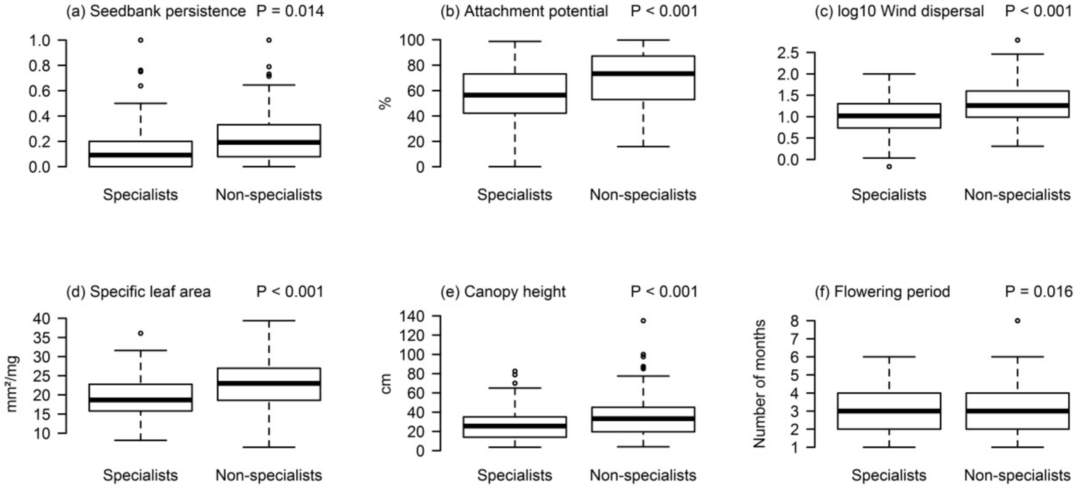


Figure 12 | Differences in six functional traits among calcareous grassland specialist (n = 106) and non-specialist (n = 100) plant species. *P*-values are from permutation t-tests using 9999 permutations.

Model-averaged effect sizes: Taxonomic community structure

The distance to source species pools (DIST.POOL) had by far the strongest effect on species richness, habitat specialist richness, and the average commonness of the species encountered (Table 3). It was also the only variable for which 95% confidence intervals did not overlap with zero in all three indices (Figure 13a-c), indicating significant effects.

Table 3 | Results of the multi-model inference of the effects of species pool influences and environmental and spatial factors on the diversity and functional community structure of secondary grasslands in south Germany. The first column shows the average conditional (c) R^2_{GLMM} of all models in the confidence set for the respective response variable and standard their errors (SE). No SE are given when only one model was included in the confidence set. A '-' in this column indicates that only the empty model was included in the confidence set. The second column gives the absolute ranges of the response variables to help the reader judge the magnitude of the model-averaged effect sizes of the explanatory variables which are reported in the remaining columns along with relative importance values (in brackets). Variables with a relative importance >0.5 are in bold. A '-' indicates that a variable was included in any model of the confidence set. Connectivity = habitat amount in a radius of 300 m (square-root transformed), PAR = perimeter-area ratio (square-root transformed), DIST.POOL = distance to historically old grassland at the time of origin of the focal secondary grassland (log$_{10}$ transformed). Seedbank persistence and canopy height were square root-transformed, and wind dispersal potential flowering period were ln-transformed prior to the calculation of community mean trait values and Functional Dispersion.

	$R^2_{\mathrm{GLMM}(c)}$ Mean ± SE	Response range |min-max|	PC1	PC2	Soil heterogeneity	Connectivity	PAR	Patch age	DIST.POOL
Species diversity									
Species richness	0.67 ± 0.00	44	0.47 (0.34)	-0.88 (0.43)	**4.69 (1.00)**	-0.08 (0.16)	0.29 (0.25)	**2.80 (0.93)**	**-6.65 (1.00)**
Specialist richness	0.77 ± 0.00	45	-0.003 (0.14)	1.05 (0.47)	**3.74 (1.00)**	-0.05 (0.23)	**4.20 (1.00)**	0.86 (0.45)	**-6.48 (1.00)**
Commonness	0.77	781.67	**-2.47 (1.00)**	**-60.33 (1.00)**	**-78 (1.00)**	**32.13 (1.00)**	**-94.76 (1.00)**	**-29.26 (1.00)**	**105.82 (1.00)**
Community mean value									
Seedbank persistence	0.46	0.14	-	-	-	-	-	-	**0.03 (1.00)**
Attachment potential	0.54 ± 0.03	9.97	0.42 (0.44)	**-1.00 (0.87)**	-	**1.09 (0.86)**	-0.19 (0.14)	-	**0.94 (0.73)**
Wind dispersal potential	0.42 ± 0.17	0.64	-	**-0.07 (0.68)**	-	-	-0.03 (0.41)	-	0.01 (0.16)
Specific leaf area	0.53 ± 0.06	4.39	-	-0.15 (0.31)	-	-	-0.07 (0.19)	-	**0.74 (1.00)**
Plant height	0.83 ± 0.01	1.29	-	**-0.21 (1.00)**	-	-	-0.04 (0.28)	-	**0.11 (0.72)**
Flowering period	0.32 ± 0.32	0.21	-	**-0.03 (0.62)**	-	-	-	-	-
Functional Dispersion									
Seedbank persistence	0.15 ± 0.15	0.27	-	-	-	-	-	-	0.01 (0.36)
Attachment potential	-	0.26	-	-	-	-	-	-	-
Wind dispersal potential	-	0.25	-	-	-	-	-	-	-
Specific leaf area	-	0.28	-	-	-	-	-	-	-
Plant height	-	0.32	-	-	-	-	-	-	-
Flowering period	-	0.23	-	-	-	-	-	-	-
Important responses	-	-	1	5	3	2	2	2	6

Species richness of secondary grasslands strongly decreased with increasing distance to source species pools but was high in grasslands with high soil spatial heterogeneity (Figure 13a). The number of habitat specialists reflected this trend but this index was also positively affected by high perimeter-area ratios (Figure 13b). Species encountered in secondary grasslands far away from source species pools (high DIST.POOL) and with low perimeter-area ratios were more common in the contemporary landscape (Figure 13c). Soil factors (PC1, PC2), connectivity, and patch age had only weak and non-significant effects on taxonomic community structure.

Model-averaged effect sizes: Functional community structure

The average seedbank persistence of species found in secondary grasslands significantly increased with DIST.POOL, whereas soil characteristics, spatial factors and patch age had no effect on this trait (Figure 13d). The average diaspore attachment potential, a measure for epizoochorous dispersal ability, tended to vary with soil properties, spatial factors and DIST.POOL, though their effects were marginally non-significant (Figure 13e). Likewise, wind dispersal ability was negatively affected by PC2 and perimeter-area ratio, but slightly increased with DIST.POOL (Figure 13f). But again, these effects were non-significant at the 95% confidence level.

Community mean specific leaf area, a trait related to resource economics, significantly increased with distance to source species pools (DIST.POOL), but was not or only little affected by soil and spatial factors, of which only PC2 and perimeter-area ratio had small negative averaged effect sizes (Figure 13g). The same three explanatory variables were also the only ones related to variation in the average canopy height of plant species among secondary grasslands (Figure 13h). Mean values of this trait decreased on permeable soils (PC2; see Table 2). Secondary grasslands far away from old-grassland pools (DIST.POOL) tended to have taller species, though this effect was not significant. Finally, the same soil characteristics that selected for small-statured plant species also favoured species with shorter flowering periods (Figure 13i). Notably, this was the only community mean trait where DIST.POOL was not included in the confidence set models (Table 3). DIST.POOL was the only explanatory variable for which an effect on FDis was observed (Table 3). This slightly positive effect on

FDis was found only for seedbank persistence, however, and was non-significant (not shown).

