

Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps

Francesco de Bello, Sandra Lavorel, Sébastien Lavergne, Cécile H. Albert, Isabelle Boulangeat, Florent Mazel and Wilfried Thuiller

F. de Bello (fradebello@ctfc.es), Inst. of Botany, Czech Academy of Sciences, Dukelská 135, CZ-379 82 Třeboň, Czech Republic. FDB also at: Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Univ. Joseph Fourier, BP 53 2233 Rue de la Piscine, FR-38041 Grenoble Cedex 9, France. – S. Lavorel, S. Lavergne, I. Boulangeat, F. Mazel and W. Thuiller, Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Univ. Joseph Fourier, BP 53 2233 Rue de la Piscine, FR-38041 Grenoble Cedex 9, France. – C. H. Albert, Dept of Biology, McGill Univ., 1205 Dr Penfield, Montreal, QC H3A 1B1, Canada. CHA also at: Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Univ. Joseph Fourier, BP 53 2233 Rue de la Piscine, FR-38041 Grenoble Cedex 9, France.

Understanding the influence of the environment on the functional structure of ecological communities is essential to predict the response of biodiversity to global change drivers. Ecological theory suggests that multiple environmental factors shape local species assemblages by progressively filtering species from the regional species pool to local communities. These successive filters should influence the various components of community functional structure in different ways. In this paper, we tested the relative influence of multiple environmental filters on various metrics of plant functional trait structure (i.e. 'community weighted mean trait' and components of functional trait diversity, i.e. functional richness, evenness and divergence) in 82 vegetation plots in the Guisane Valley, French Alps. For the 211 sampled species we measured traits known to capture key aspects of ecological strategies amongst vascular plant species, i.e. leaf traits, plant height and seed mass (LHS). A comprehensive information theory framework, together with null model based resampling techniques, was used to test the various environmental effects. Particular community components of functional structure responded differently to various environmental gradients, especially concerning the spatial scale at which the environmental factors seem to operate. Environmental factors acting at a large spatial scale (e.g. temperature) were found to predominantly shape community weighted mean trait values, while fine-scale factors (topography and soil characteristics) mostly influenced functional diversity and the distribution of trait values among the dominant species. Our results emphasize the hierarchical nature of ecological forces shaping local species assemblage: large-scale environmental filters having a primary effect, i.e. selecting the pool of species adapted to a site, and then filters at finer scales determining species abundances and local species coexistence. This suggests that different components of functional community structure will respond differently to environmental change, so that predicting plant community responses will require a hierarchical multi-facet approach.

Functional traits of species, e.g. measurable features affecting their fitness in a given environment, provide insights into how environmental factors shape biodiversity patterns at continental, regional and local scales (Diaz et al. 1998, Garnier et al. 2004, McGill et al. 2006, Albert et al. 2010a, Shipley 2010). Functional traits help to improve biodiversity predictions under environmental change since they capture different aspects of species' resource use and habitat requirements (Cornelissen et al. 2003, Suding et al. 2008, Thuiller et al. 2010). Nevertheless, understanding the processes driving the functional structure of ecological communities remains one of the central challenges of community ecology (Grime 2006, Cornwell and Ackerly 2009, Vileger et al. 2010, de Bello 2012). A substantial number of studies have shown that community trait composition is often influenced by different environmental factors, suggesting that natural communities are not only assembled through dispersal and

stochastic events (Petchey et al. 2007, Swenson and Enquist 2009, Shipley 2010, Vileger et al. 2010, Mason et al. 2011). One relatively well accepted ecological hypothesis suggests that, besides neutral processes, environmental drivers act as hierarchical 'filters' constraining the assemblage of communities, i.e. progressively selecting species best adapted to local conditions from the regional pool ('Environmental filtering', Fig. 1). Species would be filtered hierarchically according to sets of functional traits, first by large-scale environmental factors (e.g. climate), and subsequently by fine-scale environmental factors and biotic interactions ultimately determining their relative abundances (Woodward and Diament 1991, Weiher and Keddy 1995, Diaz et al. 1998).

This important theoretical axiom stating that environmental drivers act as hierarchical filters on species traits at different spatial scales remains, however, largely unverified empirically. Surprisingly, the response of trait assemblages

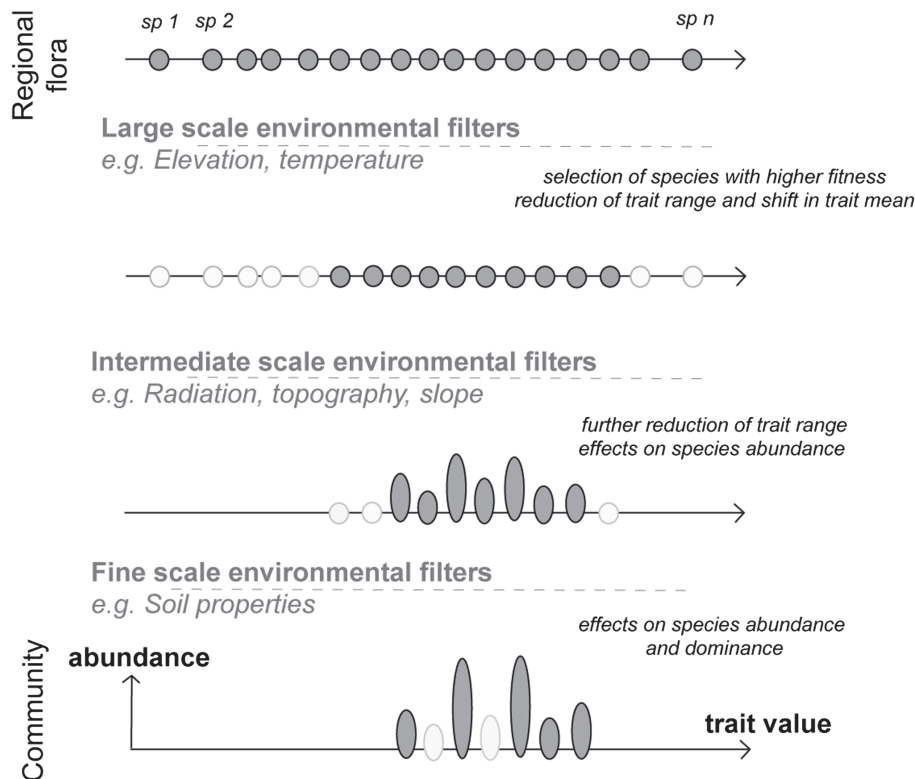


Figure 1. Expected nested filtering effects from the environmental variables considered in this study (from large-scale to fine-scale; see Introduction and Methods for more details) on the regional species pool. Given a particular regional flora formed according to different geographical and historical filters, environmental factors would filter out species whose traits reflect lower fitness for the given environmental conditions, thus reducing the range of values (e.g. compare trait ranges before and after filtering; each species is represented by a circle and ellipses expressing its position on a gradient of trait values; empty circles denote species excluded by given environmental filters; the vertical dimension of circles denotes the abundance of a given species). With increasing finer spatial scales, species with higher fitness for the given environmental conditions should become dominant and environmental filters will therefore act predominantly on the dissimilarity between species traits and on the coexistence of dominant species.

