Intraspecific variability and trait-based community assembly

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Summary

1. Trait-based approaches applied to community ecology have led to a considerable advance in understanding the effect of environmental filters on species assembly. Although plant traits are known to vary both between and within species, little is known about the role of intraspecific trait variability in the non-random assembly mechanisms controlling the coexistence of species, including habitat filtering and niche differentiation.

2. We investigate the role of intraspecific variability in three key functional traits – specific leaf area (SLA), leaf dry matter content (LDMC) and height – in structuring grassland communities distributed along a flooding gradient. We quantified the contribution of intraspecific variability relative to interspecific differences in the trait–gradient relationship, and we used a null model approach to detect patterns of habitat filtering and niche differentiation, with and without intraspecific variability.

3. Community mean SLA and height varied significantly along the flooding gradient and intraspecific variability accounted for 44% and 32%, respectively, of these trait–gradient relationships. LDMC did not vary along the gradient, with and without accounting for intraspecific variability. Our null model approach revealed significant patterns of habitat filtering and niche differentiation for SLA and height, but not for LDMC. More strikingly, considering intraspecific trait variability greatly increased the detection of habitat filtering and was necessary to detect niche differentiation processes.

4. *Synthesis.* Our study provides evidence for a strong role of intraspecific trait variability in community assembly. Our findings suggest that intraspecific trait variability promotes species coexistence, by enabling species to pass through both abiotic and biotic filters. We argue that community ecology would benefit from more attention to intraspecific variability.

Key-words: community null model, determinants of plant community diversity and structure, flood meadow, gradient analysis, habitat filtering, niche differentiation, plant functional trait, species coexistence, trait plasticity

Introduction

Trait-based approaches have recently emerged as a promising way to understand the mechanisms structuring plant communities (e.g. Stubbs & Wilson 2004; Ackerly & Cornwell 2007; Cingolani *et al.* 2007; Schamp, Chau & Aarssen 2008; Webb *et al.* 2010), so much so that McGill *et al.* (2006) proposed to rebuild community ecology from plant functional traits. Several studies have investigated community assembly processes with the view that species are filtered by the environment according to their traits (Weiher & Keddy 1995). Evidence for the existence of filtering processes has been demonstrated mainly by approaches based on mean trait values (e.g. Stubbs & Wilson 2004; Kraft, Valencia & Ackerly 2008; Schamp, Chau & Aarssen 2008), without considering intraspecific variability (Lake & Ostling 2009). Indeed, a basic assumption of comparative plant ecology (Grime, Hodgson & Hunt 1988; Keddy 1992a) is that the difference in functional trait values

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between species is larger than within species (Garnier *et al.* 2001a; Shipley 2007). However, a growing number of studies have suggested that intraspecific variability can influence community structure (e.g. Whitlock *et al.* 2007). We hypothesize that incorporating intraspecific trait variability into trait-based community ecology will improve the detection of filtering processes that control the assembly of ecological communities.

Trait-based community assembly is mostly driven by two distinct non-random processes of species sorting: habitat filtering and niche differentiation. Habitat filtering selects a set of species with similar functional attributes (Fig. 1a), leading to the under-dispersion of trait values within communities (Weiher & Keddy 1995; Díaz, Cabido & Casanoves 1998; Grime 2006). On the other hand, niche differentiation prevents coexisting species from being ecologically too similar (Fig. 1a) and leads to the over-dispersion of trait values within communities (MacArthur & Levins 1967; Weiher & Keddy 1995; Grime 2006).

Plants can display large intraspecific trait variability in response to abiotic or biotic constraints (Violle *et al.* 2007). For instance, individuals of a species have been found to increase their leaf gas exchange in response

to flooding so as to cope with oxygen limitation (e.g. Mommer *et al.* 2006). Intraspecific trait variability may arise from phenotypic plasticity or genetic diversity. Plastic and genetic variations both determine species abilities to cope with changing environmental conditions and, thus, are both potentially implied in community assembly. Here, we hypothesized that intraspecific trait variability favours the inclusion of a species within a community: (i) by adjusting its trait value to the abiotic requirements and (ii) by limiting the ecological similarity with the competing species (Fig. 1b). Thus, considering intraspecific variability should improve the detection of habitat filtering and niche differentiation. Both processes can be detected using a null model approach (Gotelli & Graves 1996), where trait distribution observed in the field is compared to trait distributions in randomly assembled communities. Such random communities should be generated with regard to both inter- and intraspecific components of trait variability (Lake & Ostling 2009).