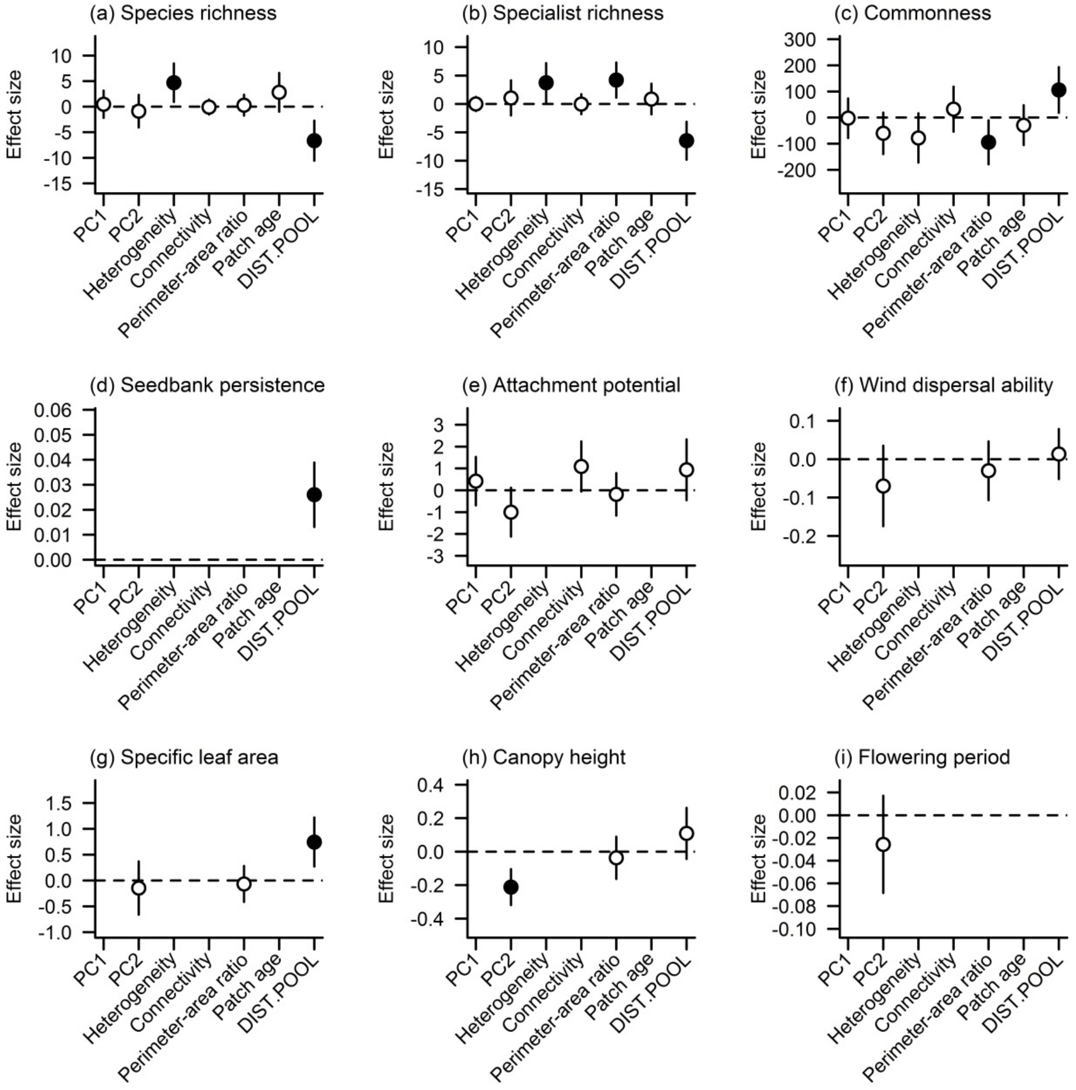


Figure 13 | Model-averaged effect sizes of explanatory variables on (a)–(c) taxonomic community structure and (d)–(i) community mean trait values in secondary grasslands in south Germany. Points are model-averaged effect sizes across all models within 2 AIC$_C$ of the most parsimonious model (‘confidence set’) and bars are their 95% confidence intervals. The further away a point is from zero, the stronger the effect of the variable. Black points highlight variables where confidence intervals do not include zero. Confidence intervals overlapping zero mainly result from some models in the confidence set not including this variable. The absence of a symbol for a variable indicates that this variable was included in any of the models in the confidence set. DIST.POOL, distance to historically old grassland at the time of origin of the secondary grassland patch.

3.4 DISCUSSION

Our study provides strong empirical support for species pools being the principal driver of taxonomic and functional community structure of secondary habitats. Most aspects of species diversity and functional composition were found to be driven by the distance to historically old patches inhabiting a rich and functionally distinct flora, and species pool influences were even more important than long gradients of soil factors, spatial characteristics of contemporary landscapes, and patch age.

Species pools, dispersal limitation, and species diversity in secondary habitats

Species richness of secondary semi-natural grasslands was mainly driven by the distance to historically old grasslands at the time of origin (DIST.POOL). When old grasslands were close, secondary patches had substantially higher species numbers (Figure 13a). Well-preserved old patches in the local landscape are often reported to have positive effects on the diversity of regenerating patches (Cousins & Lindborg 2008; Prach et al. 2015; Winsa et al. 2015), virtually serving as 'sources for diversification' (Cousins & Lindborg 2008) in modern landscapes. This view is dramatically supported if one considers that the observed decline of total richness with increasing DIST.POOL is primarily driven by a loss of habitat specialists, as can be seen from the similar average effect sizes (i.e. regression slopes) in Table 3. Obviously, the observed species diversity patterns reflect a severe dispersal limitation of calcareous grassland habitat specialists (Verkaar et al. 1983; Hutchings & Booth 1996; Diacon-Bolli et al. 2013) in combination with a reduced capability of new, intensively managed ecosystems dominating contemporary landscapes to provide colonists for vacant niches due to their low species numbers (Allan et al. 2015; Newbold et al. 2015). Because calcareous grassland specialists were less common than non-specialists in the regional flora (Figure S9), the average commonness of species found in secondary was negatively related to DIST.POOL (Figure 5c).

Soil heterogeneity but not resource availability influences species diversity

Soil spatial heterogeneity also had significant positive effects on species richness and the number of habitat specialists. Positive heterogeneity-richness relationships are often reported at large scales of observation such as in this study (Tamme et al. 2010;

Stein et al. 2014), and are usually attributed to higher numbers of available niches that can promote co-existence of higher species numbers when soil spatial heterogeneity is high (Tilman 1982; Adler et al. 2013). The effect of soil spatial heterogeneity was so important that it increased species numbers even on sites with high DIST.POOL, indicating that species-pool sizes and soil heterogeneity represent orthogonal determinants of species richness in secondary semi-natural grasslands. Higher soil heterogeneity provided niche opportunities for a wider range of species from different habitat types which then partly compensated for the absence of habitat specialists, as is reflected by only non-significant negative effects of heterogeneity on average commonness, while the numbers of rare specialist species showed significant positive responses (Figure 13b-c).