to multiple environmental factors has been assessed only in a relative small number of studies (Garnier et al. 2007, Mason et al. 2008, Cornwell and Ackerly 2009, Pakeman and Marriott 2010, Vileger et al. 2010, Meynard et al. 2011). Moreover, the functional structure of communities cannot be assessed by a single measure but rather needs a multi-faceted approach (Diaz et al. 2007, Pakeman 2011). The most relevant components of the functional structure of communities include dominant trait values (often expressed by the ‘community weighted mean’, i.e. CWM; Garnier et al. 2007, Lepš et al. 2011) and different dimensions of functional diversity, i.e. the extent of trait differences among coexisting species (Petchey and Gaston 2002, Vileger et al. 2008, Laliberte and Legendre 2010). Functional diversity can be summarized mainly by three families of metrics: functional richness (FRic), reflecting the amount (or range) of functional trait variability in a given species assemblage; functional evenness (FEve), representing the evenness of abundance distribution across species traits; and functional divergence (FDiv), capturing the degree of divergence in the abundance distribution of species functional traits (Vileger et al. 2008). These metrics are expected to express different mechanisms of community assembly and local species coexistence (Mouchet et al. 2010, Münkemüller et al. 2012). Yet, the extent to which these

different components of community functional structure respond to environmental gradients remains poorly understood (Cadotte 2011, Pakeman 2011).

The aim of this study was thus to verify empirically the hypothesis that environmental drivers act as hierarchical filters on the functional structure of plant communities. Furthermore, we tested the hypothesis that the multiple metrics of the functional structure of communities will have varying responses to environmental filtering at different spatial scales. Based on the existing literature it was expected that the prevailing climatic conditions in a region (e.g. precipitation, temperature), likely to exert larger scale filtering, would mainly affect the CWM and FRic. By excluding species possessing maladapted traits, these filters will probably reduce the range of available trait values from the regional species pool, thus shifting the mean and range of trait values in local communities across environmental gradients (Diaz et al. 1998, Grime 2006, Cornwell and Ackerly 2009, Shipley 2010). At finer scales, local environmental factors (e.g. topography, soil properties) would determine which species are expected to become dominant (Mason et al. 2011). As such, those filters should rather influence functional diversity indices which account for the relative abundance of species, i.e. this should influence FEve and FDiv, and even produce further adjustments in the values of

CWM. Specifically, environmental variables acting at smaller spatial scales related to resource availability could either reduce, or increase, trait differentiation between dominant species (Grime 2006, Mayfield and Levine 2010, Shipley 2010, Vandewalle et al. 2010, Mason et al. 2011). For example, high or low levels of resource availability at a local scale could reduce the functional dissimilarity between dominant species (therefore having lower FEve or Fdiv values) as species having traits associated with competition on the one hand, and stress tolerance on the other, would become more dominant (Grime 2006, Mayfield and Levine 2010). Alternatively, niche partitioning would favour the coexistence of functionally dissimilar dominant species (Grime 2006, Mason et al. 2011), which could be attained at high or intermediate levels of resource availability and/or when resources are locally heterogeneously distributed (Pakeman 2011, Münkemüller et al. 2012). In these cases, a significant response of functional diversity and CWM to environmental filters generally reveals non-equivalence of species in community assembly (Pillar and Duarte 2010).

In this paper, using plant community data from the Guisane Valley (French Alps) for a case study, we tested the following two hypotheses: 1) environmental factors act as filters on multiple components of community functional structure; 2) this filtering process is hierarchical, with environmental factors acting at large spatial scale shaping CMW trait values and FRic, while fine-scale factors mostly influence how trait values are distributed among the dominant species (FEve and FDiv). The environmental factors considered in the data set encompassed a wide range of climatic, topographic and fine-scale soil conditions, relevant to mountain regions. We compare these patterns with the response of taxonomical diversity, for which the connections with environmental filters are generally better known (Magurran 2004).

Methods

Study site and environmental factors

In 2007, 82 vegetation plots of 10 × 10 m were sampled along the Guisane Valley, in the French Alps (~200 km²; ~12 km long; 44.9°N, 6.6°E). In order to maximise inter-plot environmental heterogeneity, these plots were sampled according to a stratified sampling design based on two uncorrelated gradients: mean minimal temperature in winter and solar radiation in August (Albert et al. 2010b). Plots covered different vegetation and soil types (Table 1, Fig. 2). In the upper part of the valley, communities were mainly grasslands and shrublands and, in its lower part, they included also some forest stands (mainly *Larix decidua*, see Fig. 2 for more details on species composition). The herbaceous communities considered were managed with low disturbance regimes including summer grazing by sheep, cattle or horses, and mowing (Albert et al. 2010a). In each plot, we quantified species composition and percentage cover. Species cover was visually categorized into an ordinal scale (< 10%, 10–25%, 25–50%, 50–75% and > 75%).

Together with species composition, each plot was characterized by a set of environmental variables expected to

Table 1. Considered environmental variables, their units and range in the study region. Based on the results shown in Fig. 2 we expect that the variables considered in the upper part of the table are those acting at larger spatial scale on the studied plant communities; those in the lower part are those likely to be acting at a finer spatial scale. See 'Study site and environmental factors' for more details. Altitude and slope were estimated in situ. Solar radiation, topographic context and mean annual temperature were extracted from the French meteorological model Aurelhy at a 50-m resolution (Benichou and Le Breton 1987). Soil characteristics were measured using standard procedures on soil samples collected in the different plots.