We quantified the importance of intraspecific trait variability in the assembly of grassland communities distributed along a flooding gradient. Flood meadows are particularly relevant to study the role of intraspecific variability in community ecology, due to the large intraspecific trait variability that plants can display in response to hydrology (Blom & Voesenek 1996; Mommer *et al.* 2006). We focused on intra- and interspecific variability of three key functional traits potentially involved in habitat filtering and niche differentiation processes: specific leaf area (SLA), leaf dry matter content (LDMC) and height. We quantified the contribution of intraspecific trait variability relative to interspecific differences in trait variability over the gradient. We also used a null model approach to detect non-random processes of community assembly, by considering or not considering intraspecific trait variability.
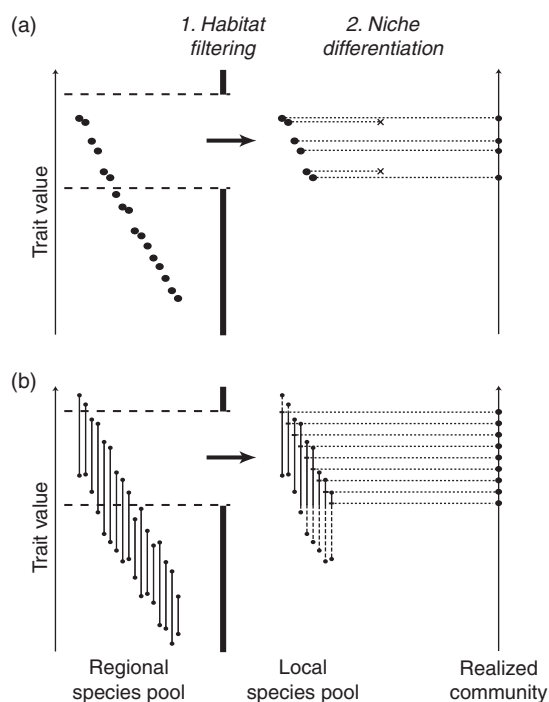
Materials and methods

STUDY AREA

The study was conducted within the Alzette floodplain (Grand-Duchy of Luxemburg, 49°31′ N, 6°01′ E) in a flood meadow. Mean annual rainfall there is 850 mm and mean annual temperature is 9 °C (Pfister *et al.* 2005). The study area is located about 100 m from the river bed. The relative elevation of the study area is 0–0.97 m. During the 2005–07 period, the area at the lowest elevation was flooded for about 7 months per year (mostly during winter and spring, see Fig. S1a in Supporting Information), while the area at the highest elevation was never flooded (Fig. S1b). Soil moisture (Time domain reflectometry probe, SDEC, Reignac sur Indre, France) measured at 16 locations along the elevation gradient decreased with increasing elevation ($r = -0.98$, $P < 0.0001$, Fig. S1c). Using elevation instead of soil moisture integrates seasonal fluctuations in soil moisture (Fig. S1a,b).

Occurrence varied significantly along the gradient for 36 of the 51 species present (results from generalized linear models, see Table S1). At low elevations, the dominant species were *Agrostis stolonifera*, *Carex disticha* and *Ranunculus repens*, accompanied by less common flood-tolerant species such as *Caltha palustris* and *Galium palustre*. At high elevations, the dominant species were *Festuca rubra*, *Trisetum*

Fig. 1. A conceptual framework describing the role of intraspecific trait variability in regulating community assembly. (a) Classical views of community assembly which do not account for intraspecific trait variability (species display mean trait values only). Within the regional pool, (1) the habitat filter selects species whose trait value matches the abiotic requirements. Within the local pool, (2) the niche differentiation leads to the selection of species that are not too ecologically similar. (b) A trait-based community assembly framework that considers intraspecific variability (a vertical bar represents the range of intraspecific trait variability displayed by a species). Intraspecific trait variability (1) improves species selection through the habitat filter by adjusting trait values to the abiotic requirements and (2) improves the niche differentiation among co-occurring species.

flavescens and *Arrhenatherum elatius*, accompanied by less common flood-intolerant species such as *Crepis biennis* and *Ranunculus bulbosus*.