Although the heterogeneity-richness patterns indicate that environmental sorting occurred within patches, soil resource availability had no effect on variation in total and specialist richness among secondary grasslands (Figure 13a-b). This is remarkable, given that the soil conditions of the study grasslands represented a considerable range of environmental soil resources that are significant drivers of plant diversity in grasslands (Gough et al. 2000; Crawley et al. 2005; Harpole & Tilman 2007; Borer et al. 2014; Ceulemans et al. 2014). It is likely that dispersal limitation of the numerous habitat specialists adapted to low resource availability might explain low species numbers in suitable resource-poor secondary grasslands (Butaye et al. 2002; Ozinga et al. 2005). On the resource-rich end of the resource gradient, mass effects (Shmida & Wilson 1985) led to comparatively high specialist and thus total richness when secondary grasslands were close to the large species pools of old grasslands at the time they originated. The opposing phenomena led to a zero net effect of soil nutrient concentrations Support for the view that high immigration rates from source pools during early stages of succession can lead to species-rich communities despite high nutrient concentrations comes from restoration experiments in our study area: Kiehl and Pfadenhauer (2007) compared spontaneous succession on nutrient-rich ex-arable soils with succession in plots on the same soils but with hay transfer from a well-preserved species-rich calcareous grassland. They found that plots with hay transfer had much higher total and specialist species richness throughout ten years of monitoring.

Effects of landscape spatial configurations on species diversity

Patch connectivity, measured as the amount of secondary and historically old semi-natural grassland in the local landscape of each patch, had no effect on community structure (Figure 13). This likely reflects that secondary habitats considered as potential propagule sources might themselves have very variable species richness and composition and suggests that studies investigating the effects of current landscape connectivity on local diversity and functional composition should explicitly account for the historical landscape context and species pools of patches considered as propagule sources (e.g. Butaye et al. 2002; Tremlová & Münzbergová 2007; Knappová et al. 2012).

High perimeter-area ratios significantly increased specialist but not total richness, thereby also decreasing the average commonness of species in secondary grasslands (Figure 13a-c). On explanation for this effect is that, as immigration progresses from patch edges to the interiors over time, and because the proportion of edge zones is smaller in large patches, immigrating habitat specialist were less likely to be detected by our sampling strategy in large patches. Alternatively, edge zones of secondary semi-natural grasslands were shown to have greater numbers of specialists than interiors because they also contain rare habitat specialists with very specific niche requirements (Knappová & Münzbergová 2015) which, for instance, are realized in grasslands with a greater structural diversity at their borders.

Contingencies in the functional trait composition of secondary habitats

The functional trait composition of secondary habitats reflected in large parts the magnitude of influences of old-grassland species pools. For example, the high average seedbank persistence of species found in patches where old-grassland species pools were absent from the local landscape (Figure 13d) reflect that most calcareous grassland specialists have only transient or short-term persistent seedbanks (Figure 12) (Bakker et al. 1996; Jacquemyn et al. 2011). This effect was larger than environmental influences which could have also been expected, considering that resource availability acts as a filter on seed size via a tolerance-fecundity trade-off (Jakobsson & Eriksson 2000; Muller-Landau 2010), and that seed size is negatively related to seedbank persistence (Bekker et al. 1998). Because higher disturbance frequencies in such systems select for species with persistent seeds (Fenner &

Thompson 2005), additional amplification of the positive relationship of average seedbank persistence with DIST.POOL might result from the partial filling of vacant niches in the absence of habitat specialists by species from more intensively managed systems dominating modern landscapes.

Likewise, specific leaf area, a trait related to resource economics (Westoby et al. 2002), was not affected by pronounced soil resource gradients, but significantly increased with increasing distance to old-grassland species pools (Table 3; Figure 13), which are characterized by species with low SLA values (Figure 12d) as an adaptation to the stressful environmental conditions in calcareous grasslands. Positive relationships of average SLA with soil fertility were found in this system in the absence of dispersal limitation (Bernard-Verdier et al. 2012), but our findings show that mass effects radiating from species pools with distinct functional characteristics rather than soil factors drive variation in this important trait among local communities.

However, we also found a role of environmental sorting on plant community functional structure. Although species numbers did not vary along soil resource gradients (Figure 13a-b), soil texture (PC2) imposed a strong environmental filter on canopy height independent of species pool associations (Figure 13g). Similarly, Sonnier et al. (2010), studying traits in successional plant communities, also found that only plant height was related to stress gradients and concluded that community assembly was driven primarily by propagule arrival order and not trait-based environmental sorting, a conclusion that receives support from our own results. Nonetheless, although this effect was marginally non-significant, considering species pool influences was important for accurate predictions of average canopy height in secondary grasslands (Table 3). When old-grassland species pools with their small-statured plants (Figure 12e) were close, secondary grasslands also tended to have higher proportions of small-statured plants (Figure 13h), again indicating the operation of mass effects (Shmida & Wilson 1985; Leibold et al. 2004).

Because plant height influences the likelihood of being dispersed by wind (Heydel et al. 2014) and being attached to animal fur (Albert et al. 2015), inclusion of PC2 as a predictor variable improved models of community average attachment potential and wind dispersal ability, although these effects were indirect and non-significant (Table 3; Figure 13e-f). Likewise, the low diaspore attachment potential of specialist species (Figure 12b) together with their lower canopy heights made the distance to old-grassland pools an important but non-significant predictor of community average attachment potential (Table 3; Figure 13e). Connectivity was also an important but marginally non-significant predictor of the average attachment potential (Table 3; Figure 13e), probably reflecting that isolated habitats are less likely to be included in foraging habitat ranges of seed dispersing ungulates and small mammals.

Because of the higher resource requirements associated with longer flowering periods (Nord & Lynch 2009), soil texture (PC2) also influenced the average duration flowering periods, although, again, this effect was non-significant at the 95% confidence level (Figure 13i).

3.5 CONCLUSION

Taken together, our results show that the magnitude of species pool influences determines most aspects of plant diversity and composition of plant traits related to resource use and dispersal in secondary grasslands. These influences operate via mass effects that gradually decrease with increasing distance from the source pools and are often stronger than environmental factors and landscape spatial configuration. However, while soil resource availability has no effect on species richness patterns and leaf economics, soil texture represents an orthogonal axis that discriminates species according to their canopy height independently of species pool association. These findings indicate that mass effects and environmental sorting are interacting assembly mechanisms that jointly determine plant community structure of secondary grasslands in human-transformed landscapes.

The results also emphasize that models of species or plant community distributions should not only account for dispersal limitation (Ozinga et al. 2005) but also for mass effects and historical contingencies that confound trait-environment relationships. Finally, our findings also have important implications for habitat restoration because they show that if the key constraint, dispersal limitation of desired habitat specialist species, is overcome during early stages of succession, for example by active species transfer, many habitat specialists can successfully establish despite non-optimal environmental conditions, although some soil factors (soil texture in this case) may impose a filter that operates within the set of successful colonists and thus set certain constraints to species' persistence.

SUPPORTING INFORMATION

Table S3 | Variation in taxonomic and functional community structure of secondary grasslands explained by the distance to historically old grasslands in the contemporary landscape and at the respective time of origin of the secondary grasslands (Historical). Univariate linear mixed effects models with a random intercept for study area and either contemporary or historical distance as fixed effects were used to model variation in the response variables (rows). Reported are conditional (c) R^2_{GLMM} representing the variation explained by the full mixed-effects models.

