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

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2016

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Cordlandwehr, V. (2016). *Functional trait patterns in grassland communities, and the importance of scale.* [Groningen]: Rijksuniversiteit Groningen.

Deterministic grassland assembly of both species and individuals

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ABSTRACT

The local structuring of communities is usually explained by two alternative mechanisms: habitat filtering and niche partitioning. These mechanisms can be considered as filters that determine the actual community composition via selecting individuals from the available species pool. We aimed to disentangle the effects and strength of these filters over the decreasing ecological scales of local communities, species, and individuals. To determine the level of trait variability at each scale, we partitioned the variance in canopy height, leaf dry matter content and specific leaf area across these nested scales in both a wet meadow and a salt-marsh grassland.

In both the wet meadow and salt-marsh grassland, traits varied most between co-occurring species with nearly the whole spectrum of trait values already appearing between species within a local community. Comparing the observed trait variance patterns to those generated by null models revealed that both filtering of species to have similar traits and filtering of individuals within species to have similar traits led to plot mean community traits being more diverse than expected by chance. The observed convergence of traits within plots streamlines the community to match the habitat characteristics of plots, which indicates that habitat filters prevail over competition filters in the assembly of these communities.

We conclude that grassland assembly is a balancing act between species versus individual level variability. The observed trait-environment relationships of grassland communities are driven by both the plot-scale filtering of species to show similar traits and filtering of individuals within species to show similar traits. Thus, both interspecific and intraspecific trait variability lead to a trait-environment relationship different from that expected by chance. This has implications for ecological research: neglecting either type of trait variability leads to reduced sensitivity to detect the trait response across communities. However, one trait measure per species, specifically measured from that plot, already seems a good proxy. Already capturing a large fraction of trait variability, this approach could form a potential basis for measuring functional diversity.

INTRODUCTION

Understanding the processes governing the assembly of species in ecological communities from the available species pool has been a central question in ecology (e.g. Belyea & Lancaster 1999). Insight into these processes provides us with important mechanistic knowledge, which may improve predictions for vegetation shifts in a changing world. These processes act as filters on the available species pool, thus defining which individuals compose the local community (Grime 2006). Under the assumption that functional traits (sensu Lavorel et al. 1997; Violle et al. 2007) determine species responses to habitat differences (Lavorel & Garnier 2002; Grime 2006; Reich 2014), a trait-based approach could be used to disentangle the filtering effects of environmental conditions (i.e. 'habitat filters') from interspecific interactions (i.e. 'competition filters') on plant community composition (Keddy 1992a; Weiher et al. 1998).

These habitat and competition filters, also called 'assembly rules' (Weiher & Keddy 1995; Götzenberger et al. 2012), are deterministic processes producing non-random trait patterns. Patterns can be distinguished based on the differences between the observed community trait compositions and those emerging from a random selection of the species pool; i.e., trait patterns are more similar or less similar than expected by chance. Theory predicts habitat filters to select for plants with similar traits, resulting in convergent trait composition due to habitat-specific adaptations. In contrast, competition filters result in niche partitioning, which leads to co-occurring plants with contrasting traits (Weiher et al. 1998; Cornwell et al. 2006; Scheffer & van Nes 2006; *c.f.* Mayfield & Levine 2010; *c.f.* de Bello et al. 2012; *c.f.* de Bello et al. 2013b). The relative importance of habitat filters, niche partitioning and stochastic processes is assumed to be scale dependent, with habitat filters predicted to be more relevant at larger spatial scales and niche-partitioning processes predicted to play a larger role at smaller spatial scales, where the strength of species interactions is strongest (Weiher & Keddy 1995; Weiher et al. 2011; Siefert 2012a; de Bello et al. 2013b). Thus, moving down along nested ecological scales, habitat filters should shape the clustering of species within sites across a gradient, whereas niche-partitioning processes could shape the segregation of locally co-occurring individuals of these species.

Understanding the assembly processes requires not only determining whether trait patterns show convergence or divergence, but also, due to the scale dependence of the assembly process, identifying the organizational level at which traits vary the most. When traits vary the most *between* communities, assembly is presumably impacted by spatial heterogeneity and environmental gradients driving communities to express different trait combinations, and individuals to cluster within communities (Scheffer & van Nes 2006). However, both of the following scenarios can lead to similarity of co-occurring individuals: the assembly of species expressing similar traits *or* individuals within species expressing similar traits. When traits vary the most *within* communities, this indicates that diversifying processes are shaping local and regional trait patterns. Again, these diverging trait values can be caused by species occupying different niches (differences in traits between species) *or* by individuals within species occupying different niches

(intraspecific niche differentiation). This highlights how considering within-species variation in contrast to using fixed species traits could amplify or dampen the ability to detect community response (Leps et al. 2011; Siefert 2012a; Jung et al. 2014). With growing evidence for the importance of trait variability between individuals of the same species across plots (Albert et al. 2010a; Leps et al. 2011), it remains to test the importance of trait variability within species at the same local plot.

   Our aim is to disentangle the effects of assembly processes on trait variability at the local community (at a few square meters), species, and individual scale. Locally co-occurring species, represented by individual plants, build a local community with 'community traits', which represents the average trait values of these individuals. First, we asked whether individuals or species are mainly responsible for shaping trait variability between plots (P-level). Second, by aggregating individuals within species within plots, we evaluated the amount of trait variation captured between co-occurring species in plots, i.e. the species-within-plot-level (SP-level). Please note here that averaging individuals' traits for each species within plots results in plot-specific mean trait values for species. Last, we compared the trait variability between individuals-within-species-and-plots (ISP-level) to the variability between communities (P-level) and species (SP-level; see Figure 2 1). These steps outline a novel method for decomposing within-species variability into between-plot and within-plot components. By comparing the observed trait variance patterns within and across these three scales with those emerging from null models and, thus, disentangling the effects of interspecific and intraspecific trait variability, we were able to evaluate the relative strength of habitat and competition filters acting at the community, species and individual scales.
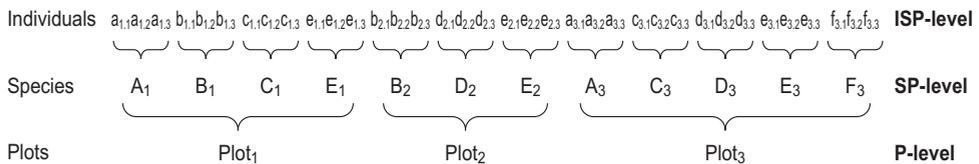
Figure 2.1 Hierarchical structure of the study design. Each letter represents a different species and each string represents an aggregated trait value. P-level = plot-level, SP-level = species-within-plot-level, ISP-level = individual-within-species-and-plot-level.

MATERIAL AND METHODS

Study sites

We surveyed two grassland sites in the Netherlands: a wet meadow and a salt marsh. The annually mown wet meadow site is located in the drainage basin of the Drentsche Aa (53° 2' N, 6° 39' E), and here we sampled 23 plots of 2 m × 2 m in an area of about 40 ha. Plots are arranged along a gradient of ground-water levels and associated soil waterlogging. The salt-marsh site is located in the Wadden Sea island of Schiermonnikoog

(53° 30' N, 6° 10' E). In total, 48 plots of 2 m × 2 m were sampled in an area of about 60 ha, covering the gradient from low (unmanaged) to high (unmanaged, grazed or mown) salt-marsh sites. Most plots studied are part of long-term monitoring projects (Bakker 1989). Details on vegetation sampling methods and a full species list can be found in Cordlandwehr et al. (2013). The two sites studied differ in species turnover between plots with a β-diversity value of 2.8 in the wet meadow and a much higher β-diversity of 6.2 in the salt marsh. β-diversity values were calculated by dividing total species richness by average species richness per plot.

