Functional trait patterns in grassland communities, and the importance of scale
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General introduction

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INTRODUCTION

The motivations to study ecological communities are manifold. Besides the intrinsic value found in detailed knowledge of natural communities, there is a growing need to apply this knowledge and make it accessible to decision makers (UK National Ecosystem Assessment 2014). Our world is confronted with global change in multiple aspects (IPCC 2014) coupled with massive loss of biodiversity (Millennium Ecosystem Assessment 2005; IUCN 2015), making it necessary to improve ecological predictions and assessment of ecosystem services (Millennium Ecosystem Assessment 2005; UK National Ecosystem Assessment 2014; IPBES 2015; MAB 2015). Such knowledge would not only help conserve biodiversity but also support human livelihood, facilitate wellbeing, and provide justice among regions, generations, and all living organisms (Eser et al. 2011). Community ecology and functional ecology are crucial for setting the foundation for this complex mission. Community ecology aims to understand and predict species co-occurrence patterns, and functional ecology aims for mechanistic insights into the processes in ecological communities and the functions of its component species.

Community assembly
For a long time, ecologists have worked on gaining insight into the processes that govern the assembly of natural communities, striving to find general ‘assembly rules’ determining species composition at a certain site and the constraints on community structure and composition (Tansley 1920; Diamond 1975; Tilman 1988; Grime 2002). Determinants of community assembly are assumed to include niche processes (niche theory (Hutchinson 1957)), dispersal processes (theory of island biogeography (MacArthur & Wilson 1967)) and neutral processes (neutral theory (Hubbell 2001)). Although there is strong evidence for the role of all three types of processes, the relative importance of different deterministic and neutral processes in the assembly of plant communities is an ongoing matter of dispute amongst ecologists (Bell 2001; Hubbell 2001; McGill et al. 2006; Cornwell & Ackerly 2010). Assuming that assembly processes are at least partly deterministic, insight into assembly rules would allow for better prediction of community composition and ecosystem function.

Trait-based approaches
An increasing number of recent publications has successfully used trait-based approaches to quantify functional characteristics of communities and ecosystems, and to gain insight into assembly processes (e.g. Garnier et al. 2007; Gross et al. 2009; Cornwell & Ackerly 2010; Jung et al. 2010). Functional traits can be defined as the morpho-physio-phenological characteristics that impact plant fitness via their effects on growth, reproduction and survival (Lavorel et al. 1997; Viole et al. 2007). Therefore, trait-based approaches have the underlying assumption that the functional traits of plant species have predictive value for their ecology (Lavorel & Garnier 2002; Grime 2006). Assembly rules (Diamond 1975) can be considered as filters that sieve out species from the available species pool (Keddy 1992a; Weiher et al. 1998). Their significance in structuring communities can be inferred
from examining distribution patterns of plant functional traits in an established community relative to the trait spectrum of the species pool (Ozinga et al. 2004; Ozinga et al. 2005; Funk et al. 2008). Defining assembly rules with respect to functional trait values instead of species identity will likely result in rules that are more general (Keddy 1992a; Díaz & Cabido 2001), independent of often changing taxonomy, and easier to construct and apply (Weiher & Keddy 1995). Rules based on functional trait values, moreover, allow for a more mechanistic view of species interactions (McGill et al. 2006).

**Role of traits in community assembly**
A mechanistic view of community assembly is possible if community assembly is deterministic and not trait-neutral. The neutral theory states that the chance of a species occurring depends solely on the abundance in the species pool, and traits are expected to make no difference with respect to local assembly processes (Hubbell 2001; Rosindell et al. 2011). Regarding the principles of deterministic community assembly, different theories exist. According to the principles of niche theory, every species occupies a distinct niche (Chase & Leibold 2003). In a strict interpretation of this theory with respect to functional traits, this would mean that the combination of trait attributes of every species is unique in a given community. However, according to the carousel model, the species within a given plant community share largely the same niche, and variation in species composition results from an individual plant’s ability to establish in microsites appearing in a dynamic, fluctuating environment (van der Maarel & Sykes 1993). This second theory would result in species of a plant community having similar trait attributes as a response to the constraints imposed by environmental factors. Nevertheless, traits linked to competition and/or dispersal might still show differences within the constraints of the environmental filters. A hybrid of the niche and carousel theories assumes that guild proportionality exists, which means that species can be grouped into guilds and species within a guild are interchangeable from a functional point of view (Wilson 1989). A third theory is the species pool concept, which considers dispersal limitation as the main factor for local species occurrence (Zobel 1997). According to this theory, community assembly is driven to a large extent by the abundance of species in the regional habitat species pool and the dispersal traits of the species (Ozinga et al. 2009).