Environmental factor	Unit and range considered (min.–max.)
Altitude	1513–2710 m a.s.l.
Mean annual temperature (T°)	1.7–6.7°C
Radiation	Solar radiation in August: 37767–74680 kJ m ⁻² d ⁻¹
Topographic context	Position with respect to mountain versants (5 semi-quantitative categories from valleys [lower values], to crests [higher values])
Slope inclination	5.4–42%
Soil pH	5.2–8.3
Sand percentage	2–74%

influence both species and trait composition (Table 1). The final list of environmental variables included in the analyses (Table 1) was a subset of the multiple variables estimated for each plot (Albert et al. 2010b), which were often correlated. In order to reduce collinearity we selected variables 1) with the lowest correlation (Supplementary material Appendix 1A, the maximum Pearson pair-wise correlation was $R = 0.37$ between all included variables) and prioritized those which 2) better predicted changes in species composition among plots (using forward selection on canonical correspondence analyses – CCA, with Monte Carlo permutations; Fig. 2). The effect of excluding variables in this selection (e.g. soil organic matter) is therefore captured by the effects of correlated variables included in the analyses (e.g. soil texture). Although temperature and altitude are correlated, they usually do not bear the same information. Indeed, altitude also contains information on precipitation and other factors, while temperature has the advantage of being a direct variable with a physiological influence on plants (Körner 2003). To keep both levels of information, we used residuals of the regression between altitude and temperature instead of altitude for the following analyses (Thuiller et al. 2006). These residuals provide information on altitude effects without the pervasive effect of temperature. Hereafter, 'elevation' refers to the residuals from altitude against temperature.

The CCA helped us to understand how different environmental variables explain changes in taxonomic composition. Temperature and 'elevation' variables drove the first CCA axis. These continuous gradients operate as primary environmental filters, acting at the landscape scale. Both variables are indeed the ones known to shape the general vegetation belts (i.e. montane, sub-alpine, alpine, nival), so that two geographically close sites with similar temperature and altitude are expected to have similar vegetation. Within these belts, variations in species composition were influenced by solar radiation and slope (the variables driving

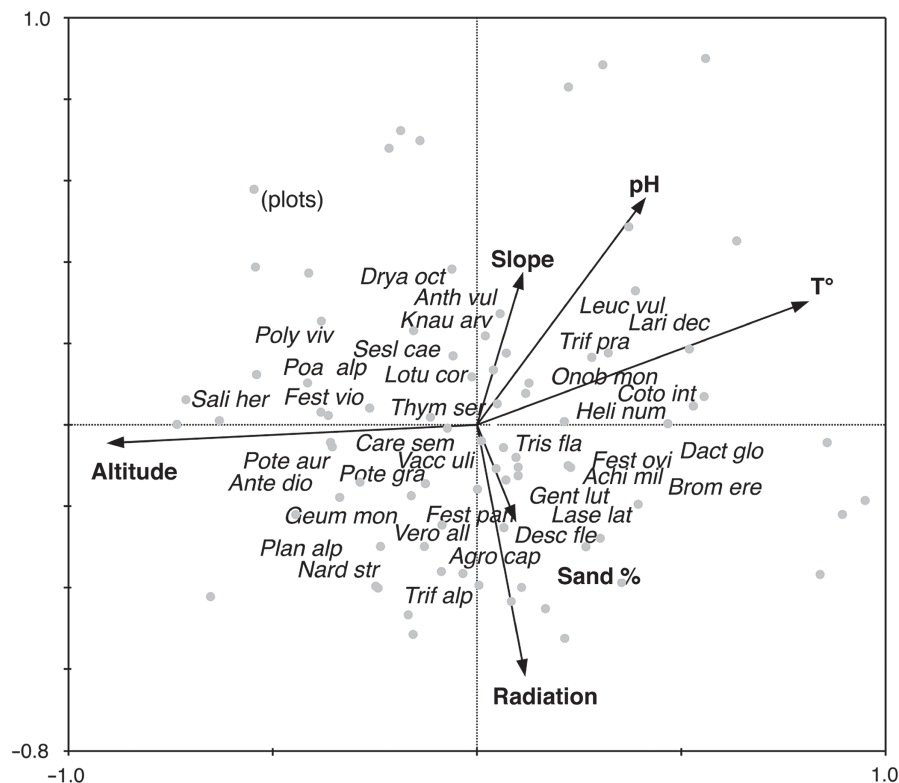


Figure 2. First two axis of canonical correspondence analysis (CCA) on community species composition. The environmental variables displayed are those selected as significant ($p < 0.05$) by a forward selection with Monte Carlo permutations (499). Grey dots indicate the 82 plots sampled. Species (labels in italics) shown are those with a higher weight on the constrained axes (their position along the axes is approximated to the centre of the labels). T° = mean annual temperature. Species: *Achillea millefolium*; *Antennaria dioica*; *Anthyllis vulneraria*; *Bromus erectus*; *Carex sempervirens*; *Cotoneaster integerrima*; *Dactylis glomerata*; *Deschampsia flexuosa*; *Dryas octopetala*; *Festuca paniculata*; *Festuca ovina*; *Festuca violacea*; *Gentiana lutea*; *Geum montanum*; *Helianthemum nummularium* subsp. *grandiflorum*; *Knautia arvensis*; *Larix decidua*; *Laserpitium latifolium*; *Leucanthemum vulgare*; *Lotus corniculatus*; *Nardus stricta*; *Onobrychis montana*; *Plantago alpina*; *Poa alpina*; *Polygonum viviparum*; *Potentilla aurea*; *Potentilla grandiflora*; *Salix herbacea*; *Sesleria caerulea*; *Thymus serpyllum*; *Trifolium alpinum*; *Trifolium pratense*; *Trisetum flavescens*; *Vaccinium uliginosum*; *Veronica allionii*.

the second CCA axis), expected to act as secondary environmental filters. Finally, soil characteristics (soil pH and sand percentage) measured at plot level drove the third CCA axis (not shown). These fine-scale variables were not spatially continuous, as two neighbouring sites could have had contrasted soil characteristics (Supplementary material Appendix 1B), and were expected to influence site productivity and resource availability. Building on these results concerning taxonomical composition (Fig. 2) and our theoretical expectations (Fig. 1), we hypothesized that the environmental variables considered would determine hierarchical filtering effects of trait community structure following the same logic. In addition to the variables significant in the forward selection ($p < 0.05$; Fig. 2), topographic position was included as another environmental variable (marginally significant in the test; $p < 0.1$) because it was not strongly correlated with the other variables already selected (Supplementary material Appendix 1A).

Plant traits

Among the 82 sampled plots, a total of 301 vascular species were found. We took a parsimonious approach by

sampling only species which represented more than 80% of the cumulated cover for each plot, being therefore considered as representative of the functional composition of the local communities (Pakeman and Quedstedt 2007). This selection resulted in a list of 211 plant species for which we measured five functional traits (see below) in at least 12 well-developed individuals per species. Traits were mostly sampled in 2008 and the previous years (Choler 2005, Lavorel et al. 2008), according to standardized protocols for plant functional trait measurements (Cornelissen et al. 2003).