Trait measurements

Species trait data were sampled at each of the plots at both sites. All trait measurements were conducted following the standard protocols of the LEDA traitbase (Knevel et al. 2003). We used three individuals of each species per sampled plot to estimate canopy height (CH), leaf dry matter content (LDMC) and specific leaf area (SLA). We measured CH from the base of the plant to the highest photosynthetic tissue (m). Leaf traits were obtained from three leaves per sampled individual (LDMC = ratio of dry to fresh leaf weight in mg g^{-1}, SLA = ratio of leaf area to leaf dry weight in mm^2 mg^{-1}). Previous research has shown these traits affect plant performance. For example, CH is positively correlated with competitive vigor of a plant (e.g. Gaudet & Keddy 1988; Tilman 1988). Additionally, LDMC is positively related to leaf life span, i.e. nutrient conservatism (e.g. Ryser & Urbas 2000). SLA is positively correlated with the photosynthetic capacity of plants, and consequently to growth rate, and negatively correlated with leaf life span (e.g. Reich et al. 1997). Further details on trait measurements as well as species trait data can be found in Cordlandwehr et al. (2013).

Data analysis

The variation in CH, LDMC and SLA was analyzed within and between three organizational levels (see Figure 2 1): i) the plot-level (P-level) representing the trait variation among plots of a site, ii) the species-within-plot-level (SP-level) representing the trait variation among species within a plot, and iii) the individual-within-species-and-plot-level (ISP-level) representing the trait variation among sampled individuals within a species in a plot.

Trait variance partitioning among these levels was extracted from nested random effects ANOVA using restricted maximum likelihood methods (REML) (Messier et al. 2010; Violle et al. 2012). Trait values were log$_{10}$ transformed prior to analysis to correct for the right-skewed distribution of all three traits. All models were implemented in R (R Development Core Team 2012) using the lme() function from the 'nlme' package (Pinheiro et al. 2013). Though species can be found in more than one plot, we used a nested random structure with species nested within plots and, thus, did not account for species effects independent of plot effects (Auger & Shipley 2013). This was because we were aiming to test the species trait concept within plots and only challenge the species trait concept across plots by comparison to null models in this study. Statistical models were calculated using this specification: model = lme(trait.value~1, random = ~1|plots/

species/individual, data = data, method = 'REML'). Estimated variance components were extracted using varcomp() from the package 'ape' (Paradis et al. 2004): varcomp (model, scale = 1).

Four alternative randomization procedures of the community data were used to determine the level at which assembly rules determine trait variations. All randomizations used a fixed species rarity value (Thompson et al. 2010). Using the described constrained randomization procedures, the models were each run 1000 times to provide four expected variance decomposition structures that were then used to answer the following questions (also see Table 2 1 for hypotheses):

i) **'Between plots' null model: Are individual plants filtered at plot level by their traits?**
   A full randomization of the trait values of individuals across plots and across species by shuffling the trait value column for each trait within sites. Thus, the link between individuals and both their plots and species is broken.

ii) **'Between species' null model: Are species filtered at plot level by their traits?**
   A randomization of species across plots by randomizing the community data matrix while maintaining species occurrence frequency and sample species richness constant (in R: package 'picante' (Kembel et al. 2010)). As individuals within species of a plot are kept together, this null model breaks the link between species and plots; however, it does not shuffle fixed species trait values but plot-specific species trait values.

iii) **'Within plots' null model: Does species identity matter within plots?**
   A randomization of individual's trait values within plots by shuffling the trait values for each trait within plots, thus breaking the link between individuals and identity of their species.

iv) **'Within species' null model: Are individual plants within species filtered at plot level by their traits?**
   A randomization of the trait values of individuals within species but across plots by shuffling the trait values for each trait within species. Thus, the link between individuals and their plots is broken.

Observed trait variance was compared to the trait variance obtained from null models by calculating the standardized effect size (SES) at each hierarchical level: SES = (observed trait variance - mean trait variance after null model)/ standard deviation of trait variance after null model (Gotelli & McCabe 2002). Large positive values (SES > 1.97) indicate trait convergence and large negative values (SES < –1.97) indicate trait divergence. The significance level was obtained per null model by using the ratio of the number of random communities with smaller or larger trait variance compared to the observed communities at a given organizational level and the total number of random runs (1000).

By testing for phylogenetic signals, we accounted for the phylogenetically linked trait variability in our dataset (Losos 2008; Münkemüller et al. 2012). For all traits (log transformed), we determined the phylogenetic signal strength and type using both the K-statistic (Blomberg et al. 2003) and Pagel's λ (Pagel 1999). The phylogeny of the species follows Prinzing et al. (2008), who used the topology of the central European species pool

(Durka 2002; checked against Bremer et al. 2003 and http://www.tolweb.org/tree/) covering all the species in our datasets (for the phylogenetic tree of the species pool see Figure S 2.6 and Figure S 2.7 in the supplementary material). For the traits showing a phylogenetic signal (Table 2.2), we recalculated nested random effects ANOVAs of observed communities incorporating a correlation matrix based on the phylogenetic tree using the corBrownian() function of the R package 'ape' (Paradis et al. 2004) with the model specification: lme(trait.value~1, random = ~1|plots/species/individual, correlation = corBrownian(1,ext.tree), data = data, method = 'REML'). Though we detected a significant phylogenetic signal for most of the traits in our dataset (Table 2.2), incorporating the phylogeny of the species in the analyses of the observed trait variance partitioning only slightly increased the variance detected at the ISP-level (see Table S 2.1 and Figure S 2.1 in the supplementary material). For clarity, and given the qualitative similarity between phylogenetically corrected and uncorrected patterns, the results presented hereafter focus on the phylogenetically uncorrected models.

RESULTS

Observed trait variance partitioning

For both sites and all traits studied, variance was not evenly partitioned among the P-level, SP-level and ISP-level (Figure 2.2 A-F). The SP-level contributed far more to the overall variability in trait values (60–90%, see bar 'obs' in Figure 2.2 A-F) than any of the other levels individually or combined; thus, trait variance was greatest between species within plots. The ISP-level, which describes the spread in trait values of individuals compared to the spread of mean species trait values within plots, consistently captured about 10% of the trait variability in both the wet meadow and salt marsh. In contrast, the contribution of the P-level to the overall trait variability differed between the two habitat types. In the wet meadow, less than 15% of the trait variability was due to the differences between community traits of plots (Figure 2.2 A-C), whereas it was about 15% to 40% in the salt marsh (Figure 2.2 D-F).

Null models

Based on the comparison of the trait variance partitioning between observed and random communities, we rejected the null hypotheses of random trait patterns for all trait-site contrasts (Table 2.1). The 'between plots' null model indicated this by predicting that most of the trait variance was concentrated at the ISP-level (Figure 2.2), which is in contrast to the observed trait data (see high positive SES at the ISP-level for the 'between plots' null model in Table 2.3).