**Soft vs. hard traits**
Plants express a variety of traits. If traits impact plant fitness, they are called functional traits (Lavorel et al. 1997; Violle et al. 2007). Trait-based approaches commonly use easily measurable morphological traits, such as canopy height, leaf dry matter content, specific leaf area, and seed mass. Often, these ‘soft’ traits are not directly linked to pertinent physiological functions of plant life. However, ‘soft’ traits can be considered indirectly functional if they can be correlated to direct functional traits. These direct functional or ‘hard’ traits have a direct impact on plant fitness, and include traits such as vegetative biomass, reproductive output or plant survival (Díaz et al. 1999; Cornelissen et al. 2003). For example, specific leaf area (SLA) can be used to replace relative growth rate (RGR) because of its strong positive correlations to RGR (Garnier et al. 1997; Wright &
Westoby 1999) and photosynthetic rates (Lavorel & Garnier 2002). Another leaf trait, leaf dry matter content (LDMC), reflects the resource use efficiency for leaf construction and reflects soil fertility (Hodgson et al. 2011).

**Trait variability**

To extrapolate using trait-based approaches from functional ecology, trait-for-species substitutions are used by assigning mean trait values to each species in a community. Such trait-based approaches focus on between-species trait variability (i.e. *interspecific trait variability*) (see approaches as in Doledec et al. (1996) or McGill et al. (2006)). This approach assumes that the majority of trait variation is captured between species (Kattge et al. 2011). To alleviate the sampling effort of measuring traits, large (global) species trait databases are being assembled (e.g. the TRY-database (Kattge et al. 2011)). Recently, there is growing evidence of the importance of within-species trait variability (i.e. *intraspecific trait variability*) (Leps et al. 2011; Albert et al. 2012; Violle et al. 2012; Jung et al. 2014). The importance of intraspecific trait variability relative to interspecific trait variability in shaping communities can be assumed to be scale dependent (Violle et al. 2012), as found in many ecological processes (Brooker et al. 2009). Moreover, the importance of intraspecific trait variability probably depends on the type of trait studied (Leps et al. 2011) as traits vary in their degree of stability within a species (Kattge et al. 2011).

Traits can be studied both at the species-level as well as at the aggregated community-level (Kleyer et al. 2012). Traits can be averaged at the community-level, and this is commonly done by weighting the species by their abundance (Lavorel et al. 2008). The basic assumption underlying the abundance-weighted community trait mean (CWM) is the ‘mass ratio’ theory, which states that the effect of a species trait is in proportion to associated primary production (Grime 1998). Besides using community-level response in mean trait values, within-community trait patterns can be quantified by different measures of functional diversity (FD) (Villeger et al. 2008). The latter measures give information on the trait variance around the mean while taking differences in richness into account (Díaz & Cabido 2001).

**Trait-neutral vs. trait-based community assembly**

A common approach is to compare observed trait patterns to those of null models drawn from a carefully defined species pool (Götzenberger et al. 2012). Patterns can be distinguished based on the differences between the observed community trait compositions and those emerging from a random selection from the species pool, i.e. trait patterns are more similar or less similar than expected by chance. When less similar than expected by chance, species occurrences are considered ‘trait-neutral’ and, thus, random with respect to plant traits (Hubbell 2001). Habitat filters are assumed to select plants with similar trait values due to habitat-specific adaptations, resulting in convergent trait composition. In contrast, competition filters are assumed to select plants with contrasting trait values due to niche partitioning, resulting in divergent trait composition (e.g. Díaz et al. 1998; Weiher et al. 1998; Cornwell et al. 2006; Grime 2006; Scheffer & van Nes 2006). Nevertheless, the interpretation of observed deviations from the null expectation can be
less than straightforward for several reasons. On the one hand, competitive exclusion may increase the similarity of the remaining species found in a community (c.f. Scheffer & van Nes 2006; Silvertown et al. 2006; Mayfield & Levine 2010; de Bello et al. 2012). To test this, null models would need to take into account the 'dark diversity', i.e. species belonging to the 'habitat species pool' but missing from the above-ground communities (Pärtel et al. 2013). On the other hand, strong micro-heterogeneity may diversify the observed species trait spectrum (de Bello et al. 2013a). Moreover, the importance of each process (i.e. stochastic processes, habitat filters and niche partitioning) is assumed to be scale dependent. Niche partitioning processes are expected to be more important at small spatial scales (e.g. at scales < 1 m in grasslands (Siefert 2012b)) because at such small scales, the strength of species interactions is greatest. Habitat filters are assumed to strengthen with increasing spatial scale (Weiher & Keddy 1995; Weiher et al. 2011; Siefert 2012a; de Bello et al. 2013b) ranging from local to habitat-level or biome-level filters. Thus, moving up nested ecological scales, niche-partitioning processes could shape the segregation of individuals from locally co-occurring species, while habitat filters could shape the clustering of species within sites along an environmental gradient. Neglecting the influence of spatial scale on observed trait patterns might explain the frequent detection of converging trait patterns found in studies conducted at coarse scales, e.g. in grasslands at scales greater than 1 m² (Siefert 2012b; de Bello et al. 2013b).