SPECIES OCCURENCE

Plant species were recorded in spring 2006 in 80 1-m^2 plots that had been distributed using a stratified random sampling scheme. The elevation gradient was divided into eight equal strata, and then 10 plots were randomly distributed within the area corresponding to each stratum (see Fig. S1). The elevation of each plot was precisely recorded using a theodolite (M3 total station, Trimble Navigation Ltd., Sunnyvale, CA, USA). In each plot, we recorded the presence of all species. Species richness within plots varied from 6 to 30 species.

TRAIT DATA

We focused on three vegetative traits expected to be involved in habitat filtering and niche differentiation: (i) SLA, the ratio of fresh leaf area to leaf dry mass, (ii) LDMC, the ratio of leaf dry mass to leaf fresh mass, and (iii) height. SLA and height are known to reflect plant flooding tolerance at both inter- and intraspecifc levels, since increasing SLA and height improve plant–atmosphere gas exchange during submergence (Mommer *et al.* 2006; Voesenek *et al.* 2006). SLA and height were therefore expected to be involved in habitat filtering driven by flooding constraints. Moreover, SLA, LDMC and height are strong markers of plant resource use strategy (Westoby 1998; Weiher *et al.* 1999; Cornelissen *et al.* 2003). They were therefore expected to display niche differentiation patterns driven by resource partitioning among co-occurring species.

We measured plant traits during May and June, the period of peak biomass production, on 10 randomly selected individuals of each species at each elevation stratum. One mature, sun-exposed, healthy leaf was sampled per individual. SLA (m^2 kg^{-1}) and LDMC (g kg^{-1}) were measured after complete rehydration (Garnier *et al.* 2001b) for all species and strata. Plant height (maximum vegetative height, Cornelissen *et al.* 2003) was measured for the most common species (i.e. 38 of the 51 species in the whole study area).

The detection of non-random patterns of trait values within communities is sensitive to measurement error. To minimize this, the 10 measurements of traits in each stratum were averaged, and intraspecific trait variability was considered at the population level. According to this procedure, we implicitly assumed that the trait value of a given species in a given stratum may be attributed to any individual in any plot within the stratum. However, this assumption implies that the study area is not affected by environmental variations (climate, soil properties, management practices, etc.) other than the gradient of interest. Especially if these variations are not parallel to the gradient of interest, they can lead to a strong environmental heterogeneity within strata, with potentially strong effects on intraspecific trait variability within strata. Our study was conducted in a continuous and relatively small area which is not affected by environmental variations other than the flooding gradient. Moreover, intraspecific trait variability between elevation strata was significant for most species (Table S2), indicating that trait values varied more between than within strata.

For subsequent analyses, the stratum-averaged values of a given trait and a given species (hereafter called 'population mean traits') were used when intraspecific trait variability was considered. The trait value averaged over all strata for a given trait and a given species (hereafter called 'species mean trait') was used when intraspecific trait variability was not considered.

DATA ANALYSIS

Quantifying intra- and interspecific trait variability

For a given species and a given trait, we quantified intraspecific trait variability over the elevation gradient by calculating the coefficient of variation of the population mean trait across all strata. For a given trait, we quantified interspecific trait variability by calculating the coefficient of variation of the species mean trait among species.

For a given trait and a given elevation stratum, we calculated a 'community mean trait' as the mean trait value of all species co-occurring in the stratum by using either population mean traits or species mean traits (log-transformed data). We calculated the slope of the linear relationship between 'community mean trait' and elevation. We then quantified the contribution of intraspecific variability, relative to change in species composition, in the trait–gradient relationship as the percentage reduction in the slope of the regression when species mean traits were used instead of population mean traits (Cornwell & Ackerly 2009).

Null models

We tested for habitat filtering and niche differentiation patterns using a null model approach that generates randomly assembled communities of equal species richness as observed in field plots (Gotelli & Graves 1996). Null models were created following a two-step procedure to ensure randomness of trait values with regard to both interspecific variability (first step) and intraspecific variability (second step). The first step consisted of randomly selecting species from the total species pool comprising all recorded species (see Fig. S2). The second step consisted of randomly allocating to each previously selected species one of its population mean traits (see Fig. S2). One thousand random communities were created for each level of species richness within plots.