Selected traits were plant vegetative height at maturity (H), leaf dry matter content (LDMC; the ratio of leaf dry mass divided by the fresh mass), specific leaf area (SLA; the ratio of dry weight leaf area), leaf nitrogen concentration (Leaf N) and seed mass. These five traits are quantitative traits reflecting key components of plant fitness and biotic interactions (Cornelissen et al. 2003, Lavergne et al. 2003, Gross et al. 2009). In particular, the leaf–height–seed combination (LHS) has proved to be a useful integrated framework to capture key plant ecological strategies (Westoby 1998, Lavergne et al. 2003). Plant height is associated to competitive vigour and to trade-offs in tolerance and avoidance of environmental stress (climate, nutrient, light), with shorter plants growing in colder conditions

(Cornelissen et al. 2003, Körner 2003). LDMC tends to scale with $1/\text{SLA}$, although the two traits may not capture the same functions (Cornelissen et al. 2003, Diaz et al. 2004). SLA and LDMC are two of a number of inter-correlated leaf traits, representing a fast–slow continuum in leaf economics across species, with slow resource-processing species expected in more stressful conditions (Diaz et al. 2004, Wright et al. 2004). Leaf nitrogen concentration, which also often correlates with SLA, tends to be closely correlated with maximum photosynthetic rate across species (on a mass base; Wright et al. 2004) and positively associated with local fertility (Lavorel et al. 2011), and is expected to increase with altitude as nitrogen mobilization increases with temperature (Körner 2003). Seed mass variation expresses a species' chance of successfully dispersing a seed into an establishment environment and a seedling's ability to survive various hazards (Westoby 1998, Cornelissen et al. 2003). Seed mass is expected to increase in dry and warmer conditions and when vegetation is taller (Pakeman et al. 2008).

Metrics of community functional structure

The functional structure of communities has multiple components which can be summarized with different metrics (Diaz et al. 2007, Lavorel et al. 2008, Vileger et al. 2008, Vandewalle et al. 2010). The first component, the 'community weighted mean' (CWM), represents the average trait value in a community weighted by relative abundance of the species carrying each value (Garnier et al. 2004, Diaz et al. 2007, Lepš et al. 2011). The index generally reflects the trait value of the dominant species in a community (Garnier et al. 2004, Vandewalle et al. 2010).

The other components describe the functional diversity within the community. They can be estimated through various metrics (Vileger et al. 2008): functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). These three diversity indices were calculated for each individual trait and also for the leaf–height–seed (LHS) scheme (Westoby 1998). For single traits, FRic corresponds to the trait range value in a given plot and reflects how much functional space is occupied in a community. As such it indicates which species possess traits well-adapted to a set of given environmental conditions (Cornwell and Ackerly 2009). FEve is calculated based on the minimum spanning tree which links all the species in a community and quantifies the regularity with which species abundances in a community are distributed among coexisting species depending on their trait values (Vileger et al. 2008). The index is expected to show whether species coexistence is based on full occupation of the niche space available (corresponding to higher functional evenness; Mason et al. 2005). FDiv quantifies how much dominant species diverge in their trait values using trait dissimilarity weighted by species abundance (Mason et al. 2005), which was computed here with the Rao quadratic entropy index of diversity (Rao 1982). This index expresses the sum of the dissimilarities in the trait space among all possible pairs of species weighted by the product of relative species abundances. High functional divergence is expected to indicate a high degree of niche differentiation (Mason et al. 2005).

For calculating indices based on multiple traits (i.e. LHS), we calculated species dissimilarities with the commonly used Gower distance (Lepš et al. 2006, Pavoine et al. 2009). Traits were log-transformed before calculations when necessary. To compute a LHS composite index for FRic, FEve and FDiv, we applied a weighted average for the different traits considered: we summed $1/3$ of the corresponding index for H and seed mass and $1/9$ for SLA, LDMC and leaf N to give leaf traits collectively the same weight as height and seed mass. All diversity calculations were made with the dbFD function implemented in the FD package in R (R Development Core Team, Laliberté and Shipley 2011). Together with these indices, we also considered the number of species (species richness) and the Simpson index of species diversity for each plot.

Data analysis

The effects of environmental variables on species diversity (i.e. species richness and Simpson index) and on the different metrics of the functional structure of the communities (i.e. CWM, FRic, FEve, FDiv) were quantified using generalised additive models in an information-theory approach (Burnham and Anderson 2002). Generalized additive models (GAMs) were used with the traditional cubic spline smoother of degree 4 (package gam in R). We used an inference-based modelling approach which, unlike stepwise model selection, was based on all possible sub-models from a set of explanatory variables. This approach reduced model selection bias and provided a relative measure of each predictor's importance (weight of evidence). The weight of evidence could be summarised with the Akaike weights, in which the average prediction is the sum of predictions from each sub-model weighted by the model's Akaike. To assess the goodness-of-fit of the inference-based model we calculated a pseudo- R^2 by correlating each observed variable of interest with the estimated values of the model. This overall strategy was repeated for the different metrics of interest (i.e. species richness, Simpson index, and the different metrics of the functional structure of the communities for each single trait).

The relative weight of evidence for each environmental predictor was estimated as the sum of the model Akaike weights over all models in which the selected predictor appeared. To estimate the absolute power of our findings, and provide a significance tests for variable importance, we used a stratified permutation test (Brook et al. 2006, Thuiller et al. 2007). This was created by random permutation of each predictor separately within the data set, recalculating the weight of evidence for each predictor and repeating this procedure 499 times for each predictor. The significance of each predictor was calculated by comparing the weight of evidence values in randomized vs original models. The original variables and model residuals did not show any strong autocorrelation patterns according to Mantel test, so no further explicit spatial regression approaches were needed. Spatial autocorrelation was limited, as only large-scale variables (mainly elevation and temperature) showed a certain spatial correlation (Supplementary material Appendix 1B).

Results

Species diversity indices (i.e. species richness and Simpson diversity) were significantly influenced by environmental factors acting at both large and fine scales. In particular, species diversity decreased with increasing elevation and with increasing sand percentage (Fig. 3, Supplementary material Appendix 2). The response of functional diversity combining the LHS traits only partially overlapped the response of taxonomic diversity to the same environmental factors (Fig. 3), highlighting the independence of metrics of functional structure relative to species diversity, particularly among fine-scale environmental filters. Species richness was independent of all the metrics describing functional structure, with the exception of a positive correlation with FRic SLA ($R = 0.26$, $p = 0.017$).