**THESIS OUTLINE**

The aim of this thesis is to broaden our knowledge on the potentials and limitations of trait-based approaches to discern the mechanistic processes driving community patterns and clarify plant community assembly, using grasslands as a representative study system. Though trait-based approaches have high potential to improve our understanding of community assembly and assessment of ecosystem services, recent results also propose limits to trait-based approaches. This thesis will focus on three issues that will likely affect the outcome regarding the value of trait-based approaches: 1) the level studied, i.e. within species-level, community-level or habitat-level; 2) the spatial scale of trait value origin, i.e. measured at the plot, measured at the site or derived from a trait database (see Figure 1.1 for the link between scales and levels); and 3) the type of trait.

The following three questions are central to this thesis:

1) **What are the relative strengths of habitat filters, competition filters, and random processes at the scales of communities, species, and individuals?**

The relative importance of three types of processes (habitat filters, competition filters, and random processes) is studied in two grassland sites, i.e. a mesic wet meadow and a stressful salt marsh, using a trait-based approach (**chapter 2**). In this study, I challenge the theory of trait-neutral community assembly and aim to differentiate between
evidence for habitat filters and competition filters using the observed deviations from random expectation. To answer this question, I tested the scale at which traits vary most: among communities of co-occurring species on a few square meters, among co-occurring species or within species. I compared these measured variance patterns to null models based on trait patterns of randomized communities. I chose the commonly used morphological plant traits canopy height (CH), leaf dry matter content (LDMC) and specific leaf area (SLA), which I measured on-site at the scale of 2 x 2 m plots.

2) How are community-level traits related to environmental gradients and management regime?

In two grassland sites, a mown wet meadow and an unmanaged salt marsh, I determined the main environmental gradients along studied plots and tested for linear relations of these gradients with community-level traits, i.e. community weighted means and functional diversity measures (chapter 4). I used on-site measurements of CH, LDMC and SLA, which are known to be linked to gradients of productivity, water stress, and salinity, respectively. For these three traits, I aimed at quantifying trait-environment relations.

The type of grassland management affects species composition (Bakker 1989). These management effects are expected to be also reflected in community-level traits. I studied the relations of both above- and below-ground traits to management treatments. I used three above-ground traits (CH, LDMC and SLA), which were also used in chapter 4, and the below-ground trait root porosity, as an indicator for adaptation to soil compaction due to trampling or traffic from heavy mowing machines. Using a long-term field experiment in a salt marsh with three management treatments (grazing, mowing, and fallow), I studied the effect of management on both species composition of the communities and community-level trait variation, i.e. trait-management relations (chapter 5). I studied the long-term effects of traditional versus mechanical mowing of mesic grasslands using a wet meadow (chapter 6). On a coarse, sandy soil and on finer sandy-organic soil, I evaluated a time-series of successional changes in vegetation composition and above- and below-ground community-level traits in a long-term experiment (38 years). With the latter two studies (chapters 5 and 6), I aim to gain more insight in the influence of management treatments on community-level traits (i.e. trait-management relations).

3) What are the benefits and drawbacks of using potential traits instead of on-site realized traits?