Refining the general statement of non-random trait patterns, the 'between species' null model showed that species are non-randomly placed across plots. For most traits, species turnover, combined with species' plot-specific trait values, resulted in traits of co-occurring species being more similar than expected by chance (see positive SES values at the SP-level for the 'between species' null model in Table 2.3). An exception to this pattern
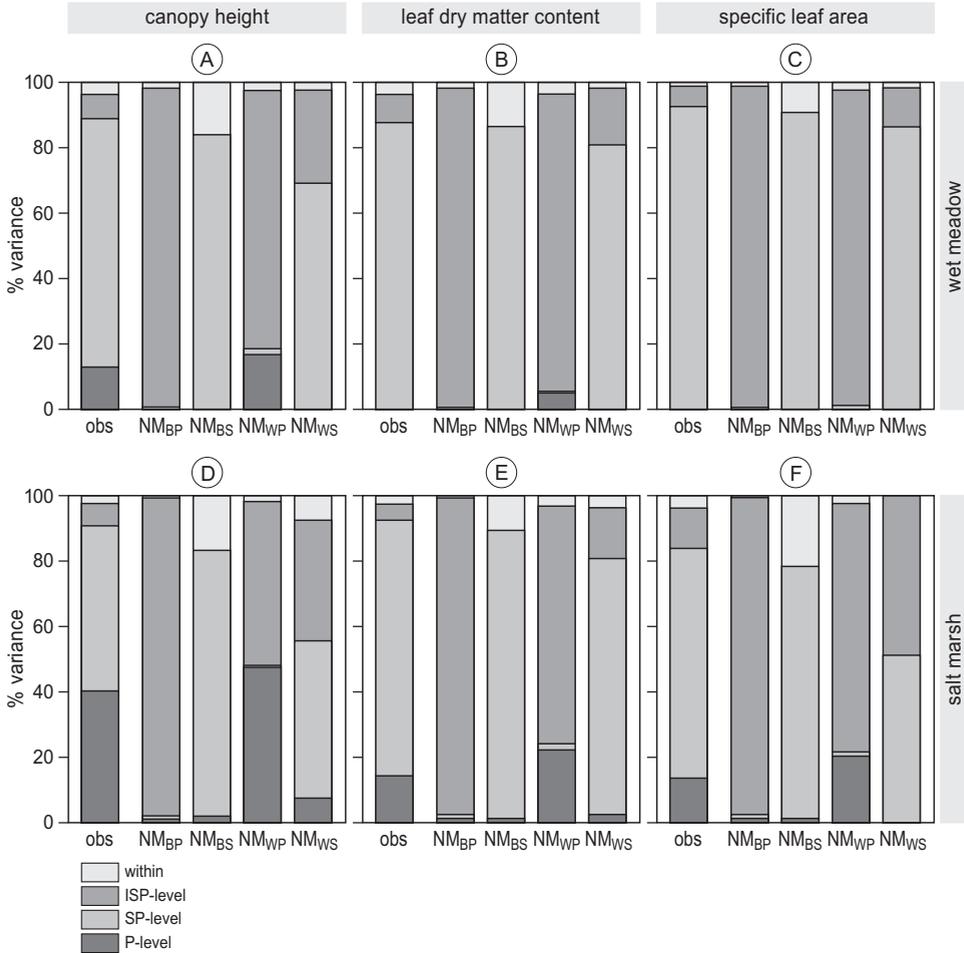
Figure 2.2 Variance partitioning of observed trait data and randomized trait data across ecological scales differ from each other. For the observed trait data, the SP-level contributed most to the overall variability in trait values and the P-level contributes more in the salt marsh than in the wet meadow site. For P-level, SP-level and ISP-level, see Figure 3.1. NM = null model, BP = between plots (full randomization), BS = between species, WP = within plots, WS = within species.

of species convergence within plots were LDMC and SLA in the wet meadow, where species within plots tended to diverge in their traits (see negative SES close to –1.97 at the SP-level for the 'between species' null model in Table 2.3).

More precisely, plots not only filtered species but also filtered specific individuals per species as shown by the 'within species' null model. This filtering resulted, for all trait-site contrasts, in traits of co-occurring individuals within a species being more similar than expected by chance. In other words, individuals within species identities were more similar in their traits within a plot than between plots (see positive SES for the 'within species' null model at the ISP-level in Table 2.3). Moreover, for most traits, the plot-

Table 2.1 Null model hypotheses.

null model	Hypothesis
between plots	$H0_{BP}$: Individuals and species are randomly assembled (no filters are present that act on individuals or species).
	$H1_{BP}$: Individuals and/or species are not randomly assembled (filters are present that act on individuals or species).
between species	$H0_{BS}$: Species are randomly placed across plots.
	$H1_{BS}$: Species within plots converge in their traits. *
	$H2_{BS}$: Species within plots diverge in their traits.
within plots	$H0_{WP}$: Individuals within plots are randomly assigned to species identities.
	$H1_{WP}$: Individuals within species and plots show a convergence in their traits.
	$H2_{WP}$: Individuals within species and plots show a divergence in their traits.
within species	$H0_{WS}$: Individuals within species are randomly placed across plots.
	$H1_{WS}$: Individuals within species are more similar in their traits within a plot than between plots. *
	$H2_{WS}$: Individuals within species are more dissimilar in their traits within a plot than between plots.

Supported hypotheses are given in bold font.
* indicates that hypotheses is true for most traits only.

Table 2.2 Phylogenetic signals could be detected for most traits in our dataset, except for CH in the wet meadow and SLA in the salt marsh. CH = canopy height, LDMC = leaf dry matter content, SLA = specific leaf area. p-values are given at the following significance levels: n.s. = not significant; . < 0.1; * < 0.05; ** < 0.01; *** < 0.001.

		Blomberg's K		Pagel's λ	
wet meadow	CH	0.283	.	0.140	n.s.
	LDMC	0.517	***	0.956	***
	SLA	1.183	***	1.000	***
salt marsh	CH	0.383	**	0.438	**
	LDMC	0.664	**	1.000	**
	SLA	0.410	n.s.	0.245	n.s.

specific trait values of individuals influenced the trait pattern at the P-level. This was very clear for CH and LDMC in the salt marsh.

The 'within plots' null model clearly showed, across all trait-site contrasts, that the trait values within a plot are species-specific. Within a plot the traits of individuals are more similar within species than across co-occurring species (see positive SES values at the P-level and ISP-level for the 'within plots' null model in Table 2.3). This, together with the fact that plots filtered specific individuals of a species at plot level (see above), led in

turn to a diversification of mean species' traits within plots, as trait values among individuals showed species-specific constraints in their trait values (Table 2.3).

In summary, plot-specific filtering of both species and individuals within species generated dissimilar community trait means. As an exception to this general pattern, leaf traits LDMC and SLA in the wet meadow showed divergence of mean species traits within plots and in turn mean community traits were not more dissimilar than expected by chance.

Table 2.3 Standard effect size (SES) for both sites and all traits resulting from the comparison of the relative variance components to the four null models. The comparison revealed deterministic community assembly. Large positive values indicate trait convergence (SES > 1.97) and large negative values indicate trait divergence (SES < –1.97, italics). Dark gray shading indicates the hierarchical level shuffled by the null model. See Figure 2.1 for P-level, SP-level and ISP-level; within = unexplained variance. p-values same as in Table 2.2.

		canopy height		leaf dry matter content		specific leaf area	
Null model	levels	wet meadow SES	salt marsh SES	wet meadow SES	salt marsh SES	wet meadow SES	salt marsh SES
Between Plots	P	*-47.31****	*-77.78****	n.s.	*-15.22****	n.s.	*-14.83****
	SP	*-55.85****	*-28.85****	*-57.55****	*-29.23****	*-60.15****	*-25.56****
	ISP	27.62***	27.37***	26.72***	21.46***	28.95***	19.5***
	within	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Between Spec	P	*-19.81****	*-23.51****	n.s.	*-11.98****	n.s.	*-8.48****
	SP	5.37***	12.86***	*-1.64***	8.37***	*-1.89****	2.7*
	ISP	*-2.72x10^7****	*-1.15x10^7****	*-48.49****	*-138.93****	*-330.82****	*-8.73x10^6****
	within	8.66***	8.07***	14.55***	9.26***	10.37***	8.01***
Within Plots	P	59.89***	44.32***	46.39***	20.18***	6.25***	21.39***
	SP	*-58.59****	*-47.2****	*-57.68****	*-28.22****	*-57.58****	*-27.25****
	ISP	19.58***	15.95***	19.51***	13.21***	22.06***	12.84***
	within	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Within Spec	P	*-49.04****	*-18.79****	*-6.19x10^5****	*-9.78****	n.s.	*-155.35****
	SP	*-6.33****	n.s.	*-10.56****	n.s.	*-13.98****	*-8.08****
	ISP	10.28***	22.78***	13.29***	7.63***	13.76***	14.65***
	within	n.s.	34.54***	*-29.76****	n.s.	9.25***	*-6.06**

DISCUSSION

Deterministic trait-based assembly filters

Our results underpin the presence of deterministic assembly processes in plant communities (Swenson et al. 2011; Siefert et al. 2013), which act both between species and within

species (Siefert 2012a). With respect to their traits, species and individuals occurred non-randomly in our grassland plots. In absolute numbers, variance at the species-level contributed most to the total variance in traits, which suggests that diversifying processes dominated by determining mean trait patterns of co-occurring species. However, the comparison between observed trait variance patterns to those generated by null models actually revealed that mean species traits in communities were predominantly conver-gent, supporting the findings of other studies (e.g. Cornwell & Ackerly 2009; Leps et al. 2011). Refining this finding, we were able to show that trait convergence in plots results from a two-fold process; the turnover of species as well as individuals within species led to trait similarity within communities. According to simple mathematical predictions, individuals converging within species should push co-occurring species traits apart, thus making species more diverse than if the same values were randomly assigned to species. The first part of this predictions was confirmed in the SES values at the species-level for the 'within plots' null-model (Table 2.3). However, this process was constrained across communities so that co-occurring species actually expressed similar traits (see "between species" null-model in Figure 3). In response to clustered trait similarity in plots, mean community traits across plots (P-level) were more diverse than expected. The observed two-fold convergence supports the theory of self-organized similarity of co-occurring individuals in saturated communities (Scheffer & van Nes 2006). Nevertheless, we could also detect a slight divergence of co-occurring species for leaf traits in the wet meadow, where species turnover and community trait variability were low.

