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

Verena Cordlandwehr
The appeal of trait-based approaches is that they reduce the multiple dimensions of communities based on assemblages of species to a more restricted number based on functional characteristics (i.e. functional traits). An additional attractive property is that they allow for comparisons across communities of very different species pools as the functional characteristics are displayed in the same dimensions irrespective of the species involved (Keddy 1992a). Trait-based approaches can contribute to more accurate predictions in ecology, which is important in the face of global change. It has been known for a long time that species can be used as indicators of habitat conditions (e.g. Ellenberg et al. 1992), thus indicating the effects of 'habitat filters'. Nevertheless, such assessments would be based upon expert knowledge valid over a distinct region and would require high-quality taxonomic skill as well as familiarity with the niche requirements of all occurring species. Including small-scale interactions between species, such as competition, increases the number of dimensions that would need to be tracked in order to account for 'competition filters'. Trait-based approaches operate on the premise that they allow for a more mechanistic understanding of the effects of habitat filters and competition filters. A critical question, however, is whether community-level trait characteristics are just another way of describing species composition. If floristically similar communities show similar traits and floristically dissimilar communities show dissimilar traits, then there would be little added value of using traits. In this thesis, however, I show that this is not the case for the two study sites, a mesic wet meadow and a stressful salt marsh. Pairwise comparisons of floristic dissimilarity and unweighted community mean differences revealed that floristically dissimilar communities can, nevertheless, be similar with respect to their traits (Figure 7.1).

Once established that communities can be functionally similar while showing dissimilar species composition, the question arises whether and how these characteristics, e.g. community-level traits, are related to processes that operate during community assembly and species interactions. This will likely depend on the level of organization studied, i.e. habitat level, community level or within-species level, and the spatial scale of trait value origin, i.e. measured at the plot scale, measured at the site scale or derived from a trait database (for an overview of levels and scales, see Figure 1.1 in Chapter 1). In order to use trait characteristics at different levels to gain mechanistic insight into community assembly, it is important to know which processes affect trait patterns and how this is modified by spatial scale. This is a fundamental requirement to be able to judge the validity of conclusions drawn from trait-based studies.

This synthesis aims to answer the following three main questions:
1) What are the relative strengths of habitat filters, competition filters, and random processes at the scales of communities, species, and individuals?

Chapter 2 addresses the partitioning of trait variance among different ecological scales, i.e. local communities, species, and individuals. It also identifies which process prevails in determining these trait patterns: habitat filters, competition filters or random processes.
2) How are community-level traits related to environmental gradients and management regime?
Figure 7.1 Scatterplots of the pairwise Bray-Curtis floristic dissimilarities vs. pairwise comparisons of community-level mean traits (CM). Paired sampling plots with high floristic dissimilarity can still have very similar CM (at log scale), although more similar community species composition is linked to less different CM. CH = canopy height; LDMC = leaf dry matter content; SLA = specific leaf area.
Chapters 4, 5, and 6 aim to ascertain trait-environment and 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 challenging the trait-for-species substitution concept.

MAIN FINDINGS

1) What are the relative strengths of habitat filters, competition filters, and random processes at the scales of communities, species, and individuals? (chapter 2)

Community assembly is not stochastic
Deterministic assembly processes act on plant communities (Wilson & Whittaker 1995; Swenson et al. 2011; Siefert et al. 2013) both between species and within species (Siefert 2012a, chapter 2). With respect to their traits, species and individuals occurred non-randomly in communities of the two systems studied (chapter 2). Mean species traits in communities seem to predominantly converge, i.e. to be more similar than expected by chance (chapter 2 and e.g. Cornwell & Ackerly 2009; Leps et al. 2011). More precisely, this process seems to be two-fold with both species turnover as well as that of individuals within species leading to trait similarity within communities (chapter 2). The observed two-fold convergence supports the theory of self-organized similarity of co-occurring individuals in saturated communities (Scheffer & van Nes 2006), which leads to diverging community mean traits between communities (chapter 2).