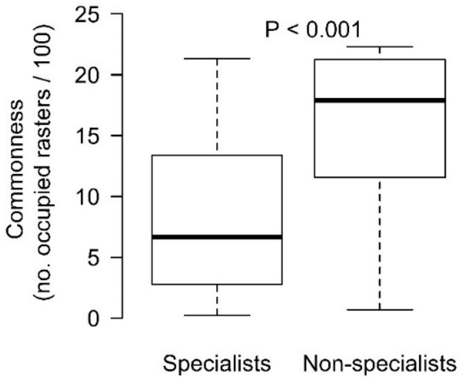
	Contemporary	**Historical**
Species diversity		
Species richness	0.30	0.62
Specialist richness	0.31	0.67
Commonness	0.29	0.60
Community mean value		
Seedbank persistence	0.12	0.46
Attachment potential	0.22	0.34
Wind dispersal ability	0.04	0.29
Specific leaf area	0.19	0.44
Canopy height	0.23	0.48
Flowering period	0.00	0.16
Functional Dispersion		
Seedbank persistence	0.13	0.30
Attachment potential	0.09	0.12
Wind dispersal ability	0.06	0.00
Specific leaf area	0.03	0.09
Canopy height	0.08	0.05
Flowering period	0.03	0.12

Table S4 | Plant functional traits used to impute missing trait values in six traits selected to investigate community assembly processes in secondary grasslands in southern Germany.

Trait	**Description**	**Data source**
Whole plant traits		
Life form	Categorical trait based on the position of buds relative to the soil surface	1, 2
Life span	Coded as a semi-metric variable where 1 = annuals, 2 = strict monocarpic biennials and poly-annuals, 4 = poly-annuals < 5 years, 25 = poly-annuals 5-50 years, 75 = poly-annuals > 50 years	3, 4
Type of reproduction	Ordinal variable with five levels indicating the degree to which a species relies on sexual (1) vs. vegetative (0) reproduction	4
Lateral spread	Ordinal variable where 1 = 0 cm, 2 = <0.01 cm, 3 = 0.01–0.25 cm, 4 = >0.25 cm	5
Canopy height	Distance between the highest photosynthetic tissue and the base of the plant [cm]	3, 6, 7
Releasing height	Distance between the highest inflorescence and the base of the plant [cm]	2, 3, 6
Root depth	Ordinal variable where 1 = <25 cm, 1.5 = at most 20% of the root depth in class 2, 2 = 25–50 cm, 2.5 = at most 20% of the root depth in class 3, 3 = 50–100 cm, 3.5 = at most 10% of the root depth in class 4, 4 = 100–200 cm, 4.5 = at most 5% of the root depth in class 5, 5 = > 200 cm	7, 8
Phenological traits		
Onset of flowering	Month in which flowering begins (ordinal)	4
End of flowering	Month in which flowering ends (ordinal)	4
Duration of flowering	Number of month with flowers	4
Seed/Diaspore traits		
Diaspore mass	Weight of the diaspore [mg]	3, 9, 10, *
Terminal velocity	Maximum speed [m s^{-1}] of a falling diaspore in still air	2, 9
Seed bank persistence	Ratio of short-term and long-term persistent records to total number of records per species	3, 11
Seed number	Total seed production per ramet of a species	3
Endozoochory	Binary trait indicating whether endozoochory occurs	2
Appendage morphology	Categorical trait describing the presence and form of diaspore appendages. Required for the calculation of diaspore attachment potential to sheep wool	9
Leaf traits		
Leaf size	One-sided projected surface area of an individual leaf or lamina [mm^2]	3, 12
Specific leaf area	Ratio of one-sided fresh leaf area to leaf dry mass [mm^2 mg^{-1}]	3, 12, 13, 14
Leaf dry matter content	Ratio of dry leaf mass to fresh leaf mass [mg g^{-1}]	3, 12, 13, 14

1 = www.floraweb.de, 2 = Jäger (2011), 3 = Kleyer et al. (2008), 4 = Klotz et al. (2002), 5 = Klimešová and De Bello (2009), 6 = Conert (2000), 7 = Jäger (2007), 8 = Landolt (2010), 9 = Hintze et al. (2013), 10 = Kreutz (1995), 11 = Bekker et al. (1998), 12 = Cerabolini et al. (2010), 13 = Pipenbaher et al. (2013), 14 = Pierce et al. (2007), * = Orchid and cryptogam species for which no data was available (n = 10) from the data sources were assigned a diaspore mass value 0.001 mg.

Figure S9 | Differences in commonness in the regional flora among calcareous grassland specialist (n = 106) and non-specialist (n = 100) plant species encountered in 24 secondary grasslands. *P*-values are from permutation t-tests using 9999 permutations.



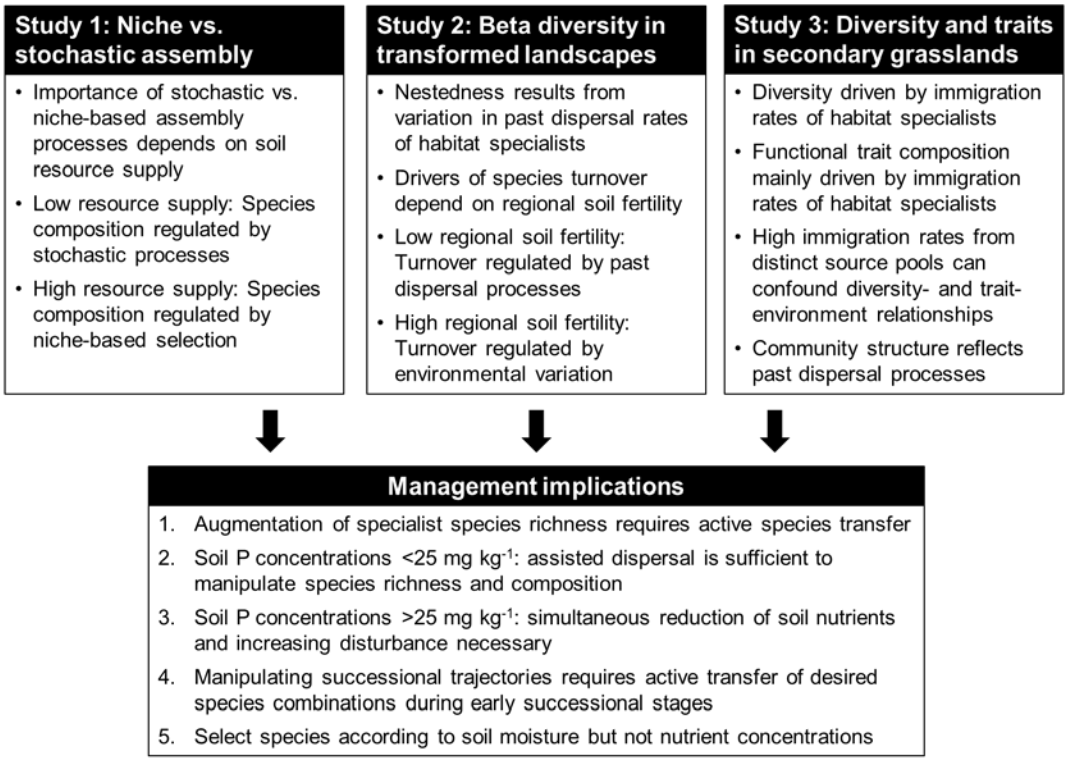
Chapter 5

Synopsis

The aims of this dissertation were to improve the scientific understanding of the drivers of plant diversity in human-transformed landscapes and to contribute to conceptual developments that consider how environmental features might regulate the effectiveness of dispersal processes in generating spatial variation in community structure. For this purpose, I combined experimental and observational approaches with innovative analytical methods in three complementary studies. This chapter synthesizes their main findings, points out directions for future research, and discusses implications for conservation and habitat restoration (Figure 14).