Deterministic trait-based assembly of species could only be detected due to the comparison with null models; thus, results are sensitive to the choice of null model (Thompson et al. 2010; Götzenberger et al. 2012). Null models based on swapping species across plots, as in the 'between species' null model, are more sensitive for detecting envi-ronmental filters when species have different fundamental niches (Thompson et al. 2010; Leps et al. 2011). This might be the case for some of the species in the salt marsh dataset, where salt tolerance is the limiting factor (Munns & Tester 2008), but negligible in the wet meadow as indicated by the leaf trait results. That our results were consistent after correction for correlation between species traits and phylogeny might be explained by the small turnover in species composition in our dataset.

Although the processes controlling biodiversity act at the scale of individuals (Clark et al. 2011), the result of aggregating individuals per plot to units of species with plot-specific traits reveals that a large fraction of trait responses are detectable at the species and plot levels. The evidence for this conclusion is the higher relative importance of between-species trait variance in the overall trait variance in our dataset. Only 10% of trait variance in the wet meadow and 10–20% in the salt marsh appeared to be due to within-species variability (see Figure S 2.3 in the supplementary material, for method see de Bello et al. 2011). However, this measure of within-species trait variability only detects intraspecific variability within a community but not between communities. The impera-tive to account for intraspecific trait variability within communities will depend on the scale and aim of a study, i.e. as in grasslands niche partitioning processes probably act on a scale smaller than 1 m (Siefert 2012b; de Bello et al. 2013a) we judge intraspecific trait

variability to be important in order to detect valuable patterns. Nevertheless, as intraspecific trait variability between communities appeared to be stronger than within communities, our results confirm that having at least one plot-specific trait measure per species is a good proxy for total trait variability of species co-occurring within a plot (Baraloto et al. 2010). We expect this type of trait sampling can even serve as a potential basis for functional diversity measures that capture a large fraction of the variability (Pakeman 2014).

Habitat filters versus competition filters in different habitats
The observed convergence of traits within plots can be explained by sorting of species and individuals according to the habitat characteristics of plots, which indicates that habitat filters prevailed over competition filters in the assembly of the communities, especially in the salt marsh (Weiher et al. 1998; Cornwell et al. 2006; Scheffer & van Nes 2006). However, the usual interpretation of converging trait patterns as habitat filters and diverging trait patterns as biotic filters is currently an active point of discussion (Mayfield & Levine 2010; de Bello et al. 2012; HilleRisLambers et al. 2012; Violle et al. 2012). Irrespective of the interpretation, our results do confirm that filter are present that act on species occurrence patterns as well as on selection processes of individuals from the locally available trait variation of each species, with both regulating the community structure in these grasslands (Whitlock et al. 2011).

While converging trait patterns predominated mean traits of co-occurring species, there was evidence for over-dispersion in LDMC and SLA at the wet meadow plots. Here, the convergence of individuals within species in plots, leading to a diversification of traits between co-occurring species, was not overwhelmed by plot differences. Plots did not seem to select for specific LDMC or SLA values. The joint presence of herbs, grasses, sedges, and rushes in each plot, typical for these *Calthion palustris* grasslands, might explain the success of different types of species in the competition for light when combined with yearly mowing disturbance (for the frequency of species ordered by mean LDMC and SLA, see Figure S 2.4 in the supplementary material). These groups showed significant differences in mean species leaf trait values, with increasing LDMC and decreasing SLA from herbs and grasses to rushes (see Figure S 2.5 in the supplementary material). In these mown wet meadows, species with the narrow and tough leaf strategy occurred jointly with species using the contrasting broad leaf strategy, and species with slower and faster growth rates also occurred together. Possibly the high species overlap between plots and, thus, sharply constrained species pool used in the null models might have made this diverse leaf strategies detectable.

The contribution of the plot level to the overall trait variability depends on the length of the environmental gradient studied, which was represented here by two systems. In the salt marsh, trait variability across plots for most traits was higher and reflected the stronger site heterogeneity along the salt stress gradient. A higher species turnover between plots suggested that the presence of abiotic stress gradients promote dissimilar communities (Guo et al. 2014). The more pronounced variability across plots in the salt marsh was accompanied by lower species diversity per plot (mean species diversity: wet meadow = 23, salt marsh = 8), suggesting less benign habitat conditions (Spasojevic et al.

2014). Though the spatial extent was comparable between the two habitats, the spatial structure of the environment in the salt marsh was more fine-grained, causing a stronger vegetation-environment relationship (Siefert et al. 2012). This result led for most traits to be detectable at the plot-level with respect to overall trait variance, in contrast to results in tropical tree species (Messier et al. 2010) where the leaf trait response to the precipitation gradient across sites seemed to be overruled by the light-availability gradient within sites.

Conclusions

Our study showed a two-fold convergence for most trait-site contrasts: converging traits of co-occurring species and converging traits of plot-specific individuals within each co-occurring species. Our interpretation of the trait convergence at these two levels is that the species level reflected long-term evolutionary processes governing species sorting and the individual level within species reflected more short-term selection processes from the locally available trait pool (i.e. long-term and short-term processes as defined in Jung et al. (2014)). The discussion on the paradox that niches can be successfully filled by being similar or dissimilar to neighboring individuals (Scheffer & van Nes 2006) continues to be a challenging task for future studies. Our results make clear that to gain insight into this question, we need to measure plot-specific traits of the co-occurring species, with each species represented by at least one individual from the plot. The sizes of the plots may possibly have to range from commonly used plots sizes ($1–25m^2$) down to very small plots sizes $<0.25m^2$ (de Bello et al. 2013b).

We conclude that both patterns, the plot-scale filtering of species showing similar traits as well as individuals within species showing similar traits, acted on the observed trait-environment relationships of the wet meadow and salt marsh communities. Thus, both interspecific trait variability and intraspecific trait variability lead to a trait-environment relationship different from random. Neglecting either type of trait variability can lead to reduced detection of the trait response across communities.

SUPPLEMENTARY MATERIAL

Figure S 2.1 Variance partitioning of observed trait data across ecological scales is very similar between uncorrected (obs) and phylogenetically corrected (obs$_{PHYL}$) data. P-level = plot-level, SP-level = species-within-plot-level, ISP-level = individual-within-species-and-plot-level.