Trait convergence is more dominant than trait divergence
The two-fold convergence in traits, i.e. converging traits of co-occurring species and converging traits of plot-specific individuals within each co-occurring species, can be explained by sorting of species and individuals according to the habitat characteristics of plots. Thus, this result is an indication that habitat filters dominated over competition filters during the assembly of communities (Weiher et al. 1998; Cornwell et al. 2006; Scheffer & van Nes 2006). This was especially pronounced in the salt marsh (chapter 2), which showed a larger spread in community weighted mean traits among plots compared to the wet meadow (Figure 7.2). However, it is an active point of discussion whether converging trait patterns should be interpreted as evidence for habitat filters and diverging trait patterns as evidence for biotic filters (Mayfield & Levine 2010; de Bello et al. 2012; HilleRisLambers et al. 2012; Violle et al. 2012; Herben & Goldberg 2014). Clearly, both types of filters acted on species occurrence patterns and selection processes of individuals from the locally available trait variation of each species (chapter 2); thus, both regulate community structure (Whitlock et al. 2011). Nevertheless, trait convergence at these two levels suggests an interpretation of species-level traits as reflecting long-term evolutionary processes governing species sorting (i.e. time perspective of evolution) and an interpretation of individual-level traits within species as reflecting
Figure 7.2 Scatterplot of site-scale species mean trait values (black dots) and plot-scale species trait values (grey dots) with cover-weighted community-level mean trait values. Community-level mean trait values varied more among plots in the salt marsh compared to the wet meadow. All traits were log-transformed. Dashed line = isocline. CH = canopy height; LDMC = leaf dry matter content; SLA = specific leaf area.
short-term selection processes from the locally available pool of trait values (i.e. time perspective of establishment). Community-level traits probably respond to long-term changes by species turnover and to short-term events by intraspecific variability (Jung et al. 2014). Additionally, as habitat filters and competition filters are assumed to be scale dependent (Weiher & Keddy 1995; Weiher et al. 2011; Siefert 2012a; de Bello et al. 2013b) a plot of 4 m² in grasslands seems too large to detect direct species interactions and, thus, too large to detect trait-based competition filters (chapter 2; Siefert 2012b; de Bello et al. 2013b).

For the wet meadow, it could be shown that communities depend on sufficient dispersal events in order to allow new species to enter the community. This was probably due to the effect of stochasticity on the establishment phase, as well as dispersal limitation (box 1), which also narrows the pool of available traits. Besides showing the importance of dispersal ability (Ozinga et al. 2009), this demonstrates the role that species abundance in the species pool has on the chance of occurring in a community (Hubbell 2001).

This trait convergence within communities at both the levels of species and individuals results in community mean traits being different among plots. These results suggest that habitat filters prevail over competition filters and that trait-neutral assembly processes act on communities at the studied scale of 2 m × 2 m (chapter 2). Next, the focus shifts to patterns across communities, which brings me to the question of trait-environment and trait-management relations.

2) How are community-level traits related to environmental gradients and management regime? (chapters 4, 5 and 6)

In both the habitats studied, a wet meadow and a salt marsh, significant trait-environment and trait-management relations were detected for some community-level traits (see summary in Table 7.1).

Trait-environment relations
Community-level mean CH was positively related to the main environmental gradient in the wet meadow, and community-level mean leaf traits were positively related for LDMC and negatively related for SLA to the main environmental gradient in the salt marsh (chapter 4). The observed increase in CH along a gradient of groundwater conductivity, i.e. increasing groundwater-level and base supply and assumed decreasing land-use intensity (chapter 4), is in line with other studies. Increasing CH has also been observed under increasing soil fertility (Violle et al. 2011; Jamil et al. 2013), high and constant water availability (Bastrup-Spohr et al. 2015) and decreasing land-use intensity (Lienin & Kleyer 2012). The slight increase in community-level FRic of LDMC with increasing groundwater conductivity in the wet meadow can be linked to stronger and more even partitioning of space between different functional groups: herbs, grasses, sedges, and rushes. This is also suggested by the over-dispersion of LDMC between species as observed in chapter 2. High iron concentrations, as in base-rich seepage groundwater, may diversify successful leaf strategies (Snowden & Wheeler 1993). In the salt marsh,
decreasing community-level mean LDMC with increasing groundwater level and increasing salinity is supported by other studies (Minden & Kleyer 2015). In contrast to other studies, however, the community-level mean SLA increased with increasing salinity when using realized species SLA values instead of potential species mean SLA values retrieved from a database (Minden & Kleyer 2011; chapter 4).