5.1 DISPERSAL, ENVIRONMENTAL FACTORS, AND THE REGULATION OF DIVERSITY PATTERNS

The first study of this thesis (Chapter 2) used an experimental approach to examine how soil resource availability drives the importance of stochastic events including dispersal, and niche-based assembly processes in grassland metacommunities. I found that the importance of stochastic events for variation in community structure was high at low resource levels, but decreased strongly with increasing resource supply towards a niche-based assembly that selected for similar combinations of few competitive species. The finding that the significance of stochasticity changes systematically along soil resource gradients provides a context into which observations from individual studies could be aligned that investigated the roles of environmental conditions vs. dispersal as drivers of diversity patterns in real metacommunities. Organizing in this way existing knowledge gained in hundreds of individual studies (Cottenie 2005; Soininen 2015) provides an opportunity to achieve a better and predictive understanding of when dispersal matters for the development of community structure.



Study 1: Niche vs. stochastic assembly

- Importance of stochastic vs. niche-based assembly processes depends on soil resource supply
- Low resource supply: Species composition regulated by stochastic processes
- High resource supply: Species composition regulated by niche-based selection

Study 2: Beta diversity in transformed landscapes

- Nestedness results from variation in past dispersal rates of habitat specialists
- Drivers of species turnover depend on regional soil fertility
- Low regional soil fertility: Turnover regulated by past dispersal processes
- High regional soil fertility: Turnover regulated by environmental variation

Study 3: Diversity and traits in secondary grasslands

- Diversity driven by immigration rates of habitat specialists
- Functional trait composition mainly driven by immigration rates of habitat specialists
- High immigration rates from distinct source pools can confound diversity- and trait-environment relationships
- Community structure reflects past dispersal processes

Management implications

1. Augmentation of specialist species richness requires active species transfer
2. Soil P concentrations <25 mg kg^{-1}: assisted dispersal is sufficient to manipulate species richness and composition
3. Soil P concentrations >25 mg kg^{-1}: simultaneous reduction of soil nutrients and increasing disturbance necessary
4. Manipulating successional trajectories requires active transfer of desired species combinations during early successional stages
5. Select species according to soil moisture but not nutrient concentrations

Figure 14 | Main findings of the dissertation and management implications.

To explore whether the experimental findings were consistent with assembly processes in real landscapes, the second study (Chapter 3) compared drivers of variation in community structure, quantified using a measure of beta diversity, among grasslands in two human-transformed grassland landscapes with contrasting regional soil fertility. Indeed, I could show that, in the fertile region, only a small fraction of beta diversity resulted from dispersal limitation, whereas compositional variation was largely driven by environmental sorting. By contrast, beta diversity in the study area with low regional soil fertility was driven by dispersal processes alone, confirming findings from Chapter 2. Together, these results suggest that soil resource availability is a critical environmental feature that determines the degree to which dispersal and other stochastic events can regulate diversity patterns in metacommunities.

Still, the underlying mechanisms that cause the transition between a niche-driven and a neutral assembly along resource gradients are not yet understood and clearly require further research. An important first step in this direction has recently been made by Fisher and Mehta (2014) who, based on mathematical modelling, suggested that system-specific thresholds of environmental stress exist, beyond which population carrying capacities are reduced to such low levels, that the importance of demographic stochasticity and/or fluctuating environmental conditions for population and community dynamics outweigh niche-based competitive interactions, leading to neutral community assembly. Below this threshold of environmental stress, the deviation from neutrality is predicted to rise quickly (Fisher & Mehta 2014), similar to my experimental findings reported in Chapter 2. Interestingly, the study region of Chapter 3 in which community assembly was driven by environmental sorting (Lech River Valley) had median soil P concentrations of ca. 25 mg kg^{-1}, what coincides with a threshold of soil P above which species richness in calcareous grasslands across Europe declines substantially (Ceulemans et al. 2014). The results from Chapter 3 showed further that this species loss was driven by a replacement of a larger number of species by few others, resulting in metacommunity dynamics being driven by environmental sorting rather than dispersal processes. These findings lend support to the suggestion of system-specific thresholds discriminating between neutral stochastic and niche-based assembly processes (Fisher & Mehta 2014).

Besides these more general findings on the varying importance of stochasticity across soil resource gradients, Chapter 3 also offered specific novel insights into the drivers of plant diversity patterns in human-transformed landscapes. Using a quantitative decomposition of beta diversity into its turnover and nestedness components, and a separate partitioning of variation in these components, I could establish a more nuanced view on how local factors, as well as past and present dispersal processes interacted to generate spatial variation in species composition. In particular, I found that sites with low historical connectivity to primary grasslands were – in parts – nested subsets of sites with higher historical connectivity, and this was independent of regional soil fertility. This nestedness pattern probably resulted from the pool of habitat specialists in primary grasslands being so large that dispersal limitation of many of them cannot be compensated by the low numbers of immigrating generalist species growing in adjacent habitats in the contemporary landscape. The factors that produced species turnover among grasslands, however, differed between landscapes with contrasting regional soil fertility. As mentioned above, in the landscape with low soil fertility, turnover was driven by dispersal limitation of habitat specialists and immigration of generalists, reflecting (neutral) dispersal assembly. By contrast, in the landscape with higher soil fertility (higher soil P concentrations), turnover resulted from niche-based environmental sorting.

In summary, these findings show that both nestedness and turnover contribute to variation in species composition among habitat patches in human-transformed landscapes. While nestedness patterns appear to be generally driven by the dispersal limitation of many species from large habitat-specific species pools, the mechanisms causing turnover are dependent on regional soil fertility and can be either dispersal limitation or environmental sorting. To test the generality of these findings, further studies are required that investigate the respective drivers of nestedness and turnover in contrasting biogeographic regions and ecosystems. The results presented in Chapter 3 are based on a standardised and detailed investigations of species composition, local environmental conditions, and past and present landscape spatial configurations in two landscapes, and are thus a basic reference for future studies that will help develop a more synthetic view on drivers of compositional variation among habitat patches in human-transformed landscapes.

These findings also have immediate implications for landscape-scale conservation management of fragmented grasslands. The observation that some grasslands were in parts nested subsets of others, and that this resulted from dispersal limitation of habitat specialist species only, suggests that their species richness is not yet saturated and can be augmented relatively easily once the dispersal limitation of specialist species is overcome. However, the facts that diversity patterns reflected past but not presented landscape connectivity, and that important historical dispersal vectors such as transhumant sheep flocks are no longer effective, emphasize the necessity for assisting the immigration of absent species. This can be achieved using seed addition from locally adapted sources (Kiehl et al. 2010) or through the re-introduction of rotational sheep herding that involves well preserved grasslands as propagule sources (Rico et al. 2014). When the management goal is to improve the species composition of some grasslands, these measures also seem to be effective management options in landscapes with low regional soil fertility, because dispersal processes strongly influence the species turnover of grasslands under these conditions. By contrast, when regional soil fertility is higher, so that species turnover is driven by environmental factors, it is less clear whether assisting immigration is sufficient or whether additional measures are required to enable long-term population persistence. For instance, it might be necessary to reduce soil nutrient concentrations and create colonisation gaps through more intensive management simultaneously to continuous assisted immigration. Alternatively, assisting immigration might be sufficient if re-activated colonisation-competition trade-offs can allow stable co-existence in nutrient-rich sites. Other approaches than analyses of beta diversity would have been necessary to tease apart this possibility, and I propose this as a relevant new research question for fundamental and applied plant ecology (see also Leibold 2011).