The most striking result was that the multiple metrics of the functional structure of plant communities responded rather differently along the investigated environmental gradients (Fig. 3, 4). First, large-scale filters (e.g. temperature, aspect, radiation) were the primary determinants of dominant trait values (CWM), while the relevance of local conditions increased for functional diversity indices (Fig. 4, Supplementary material Appendix 3). In fact, although FRic and FDiv often responded to temperature and elevation, factors such as slope, topography and soil pH were also particularly important drivers (Fig. 3, 4). Leaf N-metrics were the exception to this, as CWM leaf N was also markedly influenced by local soil characteristics (pH and sand proportion) in addition to temperature, aspect and radiation. We also expected FRic to be mainly driven by large-scale filters as opposed to FDiv and FEve, but we found little evidence for this. While FRic and FDiv often responded similarly to the environmental variables, FEve was mostly unresponsive to the different filters (see below).

In general, the community weighted mean (CWM) of different traits (e.g. height, seed mass and SLA) was better predicted by environmental predictors than diversity indices such as FRic, FEve and FDiv (26–72% of variability explained for CWM and 16–54% for FRic, FEve and FDiv, with differences in predictive capacity varying largely with the trait considered; Supplementary material Appendix 3). For plant height in particular, the response of CWM to environment was much stronger than for the three functional diversity indices ($R^2 = 0.72$ for CWM, and $R^2 = 0.42$, 0.31 and 0.43 for FRic, FEve and Fdiv, respectively). On the contrary, for traits related to resource use, such as leaf N, LDMC and SLA, the response of FRic, FEve and FDiv to environment was generally as strong as, or slightly stronger, than CWM for the same traits (Fig. 4, Supplementary material Appendix 3). Overall, the strength of response to environment was much lower for FEve than for FRic and FDiv. In addition, plant height FEve responded in a direction opposite to FRic and FDiv (Fig. 4, Supplementary material Appendix 3).

Overall, the results of the response of dominant traits (CWM) met the general expectations about plant strategies and allometry, with colder conditions and lower radiation generally selecting for short dominant species with higher leaf tissue density (Fig. 4, 5). Seed mass decreased with elevation, as taller species with higher seed mass decreased

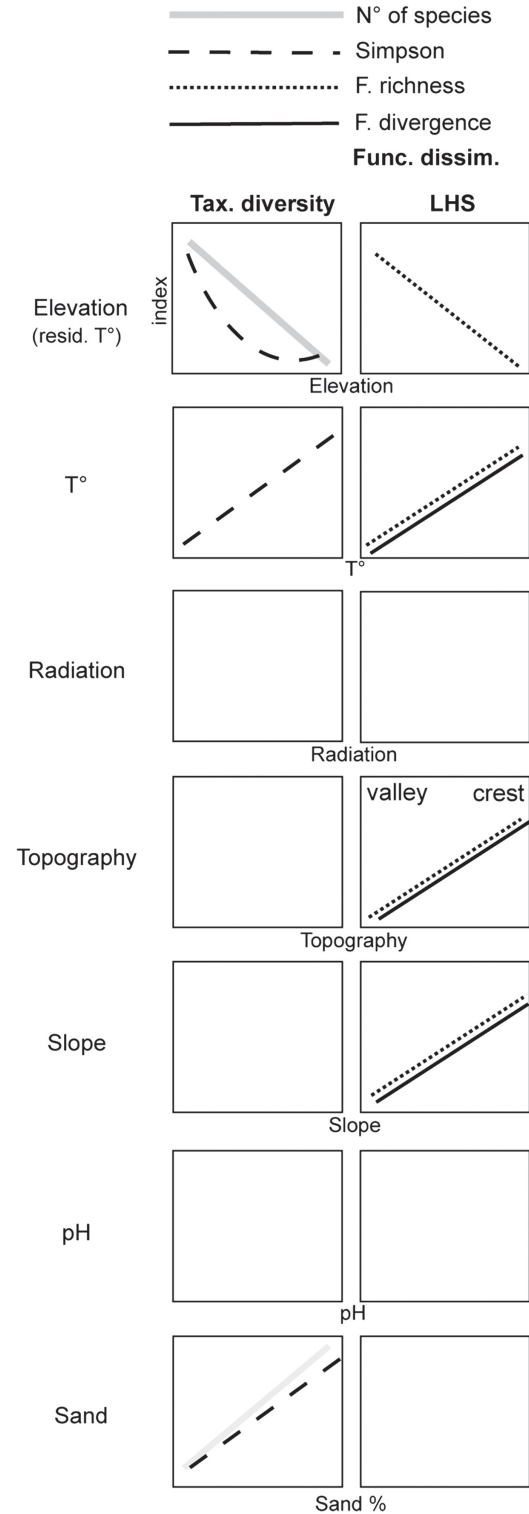


Figure 3. Schematic representation of the response of taxonomic diversity (left column) and functional diversity (right column) indices to the environmental gradients considered (the full results are shown in Supplementary material Appendix 2). For functional diversity, both functional richness and functional divergence were expressed based on multiple traits (i.e. LHS, leaf, height and seed-related traits). The relationship between environmental variables and diversity indices is schematized by using a different line for each index (the slope indicates the strength of the relationship). Only significant relationships are displayed. T° = mean annual temperature.