The stronger trait-environment relation of community-level mean leaf traits in the salt marsh compared to the wet meadow (chapter 4) is driven by the higher contribution of trait value differences among communities to the overall trait variability (chapter 2), and it also demonstrated by the range of community-level mean traits in the two sites (Figure 7.2). The stronger site heterogeneity is reflected along the salt stress gradient, which leads to higher species turnover and promotes dissimilar communities (Guo et al. 2014). The low species richness typical of salt marshes (Sharpe & Baldwin 2009) also indicates the less benign habitat conditions, which restrict the range of functional strategies (Spasojevic et al. 2014).

It is assumed that single species with an extraordinary survival strategy, such as hemi-parasitism, can have a disproportionately high influence on community structure (Press & Phoenix 2005). Drought events in the establishment phase of an annual root hemi-parasite Rhinanthus angustifolius was found to be fatal for its populations (box 2; Ameloot et al. 2006). This example shows the outcome of interactions between different traits, in this case an annual life-form together with short seed longevity of the species. Only together can they explain the response of the species to the weather fluctuations that were observed in a long-term vegetation monitoring study. As Rhinanthus angustifolius also influences the competition filter in grasslands due to its root parasitism (Ameloot et al. 2005), its effect as ‘keystone species’ (Press & Phoenix 2005) is complex due to its other traits that lead to spring-drought sensitivity.

**Table 7.1** Summary of community-level trait-environment and trait-management relations detected in this thesis. All trait-environment relations shown were based on realized, i.e. on-site measured, trait values. For root porosity and all traits in chapter 6, species mean trait values were used to calculate community-level trait values. + = positively related; - = negatively related; O = no significant relation; FRic = functional richness; CWM = community abundance-weighted mean; CH = canopy height; LDMC = leaf dry matter content; SLA = specific leaf area; RP = root porosity; SR = superficial roots with rooting depth <10 cm.

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<td>FRic ground water conductivity</td>
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Trait-management relations
The type of management regime affected floristic community composition and through this, community-level above-ground and below-ground traits in both a salt marsh (chapter 5) and wet meadow (chapter 6). In the salt marsh, a trait-management relation of higher community-level CH could be detected in the fallow treatment compared with the mowing and grazing treatments (chapter 5). The regular removal of above-ground biomass by the latter two treatments might have provided opportunities for subordinate species with low canopy height to establish (Louault et al. 2005; Díaz et al. 2007b; Lienin & Kleyer 2012), while the fallow treatment drives higher competition for light (Grime 2002). The study showed that both species with low potential CH (Westoby et al. 2002) and individuals within species with low CH are outcompeted (chapter 5). In fresh-water habitats, community SLA often decreases and community LDMC increases with intensifying land use, i.e. from leaving fallow to grazing or mowing (Garnier et al. 2007). In contrast, no trait-management relation could be detected for realized community-level leaf traits in the salt marsh; a significant relation could only be detected when using trait-for-species substitution (chapter 5). The results on intraspecific leaf trait variation of some species warrant further study on whether this relation might be inversed under salt stress. A separation of the grazing and mowing treatments was only possible based on potential community-level root porosity, which was significantly lower under mowing than grazing (chapter 5). Trampling by grazers leads to soil compaction (Schrama et al. 2013a), which can lead to adaption by forming root aerenchyma (Vartapetian & Jackson 1997). The grazing treatment compared with the mowing treatment mainly led to shifts in species abundance and, to a lesser extent, to species turnover, as only abundance-weighted community-level root porosity was able to separate the treatments (chapter 5). Thus, species less capable of forming root aerenchyma probably remain in the grazed community as subordinates.

In the wet meadow, long-term machine mowing led to soil compaction and lower soil aeration compared with hand mowing, especially on finer structured sandy-organic soil (chapter 6). This is a well-known consequence of modern agriculture (Hamza & Anderson 2005). The increasing soil compaction over a time of 38 years was reflected in an increase in abundance of species with superficial root growth and a decrease of species with low potential root porosity (chapter 6). Potential root trait-management relations, thus, depended on abiotic soil conditions. Nevertheless, the trade-off between root adaptations to water-logging and nutrient uptake (Bastrup-Spohr et al. 2015) might reveal a difference in the ecosystem service of 'productivity' between machine mowing and hand mowing. Independent of soil conditions, community-level mean CH was lower under machine mowing than under hand mowing (chapter 6), which is in line with the higher abundance of species with superficial roots, as CH and rooting depth are correlated (Douma et al. 2012).