5.2 COMMUNITY ASSEMBLY IN SECONDARY GRASSLANDS

Although beta diversity can be used to infer the importance of dispersal and local environmental factors for spatial variation in species composition in a region, still another limitation of this approach is that one cannot disentangle which aspects of community structure are actually regulated by these two drivers. More specifically, one cannot predict how many and which species (in terms of functional characteristics or certain species groups) can be found locally. To overcome this limitation, the third study (Chapter 4) used a mixed effects modelling approach to dissect local and regional drivers of species richness and functional trait composition in secondary calcareous grasslands. I found that the degree of dispersal limitation of habitat specialist species during early stages of succession, but not pronounced soil nutrient gradients, current landscape configurations, or patch age, determined most aspects of plant diversity and the composition of plant traits related to resource use and dispersal of secondary grasslands. This pattern resulted from the rich and functionally distinct species pools of primary grasslands on one hand, and the limited availability of generalist species in adjacent habitats of the transformed landscapes on the other hand, whose immigration could had counteracted the observed patterns. Besides this overarching role of past dispersal processes, I also found an important role of soil texture, which represented an orthogonal axis of community assembly that discriminated species according to their canopy height, and this acted on specialist and generalist species equally. These results emphasize that past dispersal processes, species pool characteristics and local environmental conditions act in concert to determine different aspects of plant community structure in secondary grasslands.

In the face of profound and still ongoing destruction of primary habitats, calls have been made that secondary and other man-made habitat patches should be incorporated in landscape-scale conservation management of ecosystems (Hobbs et al. 2014; Mendenhall et al. 2014; Corlett 2015). A critical component to maximize the conservation potential of secondary habitats is a thorough scientific understanding of the factors that control their diversity and composition (Chazdon et al. 2009). My findings demonstrate that dispersal is the key limiting factor for secondary habitats to be of high conservation value, and that immigration of many habitat specialists can even outweigh negative influences of high soil nutrient concentrations. The implication for habitat restoration is that community trajectories can be successfully manipulated using active species transfer during early stages of succession even when soil nutrient conditions do not seem suitable. In the case of grasslands, effective species-transfer measures include hay transfer and, again, seeding of desired species combinations, or the inclusion of secondary habitat patches in grazing networks that involve primary grasslands as source species pools (Kiehl et al. 2010; Rico et al. 2014).

The view that such measures are effective even when soil nutrients are high is supported by monitoring studies which revealed that species-rich grasslands can be successfully established even on formerly intensively used arable soils when hay from well-preserved primary grasslands is transferred in initial successional stages (Kiehl & Pfadenhauer 2007). However, I also found that soil texture imposed a (natural) environmental filter that selected for small-statured species on drier sites, independent of soil nutrient concentration. This suggests that there are still certain environmental constraints that need to be considered to achieve successful and efficient restoration efforts.

In summary, based on the results of Chapter 4, three tangible recommendations for efficient restoration efforts in secondary calcareous grasslands can be formulated. First, active species transfer at very early stages of succession is a prerequisite of successful establishment of habitat specialist species. Second, soil nutrient concentrations are not a key limiting factor. Instead, the selection of donor sites should be based on knowledge of soil moisture conditions in the target site to achieve optimal results. Third, direct seeding of desired species combinations becomes an increasingly popular restoration measure as commercially produced seeds from regional sources become available. A trait-based design of seed mixtures for restoration should consider soil moisture preferences of target species, whereas resource-economic traits are less important.

5.3 CONCLUDING REMARKS

I started this thesis with the question "*What determines species diversity?"* Three and a half years and 89 pages later I conclude that species diversity is determined by an entanglement of species' characteristics, environmental factors, dispersal processes, and historical contingencies, but that this entanglement can be resolved using comprehensive datasets, rigorous experimentation and advanced analytical methods. Together, the results presented in this thesis shall contribute to a better scientific understanding and improved management of ecological dynamics in human-transformed landscapes, and ultimately to sustaining biodiversity in the Anthropocene.

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Danksagung

Bei der Arbeit an dieser Dissertation haben mich zahlreiche Personen direkt oder indirekt unterstützt, denen ich an dieser Stelle herzlich danken möchte.

Natürlich möchte ich mich zuerst bei meinem Doktorvater Johannes Kollmann bedanken. Lieber Johannes, durch Deine großartige Unterstützung hast Du es mir stets ermöglicht, meine eigenen wissenschaftlichen Interessen zu verfolgen. Im Zweifel konnte ich mich jederzeit auf Deinen Rat verlassen – er hat sich im Nachhinein immer als richtig erwiesen. Ich habe viel von Dir gelernt und bin sehr froh, mich für eine Doktorarbeit unter Deiner Betreuung entschieden zu haben. Danke!

Als Co-Betreuerin hat mir Vicky Temperton geholfen, meine Arbeiten kritisch zu hinterfragen und hat so zum Gelingen dieser Dissertation beigetragen. Außerdem hat sie noch vor ihrem Umzug nach Lüneburg möglich gemacht, dass dort hunderte meiner Bodenproben umsonst auf Stickstoff untersucht werden. Danke Vicky!

Ohne die immense Hilfe von Hans Krimmer bei der Planung und Einrichtung meines Experiments, sowie seine ständige Bereitschaft, mir mit meinen zwei linken Händen zu helfen, wäre mein Experiment niemals so gut gelaufen. Lieber Hans, vielen Dank!

Den Kollegen am Lehrstuhl für Renaturierungsökologie danke ich für die angenehme Arbeitsatmosphäre, insbesondere meinen PhD-KollegInnen Sara Altenfelder, Naret Guerrero, Christiane Koch, Marion Lang, Anna Pahl, Wolf Saul, Maxi Schümann, Katharina Strobl, Florencia Yanelli und Emer Walker. Meinem Augschburger Spezi Thomas Wagner, danke ich für die heiter-hitzigen Diskussionen über Gott und die Welt während unserer Pendlerei sowie für die Hilfe bei den Bodenanalysen.

Pauline Böttcher-Graf, Felicia Fischer, Olivia Froehlich, Morgan McCarthy, Gustavo Paterno und Philipp Stojakowits haben sich mit mir beim Sammeln und Sieben der Bodenproben die Hände wund gerieben. Für die riesige Hilfe bei dieser Strafarbeit danke ich euch sehr!

Meine liebe Tini, Dir danke ich für die wunderbare Zeit, für Deine Geduld und dass Du immer für mich da warst. Danke!

Für diese Doktorarbeit wurde ich dankenswerter Weise durch das Promotionsstipendienprogramm der Deutschen Bundesstiftung Umwelt gefördert.

Intended publications and author contributions

The studies presented in Chapters 2–4 will be submitted as individual manuscripts to scientific journals. Intended co-authors and their contributions are outlined below.

Chapter 2

Conradi T, Temperton VM & Kollmann J. Resource availability determines the importance of niche-based vs. stochastic community assembly in grasslands.

Author contributions: TC conceived the study, collected and analysed the data, and wrote the manuscript. VMT and JK helped refine the research question and design, and contributed to writing.

Chapter 3

Conradi T, Temperton VM & Kollmann J. Disentangling the drivers of beta diversity in human-transformed landscapes.

Author contributions: TC conceived the study, collected and analysed the data, and wrote the manuscript. VMT and JK helped refine the research question and design, and contributed to writing.

Chapter 4

Conradi T & Kollmann J. Species pools, mass effects and environmental sorting interact to determine plant diversity and functional trait composition in secondary grasslands

Author contributions: TC conceived the study, collected and analysed the data, and wrote the manuscript. JK helped refine the research question and design, and contributed to writing.

Appendix

A1 – Rules for trait data extraction

For the functional trait analyses conducted in Chapters 2 and 4, values of 19 plant traits (Table S4) of 235 species were compiled. Trait values were extracted from different data sources, including databases and literature. For some traits, different ways to extract data from such sources exist that might lead to slightly different results. Therefore, I describe here in detail which rules for data usage were applied in theses.