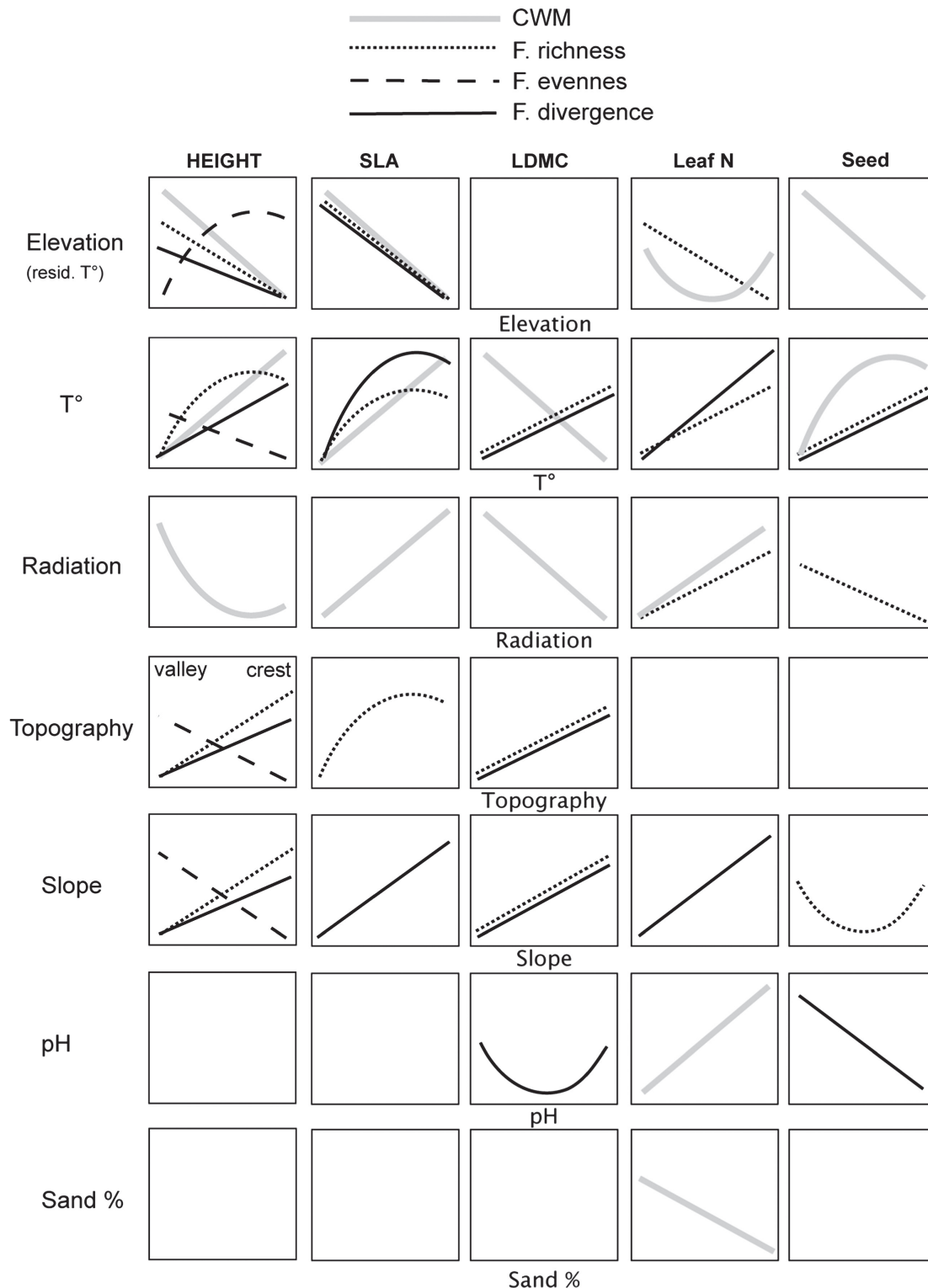


Figure 4. Schematic representation, as in Fig. 3, of the response of different metrics of plant community functional structure to the environmental gradients considered (the full results are shown in Supplementary material Appendix 3). The relationship between environmental variables and each metric is schematized for each single trait considered, by using a different line for each index (the slope indicates the strength of the relationship). Only significant relationships are displayed. T° = mean annual temperature.

(not shown). The response of CWM for leaf nitrogen was more complex, reaching lowest values at intermediate elevation and lower radiation, whereas low soil pH and high sand content partially following the presence of *Larix*

decidua and other woody species (although the relationship was generally maintained even when removing *Larix decidua* plots). Regarding the response of functional diversity, colder conditions led to lower FRic and FDiv (both for

single-trait and multi-trait measurements), indicating that such habitats were dominated by species with similar trait values. Slope inclination often increased FRic and FDiv, probably due to the coexistence of herbaceous species and various subshrubs (i.e. mostly woody chamaephytes; Supplementary material Appendix 4) and to the presence of bare ground limiting biotic interactions. FDiv for LMDC and seed mass tended to decrease towards more neutral pH values.

Discussion

In this study, we document consistent variation of various components of community functional structure along environmental gradients. These results provide interesting insights into the hierarchical effects of environmental gradients on the functional structure of plant communities (Fig. 1). First we verified that environmental factors act as filters on trait selection of species assemblages by affecting various metrics of the community trait structure (Fig. 3, 4). This confirms the lack of functional equivalence among species in their environmental preferences, which is a generally well-accepted notion especially in mountain areas worldwide, including tropical mountains (Körner 2003, Swenson et al. 2011). Second, we showed that this filtering process largely occurs at different spatial scales, i.e. species are filtered progressively from the regional species pool to local communities. To the best of our knowledge this is the first time that such patterns have been documented consistently. Third, we showed that this hierarchical filtering operates on various metrics of community functional structure at different spatial scales. In particular, we showed that dominant trait values (CWM) were, as expected, largely driven by large-scale filters, while functional diversity among coexisting species (mainly FRic and FDiv) were controlled by various filters across scales (from large to small scales).

Specifically, abiotic filtering on CWM operated mostly along large-scale environmental gradients while trait dissimilarity was more strongly affected by spatially heterogeneous factors modulating local conditions for plant growth and reproduction. Overall, in agreement with Grime (2006), the results suggest that functional diversity patterns are determined mostly after species have been ‘filtered’ from

the regional species pool by large-scale environmental factors. Once the species are selected by large-scale environmental factors (e.g. taller species with higher SLA and higher seed mass found in warmer conditions; Fig. 5), the effect of local factors on the functional dissimilarity in trait space increases. In our study, for example, sites with gentler slopes (generally associated to deeper and more productive soils, and more human disturbances) showed the lowest values in FRic and FDiv LHS (Table 2, Fig. 4). Such increased functional similarity was likely associated to an exclusion of more stress-tolerant small shrub species by more competitive herbaceous species (Supplementary material Appendix 4). This result supports findings suggesting decreased functional diversity in more benign conditions (Grime 2006, Michalet et al. 2006, Mayfield and Levine 2010, Pakeman 2011).