Some of the studied traits were related to the main environmental gradient and management regime, but significant relations of trait means at the community-level were more frequent than that of trait ranges. In the wet meadow, mean CH and FRic in LDMC were positively related to the main environmental gradient of groundwater conductivity, and
mean CH decreased and mean SLA and species with superficial rooting increased under machine mowing compared with hand mowing. In the salt marsh, mean LDMC and F Ric of SLA were positively and mean SLA was negatively correlated to the main environmental gradient of elevation. Mean CH was higher under the fallow treatment, and root porosity was lower under the mowing treatment (for a summary of relations see Table 7.1).

The results used to answer the first two questions were partly influenced by intraspecific trait variability, mainly among species across plots. This brings us to the third question, whether the results obtained from trait-based studies depend on the level of trait aggregation, i.e. species traits measured on-site at plot scale or potential traits averaged at site scale or derived from a database.

3) What are the benefits and drawbacks of using potential traits instead of on-site realized traits? (chapters 3, 4 and 5)

Currently, trait data on a vast number of species are available in large regional (e.g. Kleyer et al. 2008) and global databases (e.g. Kattge et al. 2011), which mainly contain mean species trait values from different locations. When compared with trait measurements at the site scale, species ranking is conserved to a great extent (chapter 3; Kazakou et al. 2014), but rare species are often underrepresented (Violle et al. 2015). For trait-based studies using trait-for-species substitution, these databases can supply species mean trait values, which represent potential traits for species, without the laborious work of on-site measurement of realized trait values. On-site trait measurement seems feasible only for small sample sizes, i.e. small number of sampled communities, species and traits, but the growing evidence for the importance of intraspecific trait variability (Leps et al. 2011; Albert et al. 2012; Violle et al. 2012; Jung et al. 2014) challenges the trait-for-species substitution approach. For instance, it could be shown for wet meadow and salt-marsh communities that not only species with similar traits but also individuals within species with similar traits are filtered at the plot level (chapter 2). Both these processes in turn act on community-level traits (chapter 3), partly altering trait-environment relations (chapter 4) and trait-management relations (chapter 5). Within-species trait values across communities co-vary with the average traits of the co-occurring individuals for many species, which is shown by the prevailing positive slopes of CWM linear models explaining species plot-specific trait values (Figure 7.3). Thus, both interspecific trait variability and intraspecific trait variability are important in order to understand processes at the community level. Nevertheless, the amount of intraspecific trait variability is clearly higher between individuals of a species across plots in communities of the same habitat type compared to within-plot communities (chapter 2). This means that averaging traits of individuals to species means at the within-plot community level captures a large fraction of the trait variation. The consequence of neglecting intraspecific trait variability across communities can lead to both underestimation of differences in community-level traits and, thus, to underlying environmental gradients (Leps et al. 2011) and overestimation (chapters 4 and 5) as the traits of co-occurring individuals can be more similar than their species mean trait values suggest.
Figure 7.3 Histograms of slopes from linear models of species plot-specific trait values against the CWM for all species occurring in > 3 plots. The intraspecific slopes of a number of species in both a wet meadow and a salt marsh are different from 0, mainly showing an increase of plot-scale species-level traits with increasing plot-scale community-level weighted mean traits (for method see Ackerly and Cornwell (2007)).

The studies in this thesis show that realized community-level traits at the time of sampling differed from potential community-level traits based on species optimum trait values, and that the strength and direction of the deviation depended on the habitat, trait and scale studied (chapters 3, 4, and 5). These differences were strong enough to partly skew community-level trait-environment relations (chapter 4) and community-level trait-management relations (chapter 5). The skewed community-level trait-environment and trait-management relations based on potential species trait values could result in different consequences: i) realized relations were not detected, ii) potential relations were detected that had not been realized in plots, and iii) relations became inverted (Table 7.2, chapters 4 and 5). In the salt marsh, skewing of the trait-environment and trait-management relations was slightly stronger when using trait-for-species substitution than in the wet meadow. This was especially true for SLA, which showed the strongest effect of intraspecific trait variability on these relations (chapters 3, 4 and 5).