Table S 2.1 Comparison of the results on variance partitioning between the plot-, species-, and individual-level using phylogenetic correction or not. Abbreviations for traits here and in rest of supplementary information same as in Figure S 2.1.

site	trait	phylogenetic correction	plot-level	species-level	individual-level	within
wet meadow	CH	corrected	0.0882	0.7932	0.1185	0.0000
		uncorrected	0.0882	0.7932	0.0859	0.0327
	LDMC	corrected	0.0000	0.9175	0.0825	0.0000
		uncorrected	0.0012	0.9163	0.0622	0.0202
	SLA	corrected	0.0000	0.8694	0.1306	0.0000
		uncorrected	0.0000	0.8693	0.1202	0.0104
salt marsh	CH	corrected	0.3445	0.5754	0.0558	0.0243
		uncorrected	0.3481	0.5800	0.0490	0.0228
	LDMC	corrected	0.1695	0.7283	0.1022	0.0000
		uncorrected	0.1695	0.7283	0.0719	0.0303
	SLA	corrected	0.0976	0.7341	0.1273	0.0410
		uncorrected	0.0986	0.7451	0.1159	0.0404

Table S 2.2 Standard effect size (SES) for both sites and all traits resulting from the comparison of the *absolute* variance components in the four null models. Large positive values indicate trait convergence (SES > 1.97) and large negative values indica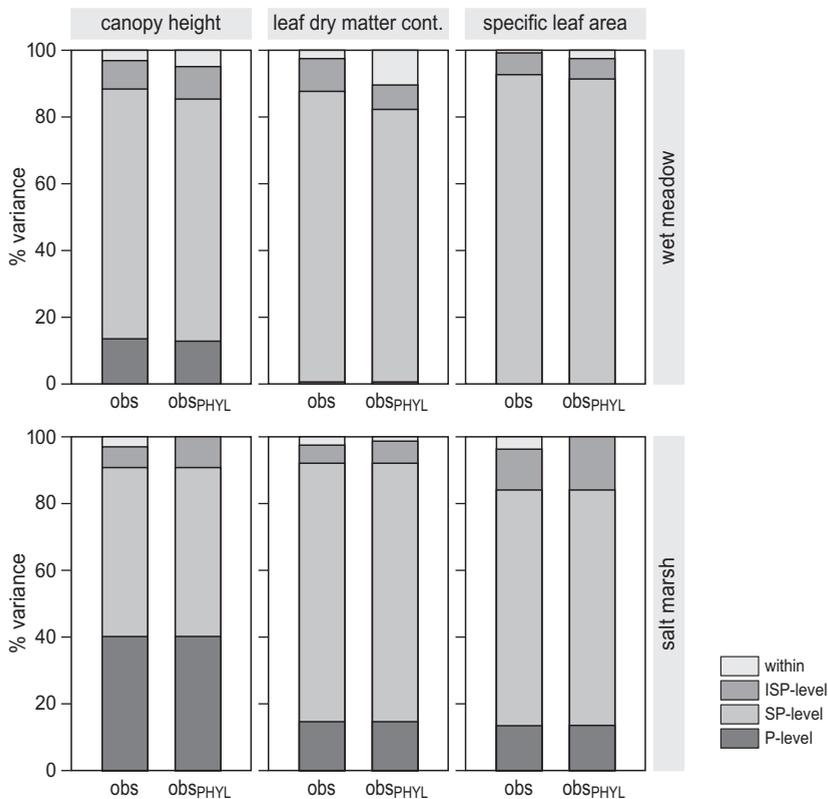te trait divergence (SES < –1.97, italics). See Figure S 2.1. Variance partitioning of observed trait data across ecological scales is very similar between uncorrected (obs) and phylogenetically corrected (obs$_{PHYL}$) data. P-level = plot-level, SP-level = species-within-plot-level, ISP-level = individual-within-species-and-plot-level. for P-level, SP-level and ISP-level; within = unexplained variance. p-values are given at the following significance levels: n.s. = not significant; .< 0.1; *< 0.05; ** < 0.01; *** < 0.001.

Null model	levels	canopy height		leaf dry matter content		specific leaf area	
		wet meadow SES	salt marsh SES	wet meadow SES	salt marsh SES	wet meadow SES	salt marsh SES
Between Plots	P	-49.58***	-81.89***	n.s.	-15.59***	n.s.	-14.87***
	SP	-58.54***	-30.40***	-56.93***	-29.95***	-59.63***	-22.06***
	ISP	27.54***	27.31***	26.79***	21.55***	28.98***	18.77***
	within	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Between Spec	P	-20.01***	-23.50***	n.s.	-12.10***	n.s.	-8.25***
	SP	2.39***	10.92***	n.s.	3.69***	n.s.	2.60*
	ISP	$-1.55x10^7$***	$-1.17x10^7$***	-49.03***	-140.33***	-354.71***	$-8.48x10^6$***
	within	9.61***	7.89***	16.52***	10.01***	15.33***	8.08***
Within Plots	P	56.09***	39.21***	45.72***	19.00***	6.25***	21.28***
	SP	-58.28***	-45.79***	-56.50***	-28.48***	-57.19***	-26.94***
	ISP	19.46***	15.74***	19.44***	13.07***	22.07***	12.80***
	within	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Within Spec	P	-51.12***	-19.60***	$-5.89x10^5$***	-10.01***	n.s.	-156.21***
	SP	-9.30***	-2.17*	-9.48***	n.s.	-11,59***	-8.22***
	ISP	10.17***	22.73***	13.37***	7.68***	13.86***	14.69***
	within	n.s.	34.07***	-30.06***	n.s.	8.97***	-6.10*
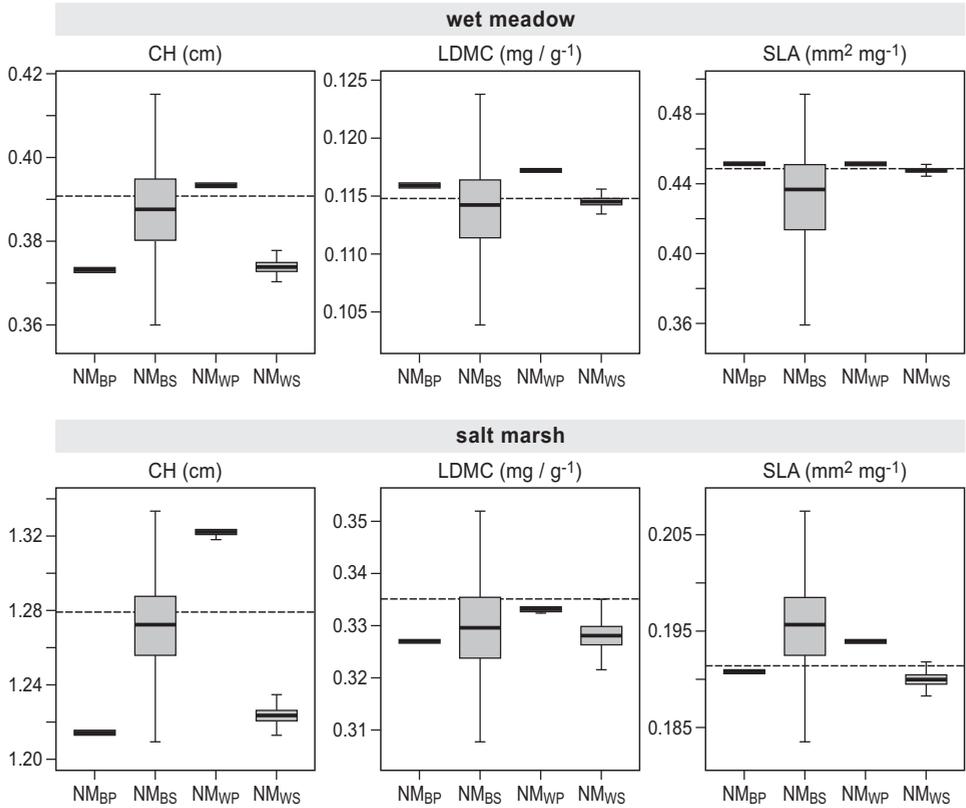
Figure S 2.2 Comparison of the total sum of variance components over all levels (including within) between null models and observed trait data. Dashed line = total sum of the observed variance. NM = null model; BP = between plots (full randomization); BS = between species; WP = within plots; WS = within species.
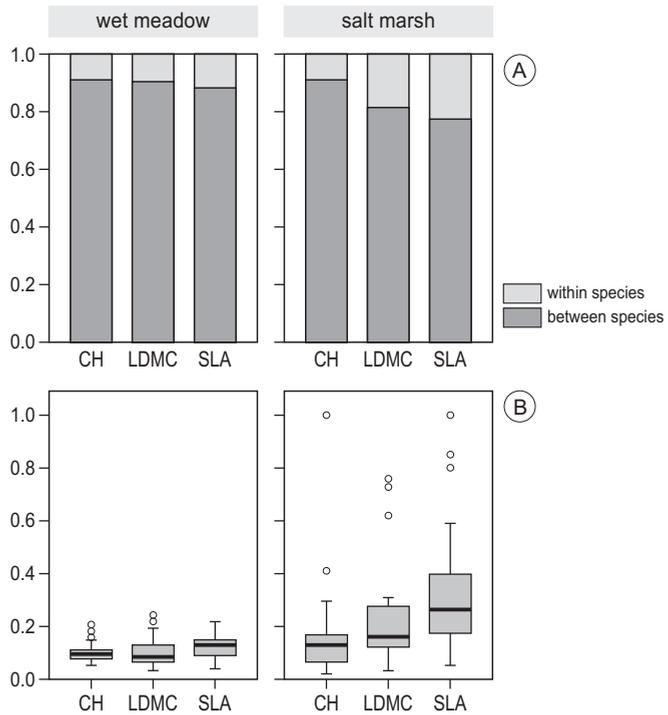
Figure S 2.3 Partitioning of trait variability in plots to 'within species' and 'between species' variability (for calculation, see de Bello et al. (2011)). A) Portion of mean trait variance over all plots of 'between species' variability (dark grey) and 'within species' variability (light grey) from total variance; B) 'Within species' variability per plot.
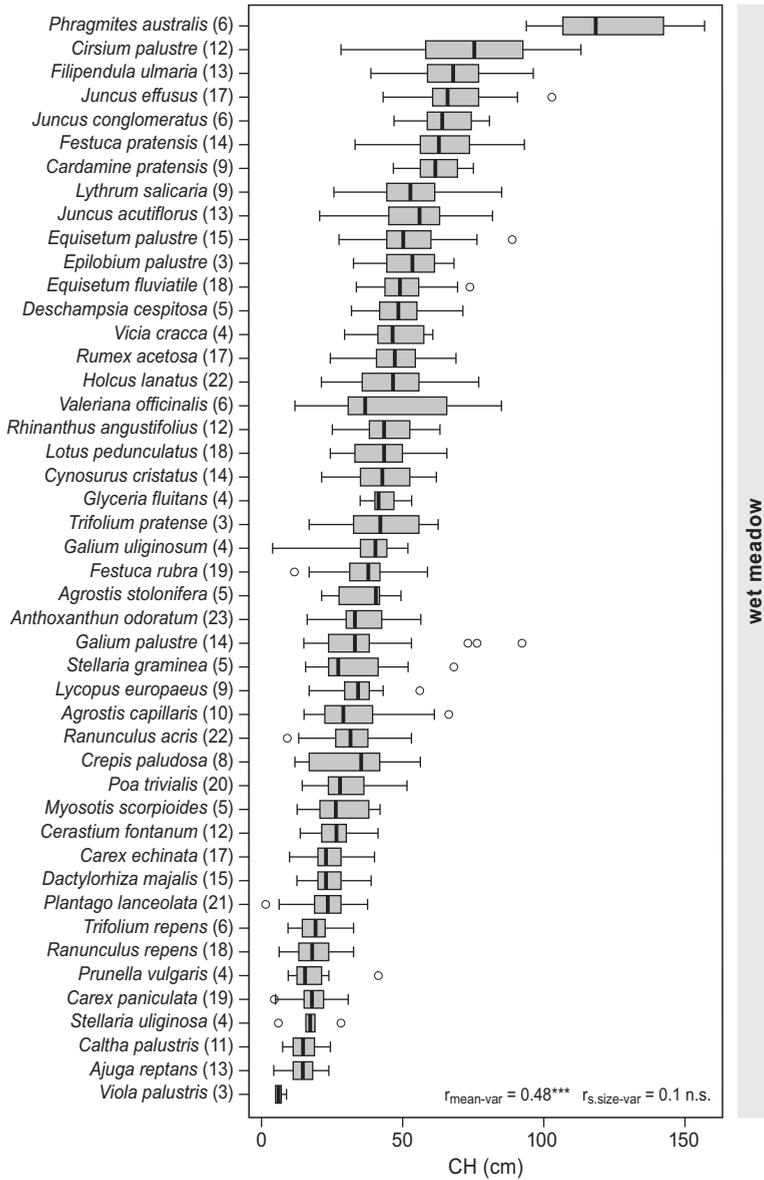
Figure S 2.4 Boxplots of species' trait data for CH, LDMC and SLA per study site for the most common species (frequency in plots > 2). Frequency in plots is given in brackets after the name. In the used data sets, mean species values and variance are correlated ($r_{mean-var}$), whereas species sample size and variance are not correlated ($r_{s.size-var}$). Indications for p-values same as in Table S2. The nomenclature of the species follows Van der Meijden (1996).

