

TECHNICAL ADVANCE

Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology

ISABELLE BOULANGEAT*, PAULINE PHILIPPE*, SYLVAIN ABDULHAK†, ROLAND DOUZET*, LUC GARRAUD†, SÉBASTIEN LAVERGNE*, SANDRA LAVOREL*, JÉRÉMIE VAN ES†, PASCAL VITTOZ‡ and WILFRIED THUILLER*

*UMR CNRS 5553, Laboratoire d'Ecologie Alpine, Université Joseph Fourier, BP 53, Grenoble Cedex 9, 38041, France, †Domaine de Charance, Conservatoire Botanique National Alpin, Gap, 05000, France, ‡Department of Ecology and Evolution, University of Lausanne, Bâtiment Biophore, Lausanne, CH-1015, Switzerland

Abstract

The pace of on-going climate change calls for reliable plant biodiversity scenarios. Traditional dynamic vegetation models use plant functional types that are summarized to such an extent that they become meaningless for biodiversity scenarios. Hybrid dynamic vegetation models of intermediate complexity (hybrid-DVMs) have recently been developed to address this issue. These models, at the crossroads between phenomenological and process-based models, are able to involve an intermediate number of well-chosen plant functional groups (PFGs). The challenge is to build meaningful PFGs that are representative of plant biodiversity, and consistent with the parameters and processes of hybrid-DVMs. Here, we propose and test a framework based on few selected traits to define a limited number of PFGs, which are both representative of the diversity (functional and taxonomic) of the flora in the Ecrins National Park, and adapted to hybrid-DVMs. This new classification scheme, together with recent advances in vegetation modeling, constitutes a step forward for mechanistic biodiversity modeling.

Keywords: biodiversity scenarios, dynamic vegetation model, emergent groups, functional diversity, functional traits, hybrid model, plant functional groups, plant functional types

Received 29 February 2012 and accepted 7 May 2012

Introduction

There is compelling evidence of a new biodiversity crisis with species already facing extinction or shifting their geographic ranges and altering their phenology in response to climate change (Parmesan, 2006; Bellard *et al.*, 2012). Effective conservation strategies to counterbalance the effects of environmental change are critical in protecting biological diversity, and need to be supported by sound biodiversity scenarios (Thuiller *et al.*, 2008). This challenge should be met by developing new tools for modeling biodiversity, which involves multiple species and aim to understand and predict changes in biological diversity (e.g., taxonomic or functional diversity). However, despite the efforts of the last 10 years, our capacity to predict the impact of environmental changes on biodiversity remains limited (Pereira *et al.*, 2010).

In this context, modeling vegetation is crucial given its pivotal role in determining overall biodiversity and ecosystem functioning. Two different approaches are traditionally used to model vegetation (Thuiller *et al.*, 2008). On one hand, phenomenological models (i.e., habitat distribution models HDMs, Table 1) can be run on thousands of species, but do not integrate certain key mechanisms (e.g., co-existence and demographic mechanisms), which could hamper their use in biodiversity and ecosystem management at regional scale (Guisan & Thuiller, 2005). On the other hand, process-based models require much more data and knowledge so they cannot be applied across large numbers of species or large spatial scales. In consequence, models depicting whole vegetation dynamics over large spatial extents, namely Dynamic Global Vegetation Models (DGVM, Table 1) usually involve just a dozen broad plant functional types (PFTs) often defined *ad hoc* and without integrating the recent knowledge of functional ecology (Harrison *et al.*, 2010). They contain consequently insufficient level of detail to represent plant diversity, in particular concerning herbaceous species

Correspondence: Isabelle Boulangeat, tel. + 33 0 476 635 733, fax + 334 76 51 42 79, e-mail: isabelle.boulangeat@gmail.com

Table 1 Main types of vegetation models. The following table lists the main types of existing vegetation models, shows how they account for the main drivers of species distribution, indicates the scale they are able to cover, and the entities they involve. A hybrid-DVM involving multiple species is the only approach to model the dynamic of biodiversity at regional scale