Overall, community-level trait-environment relations based on FD measures were more severely altered than those based on CWM (chapter 4). The deviation of commu-
nity-level mean traits calculated using trait-for-species substitution was less pronounced when species mean trait values were averaged over the site scale (chapters 3, 4 and 5). This indicates that within-species variability of traits increases with the geographic scale of measurements, which has also been confirmed by other studies (e.g. Cornwell & Ackerly 2009; Baraloto et al. 2010). For most FD indices, however, the omission of intraspecific trait variability by using the trait-for-species substitution generally leads to misleading results, even when species trait values originate from the site scale. It could be speculated that in the interactions between neighboring species within communities, intraspecific variability leads to shifts away from species mean potential trait values in both directions. Consequently, considering intraspecific trait variability has been shown to be important in studies of functional diversity in communities.

Especially in the stressful salt marsh, using potential community-level mean trait values resulted in detection of relations that were not realized (Table 7.2). In one example, fallows were assumed to promote species with resource-retentive strategies and lower growth rates (Garnier et al. 2007; Pakeman et al. 2009), which was reflected in higher community LDMC and lower community SLA. However, this was only detected when using potential traits in chapter 5. Thus, in this thesis, the assumption of Leps et al. (2011) that neglecting intraspecific trait variability will often result in underestimating the response of communities to environmental gradients seems conversely true for community-level mean traits: relations are often more pronounced than when using realized traits. The inversion of the community-level SLA-salinity relation found when using species mean trait values retrieved from a database (chapter 4) is the strongest drawback of using potential traits found in this thesis and needs to be further studied.

Table 7.2 Summary of preserved or skewed community-level trait-environment and trait-management relations between scales of trait value origin when potential species mean trait values were used. O = a realized relation was not detected; † = potential relation was detected that was not realized; ‡ = relation became inverted; = = relation was preserved; = = both detected no relation; ≠ = relation was not preserved; FRic = functional richness; CWM = community abundance-weighted mean; CH = canopy height; LDMC = leaf dry matter content; SLA = specific leaf area; site = site-scale; datab. = database-scale.

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Nevertheless, potential community-level trait values, even of very plastic traits, can contain valuable information, e.g. for predicting vegetation shifts under changing conditions, such as land-use change or climate change. Moreover, for traits where the potential of a species to respond already has a predictive value, species mean trait values retrieved from a database can give new insight into patterns of species occurrence (chapter 6). Examples of such traits include species potential to form root aerenchyma, which strongly restricts species occurrence in water-logged soils (Armstrong et al. 1991; Bastrup-Spohr et al. 2015), and species dispersal potential (chapter 6; Ozinga et al. 2009).

The main drawback of using potential traits instead of on-site realized traits is that intraspecific trait variability is not taken into account. As intraspecific trait variability can alter realized community-level traits (chapter 3) and, as a consequence, partly alter trait-environment relations (chapter 4) and trait-management relations (chapter 5), this needs to be considered in the interpretation of the results. The highest benefits occur when applied to questions and traits where a potential attribute of a species already has predictive value. Generally, species potential mean trait values measured at the site scale represent the potential in the species pool better than values derived from a database.

**FURTHER RESEARCH**

In general, this thesis shows the need to differentiate between realized and potential community-level mean traits because emerging trait-environment and trait management relations can differ between these measures (chapters 4 and 5). This should be considered in the conclusions drawn from the detected trait patterns. As potential species mean trait values retrieved from a database are averaged over various habitat conditions, they neglect intraspecific trait variability and, consequently, the extreme values found within ‘end of gradient’ communities (chapters 3, 4, and 5). This effect seems to increase with the geographic scale of measurements, as the distorting effect of using species mean trait values on the resulting trait structure is stronger at regional database scale than at site scale. Whether increasing the spatial scale of a database from regional to global level would result in further distortion effects needs further testing. Neglecting intraspecific trait variability not only dampens the response of communities to environmental gradients, as has been assumed (Leps et al. 2011), but can also invert the detected relation (chapter 4). Hence, this strong drawback of using potential traits needs to be further studied for a wider set of traits and habitat types. We need to identify the types of traits that show critical levels of discrepancy between potential and realized traits. For most functional diversity measures of communities, which focus on within-community trait patterns, trait-for-species substitution was revealed to be generally unsuitable, at least in systems with low species turnover or systems with extreme environmental conditions that restrict the range of realized species trait values (chapter 4). Moreover, when studying rather homogeneous communities where floristic differences are expressed, to a greater extent, in abundance shifts rather than species turnover, abundance-weighted community means showed a stronger link to underlying gradients (chapter 5; Wilson
2012), which is consistent with the mass-ratio hypothesis (Grime 1998). Nevertheless, using trait-for-species substitution bears a risk when communities of low evenness are studied as a single dominant species expressing traits of its potential species mean trait value can strongly skew the analysis (chapter 5). Trait shifts among communities solely based on species turnover are also more stable (Wilson 2012). Nevertheless, potential traits could be valuable when used to judge the abilities of species and communities to fill functional gaps in the community under changing land-use scenarios, as they show the potential of the species pool present. Whether these potential traits are better represented by sampling from natural populations or common garden experiments might depend on the question (Donovan et al. 2014) and on the type of trait addressed.