We calculated three metrics to detect non-random patterns of trait values within plots relatively to simulated communities. We used the mean (metric 1) and range (metric 2) of traits to detect habitat filtering. Habitat filtering is expected to shift the mean and reduce the range of the observed trait values, relatively to the null expectation (Kraft, Valencia & Ackerly 2008). We used the coefficient of variation of the nearest-neighbour distance between traits (CV_NND, metric 3) to detect niche differentiation (Kraft, Valencia & Ackerly 2008; Schamp, Chau & Aarssen 2008; Cornwell & Ackerly 2009). Niche differentiation is reflected by a lower CV_NND (i.e. trait values more evenly spaced) than expected under the null model. It is essential that the detection of niche differentiation could not be confounded with habitat filtering, i.e. that metrics of both processes are completely independent. The CV_NND is not affected by the mean of trait values, as it focuses on the distances between trait values rather than on trait values themselves. Moreover, CV_NND evaluates the variation in the relative distance between trait values but is not sensitive to the absolute value of these distances and thus to the range of trait values. In sum, the detection of niche differentiation using CV_NND cannot be confounded with the detection of habitat filtering using the mean or the range of trait values. We confirmed this by performing an additional 'restricted null model' that constrained species selection to the strata in which they have been observed, so as to control for habitat filtering. As expected, results of this supplementary analysis (Fig. S3) were equivalent to the results obtained by selecting species from the total species pool.

For a given plot, the three metrics (mean, range and CV_NND) were calculated by accounting for intraspecific trait variability (i.e. by

using population mean traits) or not (i.e. by using species mean traits, see Fig. S2). We used Wilcoxon signed-rank tests to evaluate the deviation of observed trait metrics among the 80 plots from their null expectations. Tests for the mean metric were two-tailed, since habitat filtering is expected to shift the mean of the observed trait values either above or below the null expectation. Tests for the range and CV_NND metrics were one-tailed, since habitat filtering and niche differentiation are expected to shift the range and CV_NND of the observed trait values below the null expectation. For a given plot and a given metric, we calculated the standardized effect size (SES) as:

$$SES = (I_{obs} - I_{null})/\sigma_{null}, \qquad \text{eqn 1}$$

where I_{obs} is the observed metric and I_{null} and σ_{null} are the mean and the standard deviation, respectively, of the null distribution (Gotelli & McCabe 2002). The SES quantifies, in units of standard deviation, the direction and magnitude of the deviation of each plot from the null distribution. A positive or a negative SES indicates that the observed metric is shifted above or below the mean of the null distribution, respectively.

For each plot, we quantified the contribution of intraspecific trait variability in improving the detection of habitat filtering and niche differentiation. We calculated Δ_{SES} as the difference between the SES when intraspecific trait variability was considered ($SES_{inter\ \&\ intra}$) and the SES when intraspecific trait variability was not considered (SES_{inter}). The expression of Δ_{SES} depended on whether the analysis was two-tailed or one-tailed. For the mean metric (two-tailed analysis), Δ_{SES} quantified how much intraspecific trait variability increases the deviation of the SES from the null expectation towards either positive or negative values, i.e. how much the absolute value of $SES_{inter\ \&\ intra}$ was higher than the absolute value of SES_{inter}. Therefore, Δ_{SES} was expressed as:

$$\Delta_{SES} = |SES_{inter\ \&\ intra}| - |SES_{inter}|. \qquad \text{eqn 2}$$

For the range and CV_NND metrics (one-tailed analysis), Δ_{SES} quantified how much intraspecific trait variability decreases the SES, i.e. how much $SES_{inter\ \&\ intra}$ was lower than SES_{inter}. Therefore, Δ_{SES} was expressed as:

$$\Delta_{SES} = SES_{inter} - SES_{inter\ \&\ intra}. \qquad \text{eqn 3}$$

A positive contribution of intraspecific trait variability in improving the detection of habitat filtering or niche differentiation is reflected by a positive Δ_{SES}. We used Wilcoxon signed-rank tests to evaluate the statistical significance of Δ_{SES}, by comparing $SES_{inter\ \&\ intra}$ and SES_{inter}. The randomization procedure, the calculation of trait metrics and statistical tests were carried out with the R software (R Development Core Team 2008).