Another important observation was that species diversity and functional diversity varied similarly with respect to filters operating at larger spatial scales, but rather independently with respect to filters acting at finer spatial scales (Fig. 3). The response of species diversity to soil characteristics (i.e. increase with sand %), for example, was not mirrored by a marked response of community functional structure (Fig. 3, 4). This suggests a decoupling of the process of trait filtering and the number of species capable to inhabit a site. This could suggest that once larger-scale filters have imposed constraints on functional trait composition, additional processes could shape the diversity of species coexisting at the local level. The increase in species diversity at sites with higher sand content, followed only by a reduction in FDiv for leaf nitrogen, could for instance suggest an increase in trait redundancy between species, i.e. more species having more similar traits (de Bello et al. 2009). Soils with higher sand content are generally less productive, having lower organic matter and limited ability to retain water (the correlation with sand % was -0.475 and 0.42 respectively). The results would then support the view that in more productive conditions species coexistence could be partially achieved by an increase in the functional similarity between species, instead of niche differences (Mayfield and Levine 2010). Overall, the lack of strong positive relationships between species diversity and functional diversity, which has been reported (Cadotte 2011), indicate that niche differentiation does not necessarily maximize species diversity in all types of

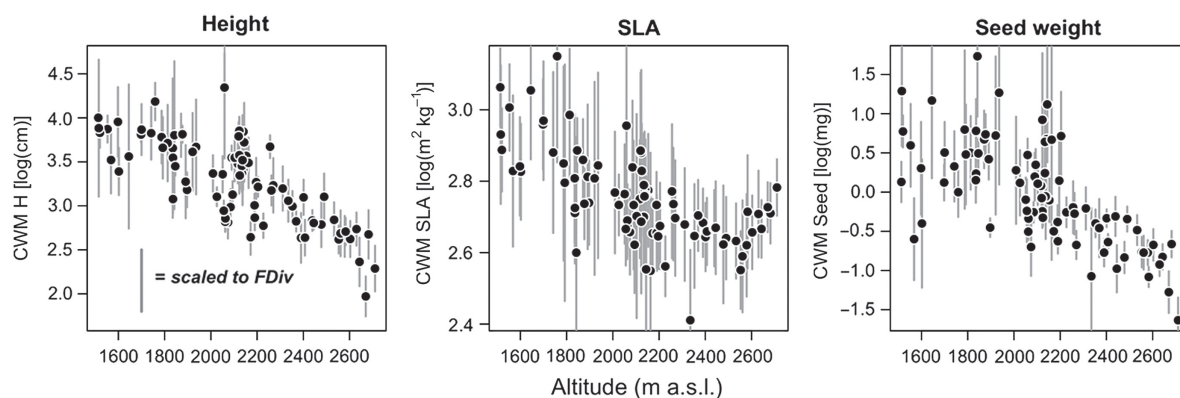


Figure 5. Variation of community-weighted means (CWM) and functional divergence (FDiv) across the altitudinal gradient considered for three traits. The extent of functional divergence is schematically expressed as a vertical bar around the CWM.

community (Gotzenberger et al. 2012). Species and functional diversities are expected to be, at least partially, correlated (Diaz and Cabido 2001), but such correlation can be dependent the ecosystem under study (Mayfield et al. 2011) and, as we show here, on the environmental filters acting on the species assembly.

The results of this study also strongly suggest that it is essential to simultaneously consider various metrics of community structure in order to assess the effect of environmental filters on biodiversity and community assembly. In this respect, the lack of strong responsiveness of FEve to the environmental filters considered, sometimes with a negative correlation to other indices of functional diversity, suggests that the behaviour of this particular index might be sometimes difficult to support with biological interpretations. This index has indeed the disadvantage of being potentially maximized by either even trait spacing or evenness in species abundance. Moreover, we suspect that FEve is also maximized at lower levels of FRic (as lower ranges will result in artificially more even trait spacing). Although FEve has proven to be of certain use (Pakeman 2011), we thus conclude here that its use should be subordinated to a better understanding of its relevance for community structure. Our results also suggest that the strength of the environmental filtering on community functional structure can largely depend on the trait considered, as hypothesized previously (Grime 2006, Mason et al. 2011). For example, for height and partially for seed weight, the response of CWM to the selected environmental factors was much stronger than for functional diversity. These results confirm the idea that the environmental filtering on dominant species with similar size and reproduction patterns is relatively more important than a filtering promoting functional differentiations for these traits (Grime 2006). On the contrary, for traits related to nutrient economy, leaf N, LDMC and SLA, which are theoretically more strongly related to nutrient partitioning between species (Cornelissen et al. 2003, Diaz et al. 2004, Stubbs and Wilson 2004), the response of trait dissimilarity indices to environmental variables was as strong, or even stronger, than for CWM. Such variability in the responses of dominant traits vs trait diversity depending on traits could remain undetected when analysing a combination of multiple traits.

Finally, the fact that particular components of community structure respond differently to environmental factors acting at various spatial scales has a crucial implication for the modelling of vegetation response to global change (Cadotte 2011, Reu et al. 2011). Our results indicate that environmental factors operating at larger spatial scales are particularly effective in predicting changes in dominant trait values (CWM) and, to a certain extent, functional diversity. However, the results also highlight that modelling trait community structure requires information on some fine-scale environmental factors (i.e. those which cannot be safely extracted from digital terrain models or are not globally available). As functional diversity is usually understood as underlying the coexistence of species and maintenance of species diversity, models overlooking such local environmental factors might produce only a partial representation and projection of vegetation, and might underestimate the importance of trait diversity (Reu et al. 2011).

Predicting biodiversity responses to environmental change will therefore require a hierarchical multi-facetted approach.

Acknowledgements – This research was conducted at the long-term research site Zone Atelier Alpes, a member of the ILTER-Europe network (ZAA publication no. 20). It was supported by the EU funded EcoChange project (FP6 European Integrated project 2007–2011, contract no. 066866 GOCE), the ANR DIVERSITALP project (ANR 2008–2011, contract no. ANR 07 BDIV 014), the CNRS PICS 4876 action and grant GACR P505/12/1296. The Station Alpine Joseph Fourier provided support during field sampling. CHA was supported by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Program (DYVERSE project, no. 272284). We thank Jan W. Jongepier for language correction.

References

- Albert, C. H. et al. 2010a. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. – *Funct. Ecol.* 24: 1192–1201.
- Albert, C. H. et al. 2010b. Intraspecific functional variability: extent, structure and sources of variation. – *J. Ecol.* 98: 604–613.
- Benichou, P. and Le Breton, O. 1987. Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. – *La Météorologie* 7: 23–34.
- Brook, B. W. et al. 2006. Minimum viable population sizes and global extinction risk are unrelated. – *Ecol. Lett.* 9: 375–382.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
- Cadotte, M. W. 2011. The new diversity: management gains through insights into the functional diversity of communities. – *J. Appl. Ecol.* 48: 1067–1069.
- Choler, P. 2005. Consistent shifts in Alpine plant traits along a mesotopographical gradient. – *Arct. Antarct. Alp. Res.* 37: 444–453.
- Cornelissen, J. H. C. et al. 2003. Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? – *J. Veg. Sci.* 14: 311–322.
- Cornwell, W. K. and Ackerly, D. D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. – *Ecol. Monogr.* 79: 109–126.
- de Bello, F. 2012. The quest for trait convergence and divergence in community assembly: are null-models the magic wand? – *Global Ecol. Biogeogr.* 21: 312–317.
- de Bello, F. et al. 2009. Relating plant species and functional diversity to community $\delta^{13}\text{C}$ in NE Spain pastures. – *Agric. Ecosyst. Environ.* 131: 303–307.
- Diaz, S. and Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. – *Trends Ecol. Evol.* 16: 646–655.
- Diaz, S. et al. 1998. Plant functional traits and environmental filters at a regional scale. – *J. Veg. Sci.* 9: 113–122.
- Diaz, S. et al. 2004. The plant traits that drive ecosystems: evidence from three continents. – *J. Veg. Sci.* 15: 295–304.
- Diaz, S. et al. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. – *Proc. Natl Acad. Sci. USA* 104: 20684–20689.
- Garnier, E. et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. – *Ecology* 85: 2630–2637.
- Garnier, E. et al. 2007. Assessing the effects of land-use change on plant traits, community and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. – *Ann. Bot.* 99: 967–985.