General rules

When no data entries for encountered subspecies were available, values of the corresponding species level were used (e.g. from *Thymus praecox* for ssp. *praecox* and ssp. *polytrichus* or from *Euphrasia officinalis* for ssp. *picta* and ssp. *rostkoviana*).

When there was no data entry for a species name, values were taken from synonymous species names or respective species aggregates (e.g. from *Aquilegia vulgaris* for *A. atrata*, from *Brachypodium pinnatum* for *B. rupestre*, from *Centaurea rhenana* for *C. stoebe*, missing values for *Festuca guestfalica* from *F. ovina*, from *Molinia caerulea* for *Molinia arundinacea*, from *Odontites vernus* for *Odontites vulgaris*, from *Potentilla cinerea* for *P. incana*, from *Taraxacum* sect. *Ruderalia* for *Taraxacum* spec., or from *Valeriana officinalis* for *Valeriana wallrothii;* leaf dry matter content (LDMC) and leaf size values for *Galium album* ssp. *album* were taken from ssp. *pycnotrichum*).

In few cases, no information on important traits was available for phylogenetically isolated taxa and this sometimes led to unreasonable statistically inferred trait values. In these situations, trait data of morphologically and ecologically similar species of the same genus that were not in encountered in the grassland survey was used. These were specific leaf area (SLA) and leaf LDMC of *Daphne striata* for *D. cneorum*, seed number of *Thesium bavarum* for *T. linophyllon* and *T. rostratum,* and seed number of *Melampyrum arvense* for *M. cristatum*.

Values measured outside Europe or in lab, greenhouse, garden or field experiments were not included except if these were the only values available.

When it was obvious that a single observation had more than one entry in a database, only one of them was used for our calculations to avoid pseudoreplication.

Single data entries (n = 11) that seemed unreasonably high or low were also not included in our trait dataset (seed number: *Briza media*, *Calamagrostis epigejos*, *Cerastium holosteoides*, *Daucus carota*, *Holcus lanatus*, *Leucanthemum vulgare*, *Lotus corniculatus*, *Pimpinella saxifraga* and *Trisetum flavescens.* Leaf size: *Hieracium pilosella, Hippocrepis comosa,* SLA: *Anacamptis pyramidalis*).

Diaspore mass

Orchid and cryptogam species for which no data was available (n = 10) were assigned a value of 0.001 mg.

Lateral spread

Lateral spread was extracted from CLOPLA (Klimešová & De Bello 2009). Only rooting horizontal stems at or above soil surface, epi- and hypogeogenous rhizoms and bulbils or tubers originating from roots (CGO type 1, 9, 10, 15 and 17 in CLOPLA) but not 'loose' bulbils or plant parts were considered for lateral spread. Only those that are 'necessary' for lateral spread or, when there were equal numbers, those CGOs that had larger values in the dtabase were selected. CGO 15, and 17 were only included when they were 'necessary'. Therophytes were assigned 0.

Leaf dry matter content (LDMC)

For the majority of species for which LDMC data was available in LEDA (Kleyer et al. 2008), measurements were performed on leaves without petioles and rachis. I also included values from measurements on leaves with petiole and rachis because 1) some species do not have leaves with petioles, 2) differences between measurement methods seemed negligible in cases where values derived from both methods applied to the same set of individuals (as obvious from information about e.g. origin of samples, date of sampling; n = 30, mean difference between methods = 7.6 mg g^{-1} ± 11.9 SE) were available, and 3) values did not differ systematically among populations measured with different methods (e.g. they were not always smaller when measured with petiole and rachis). However, when measurements were performed with both methods on the same set of individuals, only those values from without petioles and rachis-measurements were used.

Seed number

Only seed number values measured 'per ramet/tussock or individual plant' were used, and when it seemed reasonable according to drawings from Jäger (2007) and own knowledge of the species, values measured as 'per multiple flower stem' and 'per single flower inflorescence'. When only data on seed number 'per multiple flower stem' or 'per multiple flower inflorescense' where available from databases, these values were multiplied by the number of flower stems/inflorescenses drawn in Jäger (2007) (for *Carex alba*, *Carex montana*, *Globularia punctata, Euphorbia cyparissias, E. verrucosa*).

Plant life span

Data on plant life span was extracted from LEDA using the following categories:

1. Annuals

2. Strict monocarpic biennials and poly-annuals

3. Poly-annuals < 5 years (short-lived perennials)

4. Poly-annuals 5-50 years (medium-lived perennials)

5. Poly-annuals >50 years (long-lived perennials)

and coded as a semi-metric variable where category 1 = 1 year, 2 = 2 years, 3 = 4 years, 4 = 25 years, and 5 = 75 years.

When different categories were available for one species, the longest life span category was selected (except for *Carlina vulgaris, Centaurium erythraea, Crepis capillaris, Festuca ovina, Festuca rubra, Gentianella ciliata, Lolium perenne, Prunella vulgaris* which were assigned to 'strict monocarpic bi-annuals and poly-annuals' and not to 'perennials' because 'poly-annuals' is a more precise suborder of 'perennials'). When 'perennial' was the only available category in the LEDA traitbase, we first searched the BIOLFLOR database (Klotz et al. 2002) for a more precise entry. When the BIOLFLOR-search did not yield a more precise entry, species were assigned category 4.

Attachment potential

Attachment potential on sheep wool was calculated as described in Römermann et al. (2005) using data on exposure, surface structure and appendage morphology of diaspores from D^3 (Hintze et al. 2013), with one additional value from LEDA for *Primula farinosa*. Appendage morphology for ferns (n = 5) for which no such data was available was set 'none'.

Own derivations from drawings

Additional values for releasing height and canopy height for 12 and 2 species, respectively, for which no data was available from databases, were extracted from the literature (Conert 2000; Jäger 2007) (Table A1).

Terminal velocity

Data on terminal velocity were mainly extracted from D^3 with additional values for 26 species from LEDA.

Rooting depth

Rooting depth was extracted from Landolt (2010). Additional data for *Allium carinatum, A. suaveolens, Anacamptis pyramidalis, Centaurium erythraea, Crepis alpestris, Epipactis palustris, Gladiolus palustris*, *Odontites_vulgaris*, *Ophrys insectifera, Polygala_vulgaris, Polygonatum odoratum, Pulsatilla patens, Selaginella helvetica, Tetragonolobus maritimus, Thesium linophyllon* was derived from drawings in Jäger (2007) when these could confidently be estimated.