Results

Coefficients of variation of species mean SLA, LDMC and height among species were 0.24, 0.30 and 0.68, respectively, while average coefficients of variation of population mean SLA, LDMC and height among elevation strata were 0.08, 0.07 and 0.10 (see Table S2 for the details by species). Interspecific trait variability in SLA, LDMC and height was therefore 2.8-, 4.5- and 6.8-fold higher, respectively, than their average intraspecific variability among elevation strata. Community mean SLA and height within the eight elevation strata showed significant negative relationships with elevation, and intraspecific variability accounted for 44% and 32%, respectively, of their slopes (Table 1). LDMC did not significantly vary along the elevation gradient.

Based on the analysis of the mean and range of traits values, we found evidence for habitat filtering acting on SLA and height. Indeed, mean SLA and height within plots were distributed above the null expectation at low elevations, and below the null expectation at high elevations (Fig. 2a–d). The range of SLA and height was, in aggregate, below the null expectation (Table 2). Intraspecific variability significantly contributed to shift the mean SLA and height towards greater departure from the null expectation, as indicated by positive and significant Δ_{SES} values (Table 3). SLA is the trait for which intraspecific variability contributed the most to the habitat filtering processes. As a consequence, accounting for intraspecific variability increased from 1% to 25% the proportion of the 80 plots where the observed mean was situated outside the 95% confidence interval of the null expectation (Fig. 2a,b). For LDMC, intraspecific variability did not significantly improve the detection of habitat filtering (Table 3).

The CV_NND was, in aggregate, below the null expectation for SLA (Fig. 2f, Table 2) and height (Table 2), providing evidence for niche differentiation. Intraspecific variability significantly decreased the CV_NND for SLA (Fig. 2e,f, Table 3) and height (Table 3), and we detected significant niche differentiation in these traits only when intraspecific variability was considered (Table 2). For LDMC, intraspecific variability tended to reduce the CV_NND ($P < 0.1$, Table 3), but not sufficiently to allow the detection of significant niche differentiation (Table 2).

Table 1. Community mean trait–gradient relationships. We give the results of linear regressions between elevation and community mean trait value calculated in each elevation stratum, by accounting for intraspecific variability (i.e. by using population mean traits) or not (i.e. by using species mean traits)

Trait	Source of trait variability	Slope	R^2	P-value
SLA	Inter- and intraspecific	−0.0079	0.52	0.043
	Interspecific	−0.0044	0.61	0.022
LDMC	Inter- and intraspecific	0.0022	0.14	0.358
	Interspecific	−0.0011	0.05	0.590
Height	Inter- and intraspecific	−0.0238	0.75	0.005
	Interspecific	−0.0161	0.66	0.014

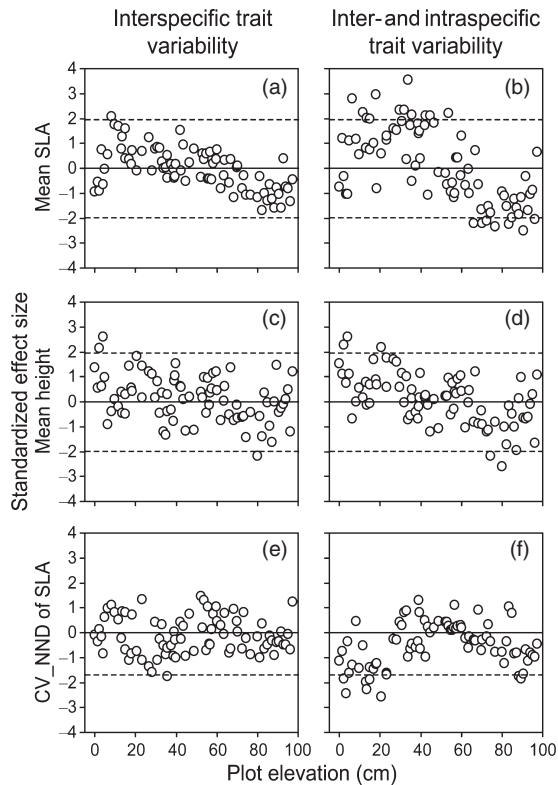SLA, specific leaf area; LDMC, leaf dry matter content.