Chapter 3, and also parts of chapters 4 and 5, are dedicated to evaluate the suitability of trait-for-species substitutions, especially when using species mean trait values aggregated over large scales from databases. Aggregating trait data per species is assumed to cover a high fraction of the variation in traits (Kattge et al. 2011), but this assumption needs to be tested for the traits, scales, and habitats at which we evaluate how community assembly drives local and regional trait patterns. I tested whether using realized traits (i.e. measured on-site) or potential traits (i.e. derived from a database) results in different
outcomes. One aspect is the deviation of traits aggregated at the habitat level (i.e. the species pool of a site) and traits aggregated at the community level (i.e. co-occurring species in small plots) between on-site measured traits and traits derived from a database, which I studied in a wet mesic meadow and a stressful salt marsh (studied in chapter 3). In chapter 3, I addressed two related questions representing the two levels of aggregation. (i) Can habitat species pool traits retrieved from a regional database be used as a proxy for habitat species pool traits measured at the site? (ii) Can plant community traits calculated using species trait values retrieved from a database and those calculated using species trait values measured at the site be used as a proxy for community traits measured at the plot? Additionally, I studied the consequence of these deviations at the community level on observed trait-environment relationships (chapter 4) and trait-management relations (chapter 5). A good proxy of realized community-level traits would detect the same trait-environment and trait-management relations as those detected by traits measured per plot. I wanted to test whether traits derived from a regional database and traits measured at the site-scale can indeed serve this aim. In chapter 4, I tested the consistency of linear relations between the main environmental gradient across plots and different community-level traits at the three spatial scales of
trait value origin: measured at the plot-scale, measured at the site-scale and species mean trait values derived from a database. I aim to evaluate the scale effect of the different proxies on community-level trait-environment relations in a mesic and a stressful habitat. In chapter 5, I challenge the use of trait-management relations based on database-derived potential community-level traits as proxies for realized community-level traits in a salt marsh site.

The limited availability of propagules of target species, resulting from limited soil seed bank persistency and long-distance dispersal capacity (Bakker et al. 1996), is assumed to be a major factor when restoration measures fail to restore target communities. Therefore, this thesis additionally contains the results of a field experiment on seed limitation in the wet meadow site (box 1). I tested the hypothesis of propagule limitation using a field experiment mimicking seed dispersal by sowing seeds of a few typical wet meadow species into the established vegetation.

It is assumed that single species with extraordinary survival strategies, such as hemi-parasitism, have disproportionately high influences on community structure (Press & Phoenix 2005). In a long-term study, Ameloot et al. (2006) revealed a high degree of sensitivity of the annual hemi-parasite Rhinanthus angustifolius to spring droughts. Extending the data of this study with observations from permanent plots in another year with extreme spring drought, the long-term impact of this hemi-parasite on the resident community is discussed (box 2).

Finally, chapter 7 is a synthesis of the results from this thesis evaluating the answers to the central questions of this thesis. It is devoted to discussing the potentials and limitations of using trait-based approaches to reveal the drivers of plant community assembly so that we can more accurately predict changes in community composition and ecosystem services of landscapes.

**STUDY SYSTEMS**

To answer the questions posed in this thesis, I studied two grassland habitats in the Netherlands: a mown wet meadow area of about 40 ha located in the catchment of the Drentsche Aa brook (53° 2' N, 6° 39' E) and an unmanaged salt-marsh area of about 60 ha located on the Wadden Sea island of Schiermonnikoog (53° 30' N, 6° 10' E) (see map in Figure 1.2). The wet meadow represents a mesic habitat hosting a large pool of species. At this study site, the almost water-impermeable layers of boulder-clay from the Saalian ice age result in different channels of groundwater: a base-poor and oxygen-rich channel above the boulder-clay layer recharged by local rainwater, and another base-rich deeper seepage channel. This results in spatially variable hydrological conditions (Grootjans 1980). In many parts of this study site, the practice of haymaking without using fertilizer was applied, which led to a depletion of soil nutrients and, consequently, vegetation changes (Bakker & Ollf 1995). In contrast to the mesic wet meadow, the salt marsh represents a habitat with extreme abiotic conditions and strong environmental filtering, which
results in a small species pool consisting of specialized species (Sharpe & Baldwin 2009). The salt-marsh site covers a gradient from about 100 cm to 260 cm above sea level. The height above sea level is a strong indicator for inundation frequency, salt stress and soil water condition in a salt marsh (Olff et al. 1997). Both sites are part of long-term monitoring projects (40 years) with regularly sampled permanent plots of 2 m × 2 m (Bakker 1989).

Figure 1.2 The two study sites are located in the Netherlands. (raw data source OpenStreetMap).