Habitat specialism

Species characteristic for or occurring mainly in European dry grasslands (phytosociological class Festuco-Brometea; Oberdorfer 2001) were classified as habitat specialists. In addition, some species of

thermophilous fringe communities (*Trifolio-Geranietea*: *Agrimonia eupatoria, Anthericum ramosum, Aster amellus, Campanula rapunculoides, Fragaria viridis,* *Geranium sanguineum, Hypericum perforatum, Laserpitium latifolium, L. siler, Medicago falcata, Melampyrum cristatum, Peucedanum oreoselinum, Polygonatum odoratum, Scabiosa canescens, Securigera varia, Silene nutans, Trifolium medium, Vincetoxicum hirundinaria, Viola hirta*),

calcareous Pine forests (*Erico-Pinetea*: *Aquilegia atrata*, *Asperula tinctoria, Carex ornithopoda, Chamaecytisus ratisbonensis, Coronilla vaginalis, Crepis alpestris, Daphne cneorum, Dorycnium germanicum, Erica carnea, Festuca amethystina, Leontodon incanus, Polygala chamaebuxus, Rhamnus saxatilis, Thesium rostratum*),

steppe Pine forests (*Pyrolo-Pinetum: Carex ericetorum, Potentilla patens, Viola collina, Viola rupestris ssp. rupestris*),

thermophilous Oak forests (*Potentillo-Quercion petraeae: Inula hirta, Potentilla alba*),

natural alpine limestone habitats (*Campanula cochleariifolia, Carduus defloratus, Carex sempervirens, Euphrasia salisburgensis, Gentiana clusii*, *G. verna, Globularia cordifolia, Gypsophila repens, Phyteuma orbiculare ssp. orbiculare, Sesleria albicans, Thymus praecox subsp. polytrichus*),

the *Cirsio tuberosi-Molinietum arundinaceae* (*Cirsium tuberosum, Molinia arundinacea, Tetragonolobus maritimus*), and

the Sedo-Scleranthetea species (*Alium montanum, Echium vulgare, Sedum sexangulare, Veronica arvensis*)

were also classified as habitat specialists as they are characteristic elements of well-preserved calcareous grasslands in southern Germany (Ellenberg & Leuschner 2010).

Table A1 | Species for which data on seed releasing height and canopy height was extracted from the literature.

	Releasing height (m)			**Canopy height (m)**		
	min	**max**	**mean**	**min**	**max**	**mean**
Agrostis stolonifera	-	-	-	0.065	0.65	0.3575
Asperula cynanchica	0.05	0.3	0.175	-	-	-
Campanula cochleariifolia	0.05	0.15	0.1	-	-	-
Carex ericetorum	0.1	0.3	0.2	-	-	-
Carex muricata s. str.	0.2	0.6	0.4	-	-	-
Carex ornithopoda s. str.	0.08	0.15	0.115	-	-	-
Euonymus europaea	1.5	3.0	2.25	-	-	-
Euphrasia salisburgensis	0.02	0.2	0.11	-	-	-
Odontites vulgaris	0.1	0.45	0.275	-	-	-
Ononis spinosa ssp. spinosa	0.3	0.6	0.45	-	-	-
Phleum pratense s. str.	0.2	1.0	0.6	-	-	-
Potentilla incana	0.05	0.15	0.1	-	-	-
Seseli annuum	0.1	0.9	0.5	0.062	0.555	0.3085

A2 – Curriculum vitae

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Naturwissenschaftlicher Verein für Schwaben

PROFESSIONAL SERVICE

Manuscript reviewer for: *Journal of Vegetation Science*, *Restoration Ecology*, *Tuexenia, Peerage of Science*

COMPUTATIONAL SKILLS

R
GIS (ArcGIS, QGIS and R-based)

LANGUAGES

German (mother tongue), English (fluently), Portuguese (basic) and French (basic)

A3 – Publications

INTERNATIONALLY PEER-REVIEWED PUBLICATIONS

In review	Kollmann J, Meyer ST, Bateman R, **Conradi T**, de Souza Mendonça M, Fernandes GW, Gossner MM, Herrmann J-M, Koch C, Müller SC, Oki Y, Overbeck GE, Paterno GB, Toma TSP, Rosenfield MF & Weisser WW. Towards a functional restoration ecology – recent advances and future directions.
In review	Koch C, **Conradi T**, Gossner MM, Hermann J-M, Leidinger J, Meyer ST, Overbeck GE, Weisser WW & Kollmann J. The effect of management intensity and temporary conversion to other land use on subtropical grasslands in southern Brazil.
2015	**Conradi T**, Strobl K, Wurfer A-L & Kollmann J. Impacts of visitor trampling on the taxonomic and functional community structure of calcareous grassland. ***Applied Vegetation Science***, 18, 359–367. • **Highlighted** in a comment by Rasmus Ejrnæs (Aarhus University)
2015	Walker EA, **Conradi T**, Meimberg H & Kollmann J. Seed selection for grassland restoration: Competitive effect of a dominant grass is mediated by seed source and nutrient availability. ***Restoration Ecology***, 23, 261–267.
2014	Andrade BO, Overbeck GE, Pilger GE, Hermann J-M, **Conradi T**, Boldrini II & Kollmann J. Intraspecific trait variation and allocation strategies of calcareous grassland species: results from a restoration experiment. ***Basic and Applied Ecology***, 15, 590–598.
2013	**Conradi T** & Friedmann A. Plant communities and environmental gradients in mires of the Ammergauer Alps (Bavaria, Germany). ***Tuexenia***, 33, 133–163. • **Best young author paper** and featured on the issue cover

OTHER PUBLICATIONS

2015	**Conradi T.** Plant diversity in calcareous grasslands: patterns, processes and restoration. ***Nodium***, 7, 88–89. [In German]
2012	**Conradi T**. Welcome to Africa! Restoration ecological excursion to South Africa. ***Nodium***, 5, 38–39. [In German]
2011	**Conradi T** & Zehm A. *A review of the* Senecio-*situation – recent knowledge and management*. Regierung von Schwaben and Bayerisches Landesamt für Umwelt, Augsburg, 16 pp. [In German]

INVITED TALKS

2014	Drivers of plant species diversity in calcareous grassland metacommunities in southern Germany: Community assembly and regional processes. *Universidade Federal do Rio Grande do Sul*, Porto Alegre, Brazil.

CONFERENCE CONTRIBUTIONS

2015	**Conradi T**, Temperton VM & Kollmann J. Beta diversity in human-transformed landscapes: the roles of resource competition, environmental filtering, landscape structure and historical contingency. ***International Association for Vegetation Science***, Annual Meeting, Brno, Czech Republic (oral).
2015	Kollmann J, Walker EA, **Conradi T** & Hermann J-M. Implications of using cultivars for grassland restoration: The competitive effects of a dominant grass on subordinate forbs. ***Society for Ecological Restoration***, Annual Meeting, Manchester, UK (oral).
2014	**Conradi T** & Kollmann J. Site productivity and community assembly in initial restored grasslands. ***Society for Ecological Restoration (European Chapter)***, Annual Meeting, Oulu, Finland (oral).
2014	**Conradi T** & Kollmann J. Species interactions and environmental filtering across spatial scales in initial grassland communities. ***Plant Population Biology Conference (PopBio)***, Annual Meeting, Konstanz, Germany (oral).
2014	Walker EA, **Conradi T**, Meimberg H & Kollmann J. Nature and nurture: how site productivity and seed source of a dominant species affect a subordinate grassland species. ***Society for Ecological Restoration (European Chapter)***, Annual Meeting, Oulu, Finland (poster).
2014	Weidlich E, **Conradi T**, Kollmann J & Temperton VM. Exploring plant community assembly for its potential for grassland restoration: the role of traits and functional diversity in assembling grasslands. ***Ecological Society of Germany, Austria and Switzerland***, Annual Meeting, Hildesheim, Germany (poster).
2013	**Conradi T**, Albrecht H & Kollmann J. Functional re-connection of calcareous grassland remnants: Incorporating local and landscape-scale factors in management and restoration. ***Ecological Society of Germany, Austria and Switzerland***, Annual Meeting, Potsdam, Germany (poster).
2013	**Conradi T** & Kollmann J. Integrating local and regional processes in management and restoration of calcareous grassland metacommunities. ***Open Landscapes***, Hildesheim, Germany (oral).
2013	**Conradi T**, Staab K, Temperton VM & Kollmann J. Community assembly processes along environmental gradients in restored calcareous grasslands. ***Society for Ecological Restoration World Conference***, Madison, USA (poster).