Fig. 2. Standardized effect size (SES) of the mean specific leaf area (SLA, a, b), the mean height (c, d) and the coefficient of variation of the nearest-neighbour distance (CV_NND) of SLA (e, f) within the 80 plots as a function of elevation (the lowest elevation corresponds to the most frequently flooded site). For each trait and each metric, SES is calculated by considering intraspecific variability (right) or not (left). The dotted lines indicate the 95% confidence intervals of the null distributions (two-tailed procedure for the mean and one-tailed procedure for CV_NND). The most important and significant results are shown here; see Fig. S4 for results for all traits and all metrics.

Discussion

We used a trait-based approach to investigate the assembly of meadow communities along a flooding gradient. While most previous studies have focused only on species mean traits (e.g. Stubbs & Wilson 2004; Kraft, Valencia & Ackerly 2008; Schamp, Chau & Aarssen 2008), we also considered population mean traits in order to account for intraspecific trait

variability. For all traits, interspecific variability was higher than the intraspecific variability recorded over the gradient, confirming the general assertion that trait values vary more between than within species (Keddy 1992a; Garnier *et al.* 2001a; Shipley 2007). Nevertheless, intraspecific variability in SLA and height accounted for a considerable part (44% and 32%, respectively) of the trait–gradient relationship. These results indicate that intraspecific trait variability is important with regard to change in species composition in the response of plant communities to the flooding gradient. Community mean SLA and height significantly decreased from high to low flooding constraints. This result is consistent with ecophysiological studies that underlined the importance of these traits for species' tolerance to flooding (Mommer *et al.* 2006; Voesenek *et al.* 2006). Intraspecific variability accentuated the decreasing trend of SLA and height along the elevation gradient (Table 1). This demonstrates that intraspecific trait variability follows the same directional pattern than interspecific variability, which is a pre-requisite for intraspecific variability to be involved in species sorting through environmental filters.

Mechanisms underlying species sorting through abiotic and biotic filters were revealed thanks to a null modelling approach, which provides evidence for non-random processes of community assembly (Weiher & Keddy 1995). In accordance with the concept of habitat filtering (Keddy 1992b), we demonstrated that trait values for SLA and height within plots were more similar than expected by chance. For instance, tall species with high SLA were selected at high flooding constraints. We also provide evidence for niche differentiation, reflected by trait values more evenly spaced than expected by chance. Here, significant niche differentiation patterns were found for SLA and height, two traits already involved in habitat filtering. SLA and height are key plant functional traits reflecting the trade-off between resource capture and conservation (Westoby 1998; Wright *et al.* 2004). Even spacing of trait values is therefore consistent with the concept of niche differentiation driven by resource partitioning (MacArthur & Levins 1967; Schoener 1974).

Recently, Kraft, Valencia & Ackerly (2008) demonstrated that two distinct niche-based processes, habitat filtering and niche differentiation, structure plant communities in a tropical forest. Here, we found similar results for temperate meadow

Table 2. Detection of habitat filtering and niche differentiation using a null model approach. For each studied trait, we give the Wilcoxon signed-rank *P*-values for the deviation of the mean, range and coefficient of variation of the nearest-neighbour distance (CV_NND) within each plot from their null distribution, by considering intraspecific variability or not. The mean test was two-tailed and the range and CV_NND tests were one-tailed

Trait	Source of trait variability	Mean	Range	CV_NND
SLA	Inter- and intraspecific	0.090	0.045	< 0.0001
	Interspecific	0.935	< 0.0001	0.094
LDMC	Inter- and intraspecific	0.058	0.009	0.998
	Interspecific	0.001	0.001	0.996
Height	Inter- and intraspecific	0.125	0.038	0.021
	Interspecific	0.095	0.026	0.143

SLA, specific leaf area; LDMC, leaf dry matter content.