Figure S 2.4 Continued.

The plot shows LDMC (mg/g⁻¹) box-plots for species in two habitats.

Wet meadow species (top to bottom):
Phragmites australis (6), *Juncus conglomeratus* (5), *Juncus effusus* (17), *Filipendula ulmaria* (13), *Cardamine pratensis* (9), *Carex echinata* (17), *Juncus acutiflorus* (12), *Festuca rubra* (19), *Deschampsia cespitosa* (5), *Agrostis capillaris* (8), *Galium palustre* (13), *Vicia cracca* (3), *Glyceria fluitans* (3), *Agrostis stolonifera* (4), *Galium uliginosum* (3), *Lythrum salicaria* (7), *Cynosurus cristatus* (13), *Festuca pratensis* (13), *Equisetum palustre* (14), *Poa trivialis* (9), *Equisetum fluviatile* (16), *Rhinanthus angustifolius* (10), *Holcus lanatus* (23), *Myosotis scorpioides* (4), *Anthoxanthun odoratum* (21), *Caltha palustris* (8), *Carex paniculata* (11), *Lotus pedunculatus* (18), *Stellaria graminea* (4), *Valeriana officinalis* (7), *Ranunculus acris* (20), *Crepis paludosa* (7), *Trifolium repens* (7), *Viola palustris* (3), *Plantago lanceolata* (22), *Lycopus europaeus* (9), *Rumex acetosa* (19), *Dactylorhiza majalis* (8), *Cirsium palustre* (12), *Ranunculus repens* (16), *Ajuga reptans* (10), *Cerastium fontanum* (10)

$r_{mean-var} = 0.26*$ $r_{s.size-var} = 0.26*$

Salt marsh species (top to bottom):
Agrostis stolonifera (4), *Elymus pycnanthus* (14), *Festuca rubra* (14), *Juncus gerardi* (11), *Armeria maritima* (7), *Puccinellia maritima* (8), *Glaux maritima* (10), *Triglochin maritima* (6), *Artemisia maritima* (14), *Spergularia media* ssp. *Angustata* (11), *Plantago maritima* (6), *Atriplex portulacoides* (10), *Atriplex prostrata* (12), *Aster tripolium* (6), *Suaeda maritima* (8)

$r_{mean-var} = 0.62***$ $r_{s.size-var} = 0.14$ n.s.