For accurately detecting trait-based competition filters in grasslands, a plot size of 4 m² was revealed to be too large (chapter 2), which has been confirmed by other studies (Siefert 2012b; de Bello et al. 2013b). To test the assumption that competition filters become more important at small spatial scales, further studies with varying plot sizes from commonly used plots sizes (1–25 m²) down to very small plots sizes (<0.25 m²) could be conducted. Such fine-grained studies can be assumed to be very sensitive to intraspecific trait variability. Thus, on-site measurement of traits would be advisable. Plot-specific traits of the co-occurring species, with each species represented by at least one individual from the plot, will already capture a large fraction of trait variability in the community (chapter 2; Baraloto et al. 2010), which is also needed to judge the functional diversity in communities (Pakeman 2014). Nevertheless, under approaches aiming to compare directly neighboring individuals (Semchenko et al. 2013), this conclusion would need further validation. The importance of intraspecific trait variability relative to interspecific trait variability is assumed to be scale dependent (Viole et al. 2012) as are many ecological processes (Brooker et al. 2009). Thus, a practical solution might be to measure the traits at the scale of the studied processes: biotic interactions at a neighborhood scale of <1 m; and environmental stress gradients at a local scale of <1 km or regional scale of <1000 km, dependent on the scale of the study (scale of filters as in Brooker et al. (2009)).

The results of the studies in this thesis, moreover, indicate a need to further compare relations to gradients of the within species-level to the relations to gradients of the community-level. In chapter 5, some grass species showed the trend of opposite within species response in SLA to land-use intensity compared with the response of potential community-level traits. An intraspecific response of increasing SLA to decreasing land-use intensity was experimentally shown to be one strategy that grass species use to cope with increasing shade in fallows (Gubsch et al. 2011). This is opposite to what has been revealed at the community-level, where decreases in SLA and increases in LDMC with increasing land-use intensity were detected (Garnier et al. 2007). Such discrepancies between species-level and community-level trait relations were also shown for decomposability (Jackson et al. 2013). This might be linked to the paradox that niches can be successfully filled by being either sufficiently similar or sufficiently dissimilar to neighboring individuals (Scheffer & van Nes 2006). Disentangling this paradox is a challenging task for future studies.
CONCLUSIONS

Trait-based studies can be used to detect deterministic processes that are involved in community assembly by identifying the filters acting on species sorting and abundance. Both interspecific trait variability and intraspecific trait variability determine the trait patterns among habitats, communities and species. Neglecting either type of trait variability by relying on species potential trait values derived from a much larger scale than the processes studied can lead to misleading conclusions when imposed on the levels of realized trait values, e.g. using species trait values from the regional database scale when studying local differences among communities. Thus, the benefits of using species mean trait values derived from databases for a trait-based study will strongly depend on the level and scale of the question. Species potential trait values are probably more valid for questions regarding the potential of communities to respond to the effects of future changes, such as land-use dynamics or climate change, than for questions regarding understanding the roles that realized traits play in assembly processes on a mechanistic perspective. Another aspect is the type of trait as the degree of plasticity probably differs widely between traits, but comparative studies are scarce.

I show in this thesis that the value of using large-scale databases to link species trait data to species occurrence data at smaller scale is more limited than hoped for when using the traits CH, LDMC and SLA. Nevertheless, the general idea of trait-based approaches is still valid, but this requires a more laborious approach as plot-scale measurements of traits are still necessary for some questions. Though more laborious than approaches based solely on vegetation recording (i.e. species composition), trait-based approaches leading to functional descriptions of communities can give valuable insights into assembly processes and allow for comparisons among communities independent of species taxonomy; therefore, they are worth the effort. This thesis demonstrates that by using such a fine-scale approach, functional comparisons became possible between a mesic wet meadow and a stressful salt marsh with different species pools.