- Gotzenberger, L. et al. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. – *Biol. Rev.* 87: 121–127.
- Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. – *J. Veg. Sci.* 17: 255–260.
- Gross, N. et al. 2009. Linking individual response to biotic interactions with community structure: a trait-based framework. – *Funct. Ecol.* 23: 1167–1178.
- Körner, C. 2003. Alpine plant life – functional plant ecology of high mountain ecosystems. – Springer.
- Labarte, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. – *Ecology* 91: 299–305.
- Labarte, E. and Shipley, B. 2011. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. – R package ver. 1.0–11.
- Lavergne, S. et al. 2003. Do rock endemic and widespread plant species differ under the leaf–height–seed plant ecology strategy scheme? – *Ecol. Lett.* 6: 398–404.
- Lavelle, S. et al. 2008. Assessing functional diversity in the field – methodology matters! – *Funct. Ecol.* 22: 134–147.
- Lavelle, S. et al. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. – *J. Ecol.* 99: 135–147.
- Lepš, J. et al. 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. – *Preslia* 78: 481–501.
- Lepš, J. et al. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. – *Ecography* 34: 856–863.
- Magurran, A. E. 2004. Measuring biological diversity. – Blackwell.
- Mason, N. W. H. et al. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. – *Oikos* 111: 112–118.
- Mason, N. W. H. et al. 2008. Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. – *J. Anim. Ecol.* 77: 661–669.
- Mason, N. W. H. et al. 2011. Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. – *J. Ecol.* 99: 788–796.
- Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – *Ecol. Lett.* 13: 1085–1093.
- Mayfield, M. M. et al. 2011. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. – *Global Ecol. Biogeogr.* 19: 423–431.
- McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – *Trends Ecol. Evol.* 21: 178–185.
- Meynard, C. N. et al. 2011. Beyond taxonomic diversity patterns: how α , β and γ components of functional and phylogenetic diversity respond to environmental gradients across France? – *Global Ecol. Biogeogr.* 20: 893–903.
- Michalet, R. et al. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? – *Ecol. Lett.* 9: 767–773.
- Mouchet, M. A. et al. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. – *Funct. Ecol.* 24: 867–876.
- Münkemüller, T. et al. 2012. From diversity indices to community assembly processes: a test with simulated data. – *Ecography* 35: 468–480.
- Pakeman, R. J. 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. – *J. Ecol.* 99: 1143–1151.
- Pakeman, R. J. and Quested, H. M. 2007. Sampling plant functional traits: what proportion of the species need to be measured? – *Appl. Veg. Sci.* 10: 91–96.
- Pakeman, R. J. and Marriot, C. A. 2010. A functional assessment of the response of grassland vegetation to reduced grazing and abandonment. – *J. Veg. Sci.* 21: 683–694.
- Pakeman, R. J. et al. 2008. Impact of abundance weighting on the response of seed traits to climate and land use. – *J. Ecol.* 96: 355–366.
- Pavoine, S. et al. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. – *Oikos* 118: 391–402.
- Petchey, O. L. and Gaston, K. J. 2002. Functional diversity (FD), species richness and community composition. – *Ecol. Lett.* 5: 402–411.
- Petchey, O. L. et al. 2007. Low functional diversity and no redundancy in British avian assemblages. – *J. Anim. Ecol.* 76: 977–985.
- Pillar, V. D. and Duarte, L. D. S. 2010. A framework for metacommunity analysis of phylogenetic structure. – *Ecol. Lett.* 13: 587–596.
- Rao, C. R. 1982. Diversity and dissimilarity coefficients – a unified approach. – *Theor. Popul. Biol.* 21: 24–43.
- Reu, B. et al. 2011. The role of climate and plant functional trade-offs in shaping global biome and biodiversity patterns. – *Global Ecol. Biogeogr.* 20: 570–581.
- Shipley, B. 2010. Community assembly, natural selection and maximum entropy models. – *Oikos* 119: 604–609.
- Stubb, W. J. and Wilson, J. B. 2004. Evidence for limiting similarity in a sand dune community. – *J. Ecol.* 92: 557–567.
- Suding, K. N. et al. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. – *Global Change Biol.* 14: 1125–1140.
- Swenson, N. G. and Enquist, B. J. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. – *Ecology* 90: 2161–2170.
- Swenson, N. G. et al. 2011. Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. – *Proc. R. Soc. B* 278: 877–884.
- Thuiller, W. et al. 2006. Predicting patterns of plant species richness in megadiverse South Africa. – *Ecography* 29: 733–744.
- Thuiller, W. et al. 2007. Stochastic species turnover and stable coexistence in a species-rich, fire-prone plant community. – *PloS One* 2: e938.
- Thuiller, W. et al. 2010. Variation in habitat suitability does not always relate to variation in species' plant functional traits. – *Biol. Lett.* 6: 120–123.
- Vandewalle, M. et al. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. – *Biodivers. Conserv.* 19: 2921–2947.
- Villegier, S. et al. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – *Ecology* 89: 2290–2301.
- Villegier, S. et al. 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. – *Ecol. Appl.* 20: 1512–1522.
- Weih, E. and Keddy, P. A. 1995. Assembly rules, null models, and trait dispersion – new questions from old patterns. – *Oikos* 74: 159–164.
- Westoby, M. 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. – *Plant Soil* 199: 213–227.
- Woodward, F. I. and Diament, A. D. 1991. Functional approaches to predicting the ecological effects of global change. – *Funct. Ecol.* 5: 202–212.
- Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – *Nature* 428: 821–827.

Supplementary material (Appendix E7438 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.