LDMC (mg/g⁻¹)

Species (axis labels, top panel — wet meadow):
Anthoxanthun odoratum (21)
Galium uliginosum (3)
Agrostis stolonifera (4)
Myosotis scorpioides (4)
Stellaria graminea (4)
Ajuga reptans (10)
Holcus lanatus (23)
Agrostis capillaris (8)
Lotus pedunculatus (18)
Trifolium repens (7)
Cynosurus cristatus (13)
Glyceria fluitans (3)
Viola palustris (3)
Carex paniculata (11)
Rhinanthus angustifolius (10)
Cerastium fontanum (10)
Crepis paludosa (7)
Festuca pratensis (13)
Lycopus europaeus (9)
Ranunculus repens (16)
Lythrum salicaria (7)
Festuca rubra (19)
Carex echinata (17)
Ranunculus acris (20)
Rumex acetosa (19)
Plantago lanceolata (22)
Dactylorhiza majalis (8)
Valeriana officinalis (7)
Filipendula ulmaria (13)
Vicia cracca (3)
Caltha palustris (8)
Cardamine pratensis (9)
Phragmites australis (6)
Deschampsia cespitosa (5)
Cirsium palustre (12)
Equisetum palustre (14)
Equisetum fluviatile (16)
Juncus acutiflorus (12)
Juncus conglomeratus (5)
Juncus effusus (17)

$r_{mean-var} = 0.48^{***}$ $r_{s.size-var} = 0.14$ n.s.

wet meadow

Species (axis labels, bottom panel — salt marsh):
Atriplex prostrata (12)
Suaeda maritima (8)
Glaux maritima (10)
Aster tripolium (6)
Puccinellia maritima (8)
Artemisia maritima (14)
Agrostis stolonifera (5)
Triglochin maritima (6)
Sagina maritima (4)
Atriplex portulacoides (10)
Spergularia media ssp. Angustata (11)
Festuca rubra (15)
Plantago maritima (6)
Armeria maritima (7)
Juncus gerardi (11)
Elymus pycnanthus (14)

$r_{mean-var} = 0.48^{*}$ $r_{s.size-var} = 0.14$ n.s.

salt marsh

SLA (mm^2 mg^{-1})

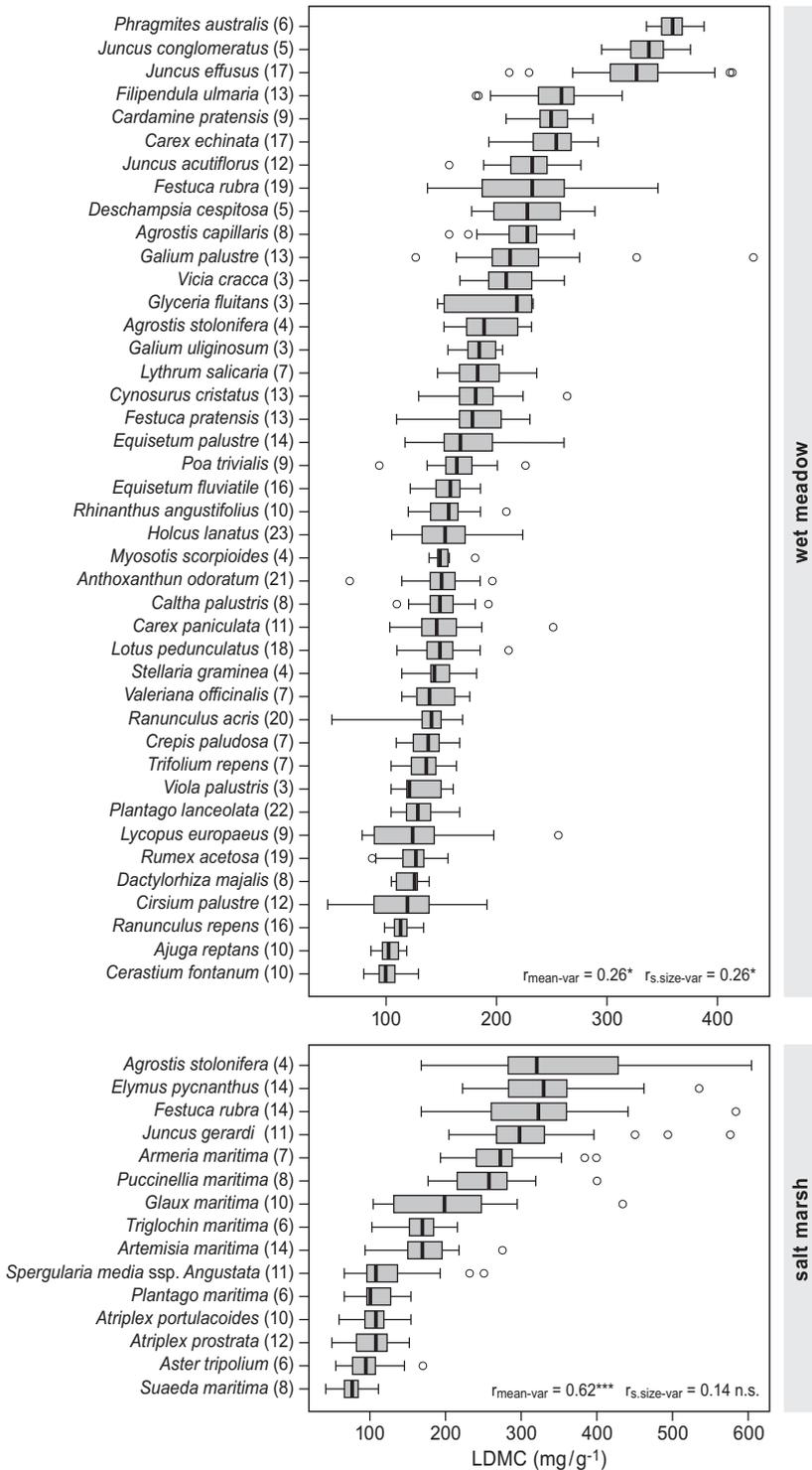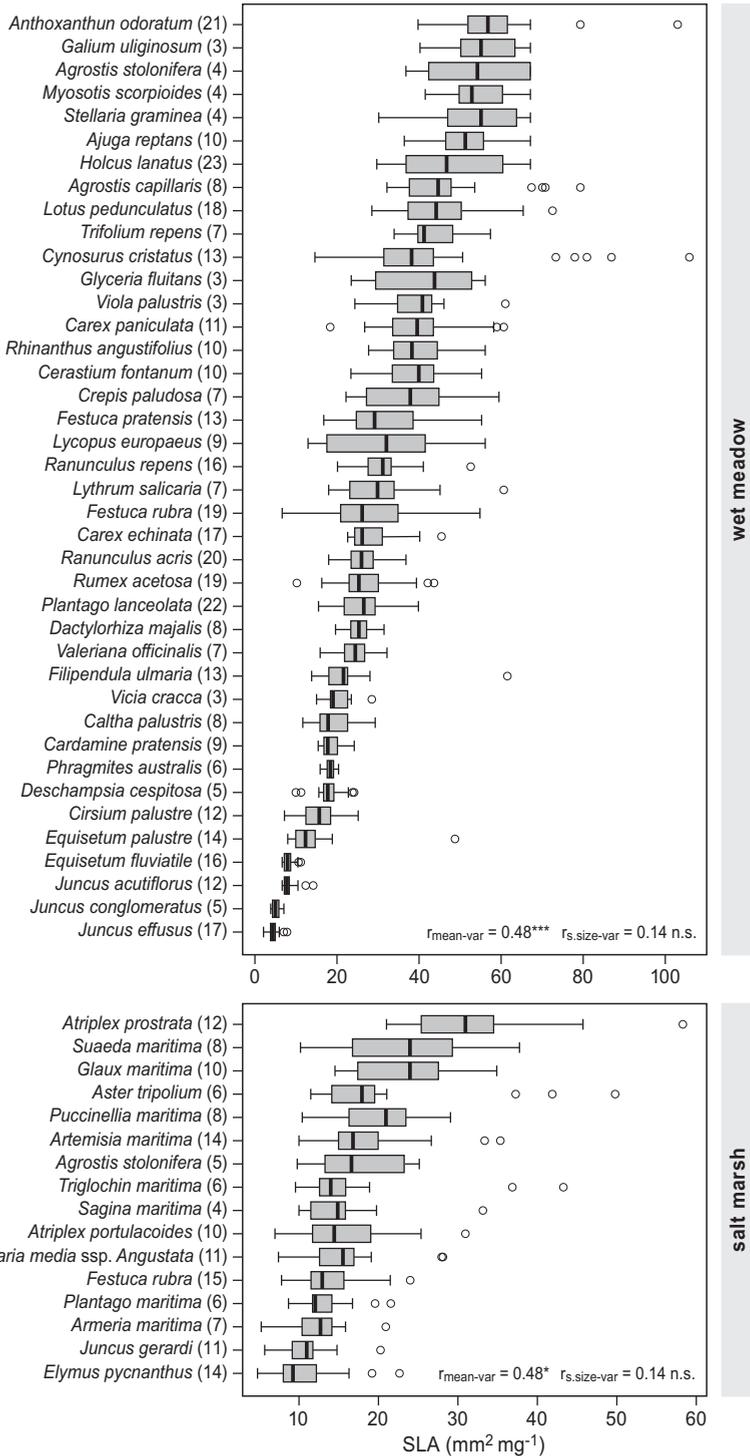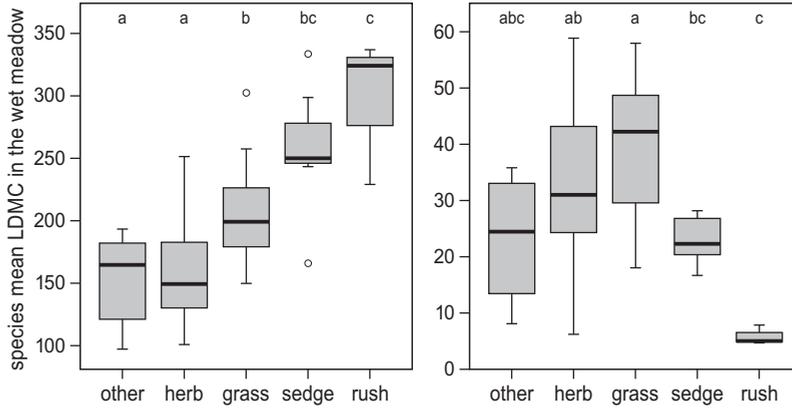**Figure S 2.4** Continued.