Table 3. Contribution of intraspecific trait variability to habitat filtering and niche differentiation. Δ_{SES} quantifies the deviation of trait metrics – mean, range and coefficient of variation of the nearest-neighbour distance (CV_NND) – calculated by considering intra-specific variability from trait metrics calculated without considering intraspecific variability. Δ_{SES} is in units of standard deviation of the null distributions. Positive values indicate a shift in trait metrics towards patterns of habitat filtering (mean and range) or niche differentiation (CV_NND) when intraspecific variability is considered. Data for Δ_{SES} correspond to the mean values calculated across the 80 plots. *P*-values from Wilcoxon signed-rank tests are given

	Mean		Range		CV_NND	
	Δ_{SES}	*P*-value	Δ_{SES}	*P*-value	Δ_{SES}	*P*-value
SLA	0.645	< 0.0001	−0.043	0.523	0.388	0.002
LDMC	0.078	0.221	−0.051	0.820	0.183	0.067
Height	0.075	0.017	−0.004	0.644	0.223	< 0.0001

SLA, specific leaf area; LDMC, leaf dry matter content.

communities distributed along a small-scale flooding stress gradient. Most strikingly, we demonstrated that incorporating intraspecific variability improved the detection of both habitat filtering and niche differentiation. Significant patterns of niche differentiation were revealed only when intraspecific trait variability of SLA and height was considered. For LDMC, although no significant niche differentiation was detected, it is notable that considering intraspecific trait variability slightly decreased the CV_NND, i.e. led to more evenly spaced trait values. Thus, our study highlights the fundamental role of intraspecific trait variability, which simultaneously drives trait convergence through habitat filtering and trait divergence through niche differentiation. On this last point, our findings reinforce the evidence provided by a recent study (Ashton *et al.* 2010) that plasticity in resource use is an important mechanism of niche differentiation among plants. We therefore support the theoretical prediction that intraspecific variability promotes species coexistence through resource partitioning (Callaway, Pennings & Richards 2003; Miner *et al.* 2005). We considered intraspecific trait variability at the population level rather than at the individual level. Since niche differentiation operates at a local scale among directly competing plants, we can expect the detection of niche differentiation to be further improved by accounting for intraspecific trait variability at the individual level. We encourage future biodiversity studies to focus on the ecology of individuals instead of populations or species to improve our understanding of species coexistence (Bolnick *et al.* 2003; Clark 2010).

This study has important implications for understanding how environmental filters influence the structure of ecological communities. We demonstrated that species are sorted according to both their species-specific mean trait value and their ability to 'fit' their trait value to the abiotic and biotic requirements. Such a mechanism of species selection implies that *a priori* 'unexpected species' (species whose mean trait values do not satisfy the abiotic and biotic requirements) are still able to pass through environmental filters (Fig. 1b). More

broadly, we demonstrated that the realized trait value – rather than species identity *per se* – is of great importance in driving community assembly (Messier, McGill & Lechowicz 2010). Our findings therefore provide support to the shift from species-centred to trait-centred community ecology (McGill *et al.* 2006; Violle & Jiang 2009). We focus on specific environmental conditions and further studies are needed to determine whether our results are generalizable to other environmental gradients involving other response traits. However, many species in different biomes are known to display intraspecific variability along various environmental gradients (e.g. Burns 2004; Hulshof & Swenson 2010). Our study is the first to address the contribution of such intraspecific variability in non-random processes of community assembly and we believe our results are likely generalizable to other ecological contexts.

Despite the growing interest in trait-based approaches to community assembly, intraspecific trait variability has not been considered in most published studies. Our results clearly call for more attention to the functional importance of intraspecific variability in community assembly. Previous studies (Madritch & Hunter 2002; Boege & Dirzo 2004; Lecerf & Chauvet 2008) have demonstrated that intraspecific trait variability can also strongly regulate ecosystem processes like decomposition or response to herbivory. While the functional structure of plant communities is increasingly used to explain ecosystem processes (Hillebrand & Matthiessen 2009), we argue that incorporating intraspecific trait variability should improve our mechanistic understanding of the effects of environmental changes on both biodiversity and ecosystem functioning.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Habitat distribution modelling of the 51 species of the study area

Table S2. Trait data for each species

Figure S1. Hydrological conditions measured in the field.

Figure S2. Detailed procedure used to collect species and trait data and to detect non-random patterns of trait values within plots.

Figure S3. Detection of niche differentiation using a 'restricted null model'.

Figure S4. Complete results of the null model approach.

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