Figure S 2.5 Mean species LDMC in the wet meadow for different taxonomic groups of species. Herbs have different LDMC values than grasses, sedges and rushes. Pairwise comparison between group means using R function pairwise.t.test(), significance level alpha < 0.05.
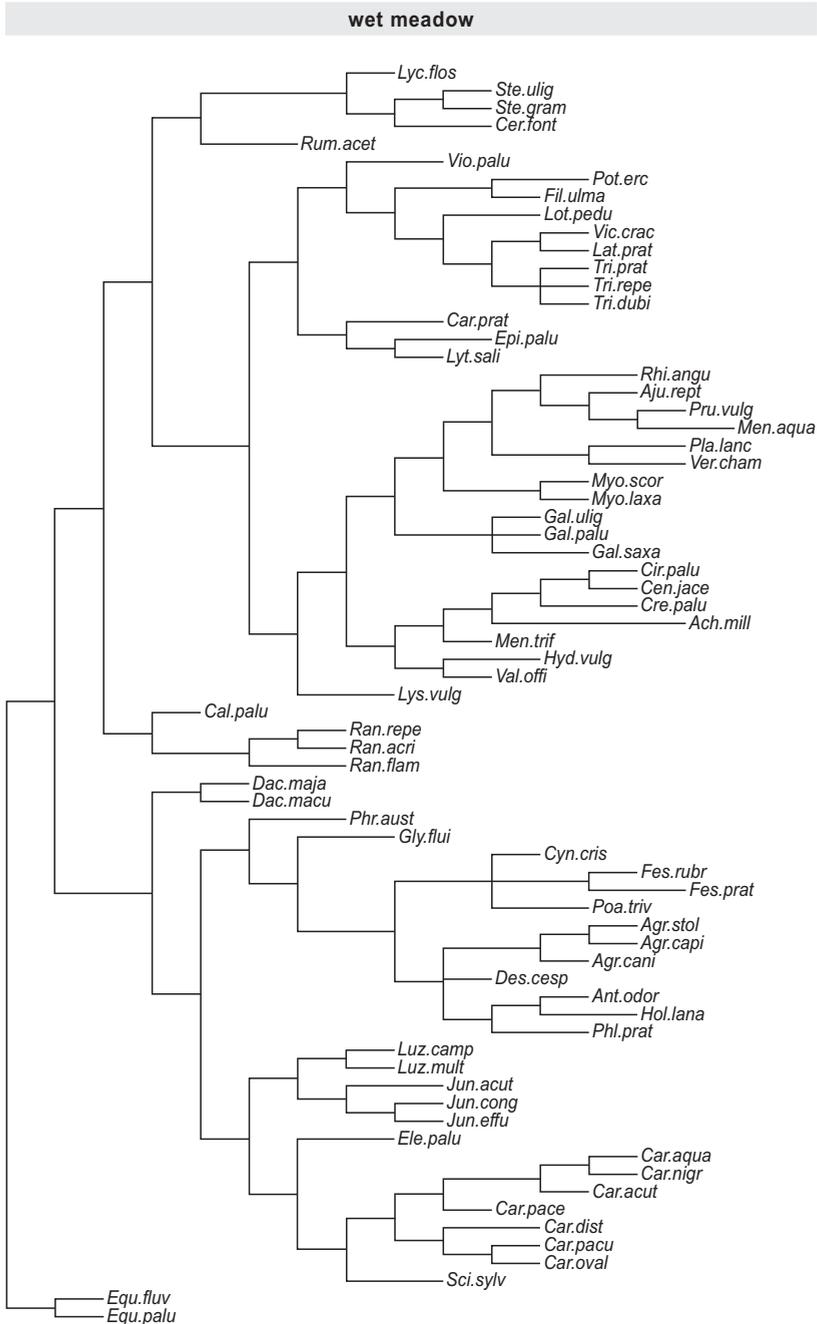
Figure S 2.6 Phylogenetic tree of the wet meadow species pool. The phylogeny of the species follows Prinzing et al. (2008), who used the topology of the central European species pool (Durka 2002; checked against Bremer et al. 2003 and http://www.tolweb.org/tree/). The nomenclature of the species follows Van der Meijden (1996).
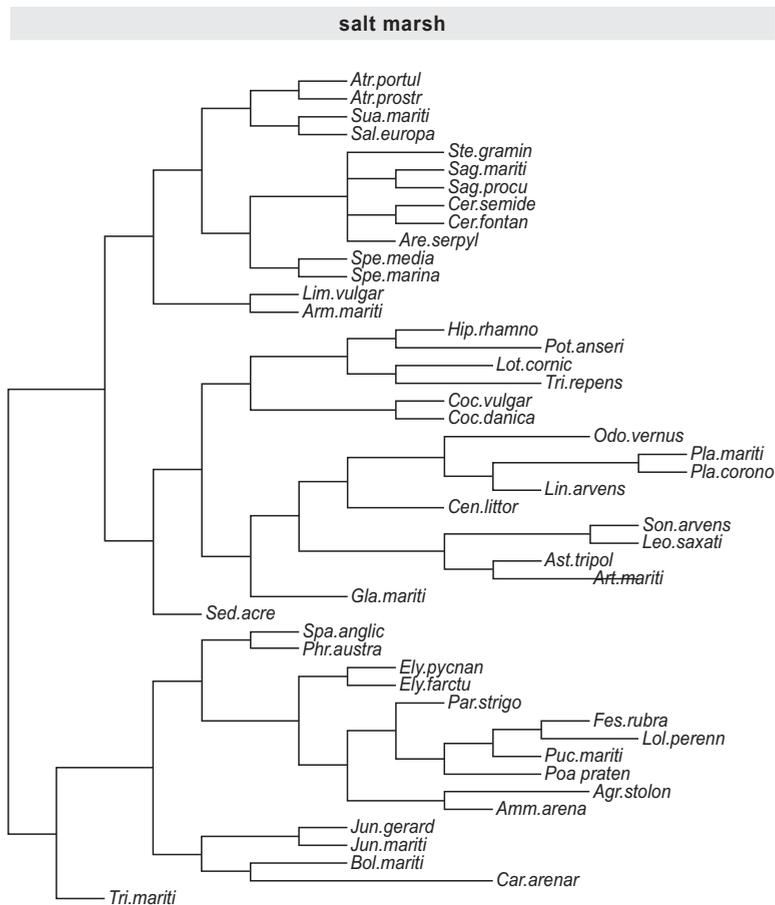
Figure S 2.7 Phylogenetic tree of the salt marsh species pool. Source for phylogeny same as in Figure S 2.6. Same nomenclature as in Figure S 2.6.