Model type	Abiotic	Biotic	Dispersal	Scale	Entities	Examples
Process-based						
DGVMs	Based on plant physiology and biogeochemical cycles	Sometimes competition for light/water/space	No	Low resolution (Large regions or globe)	PFT representing main forest types and 2 for grasses	LPJ (Sitch <i>et al.</i> , 2003)
Forest Gap Models	Temperature and precipitations	Competition for light and soil water	In most of the recent models	Forest patches	Only trees	TreeMig (Lischke <i>et al.</i> , 2006)
Phenomenological						
Habitat suitability models	Relationship between abiotic variables and species presence/absence observations	No	Unlimited or nothing	Regional to global, high resolution	Species	BIOMOD (Thuiller <i>et al.</i> , 2009)
Hybrid Single species	Relationship between abiotic variables and species presence/absence observations	No	Yes	Landscape	Species	Keith <i>et al.</i> (2008)
Multiple species	Relationship between abiotic variables and species presence/absence observations	Competition for light	Yes	Landscape	PFG representing dominant species	LAMOS (Albert <i>et al.</i> , 2008)

(e.g., MC1, Daly *et al.*, 2000; IBIS, Foley *et al.*, 1996; LPJ, Sitch *et al.*, 2003).

Over the last decade, hybrid dynamic vegetation models of intermediate complexity (hybrid-DVMs, Table 1) have been developed. They usually combine existing process-based models to depict successional dynamics and/or dispersal, with habitat suitability models to constrain species distribution by abiotic factors (Gallien *et al.*, 2010). To involve a sufficient number of species to represent the whole vegetation diversity at regional scale, hybrid-DVMs require modeling entities of intermediate complexity between species level and broad PFT classifications. These newly defined plant functional groups (PFGs) should be explicitly constructed in relation to the hybrid-DVM sub-models, which have to include the main factors of species distribution and dynamic. Although abiotic constraints, biotic interactions, and dispersal are explicitly included in some DGVMs, the available PFTs are not usually built to model all these ecological mechanisms. For instance, few classifications have used both the species' vegetative properties (representing their dynamic responses to environment) and species' climatic affinity (but see Laurent *et al.*, 2004).

Quite independent of the modeling field of research, functional ecology has always searched for associations

between abiotic and biotic environment and species characteristics (Calow, 1987). Significant efforts have been put into grouping species by functional characteristics to predict grassland (e.g., Lavorel *et al.*, 1998) and forest ecosystem (e.g., Verheyen *et al.*, 2003) responses to global changes. These approaches provide much more detailed PFT than the one usually modeled in DGVMs. They constitute a sensible theoretical basis for selecting relevant species characteristics with which to design new PFGs (Lavorel *et al.*, 1997; Pausas & Lavorel, 2003; Harrison *et al.*, 2010). However, moving from species-level responses to modeling biodiversity dynamics requires the inclusion of species characteristics involved in community assembly mechanisms. In this direction, Herault (2007) for instance proposed an emergent group approach that aimed to both maximize niche differentiation between groups and functional equivalence within groups.

These two different lines of investigation, on the one hand the biogeochemical approach to build PFT for DGVMs and on the other hand the functional groups defined in response to disturbance, require to be merge to enhance current plant classifications (Harrison *et al.*, 2010). In this article, we present a framework for building PFGs for hybrid-DVMs to represent vegetation dynamics and ecosystem functioning while

also depicting biodiversity. We first present the principles of the framework, its features and adaptation to different regional settings. We then apply it to regional flora (National Park in the French Alps) and test its robustness in relation to the aims of biodiversity modeling.

Conceptual and methodological framework

The framework relies on the emergent group approach (Lavorel *et al.*, 1997; Herault, 2007). A set of representative species is classified based on key biological characteristics, to determine groups of species sharing ecological strategies. We divided the framework into four steps (Fig. 1), presenting the associated concepts and underlying ecological hypotheses for each.

Selecting representative species

Dominant species are usually seen as the main drivers of vegetation dynamics and ecosystem functioning ('Biomass ratio hypothesis' (Grime, 1998). Moreover, according to the well-known species-abundance distribution (Whittaker, 1965), just a few species produce most of the community's biomass. In each vegetation strata (herbaceous, shrub, trees), these species are the most important, not only for structuring the landscape, but also explaining patterns of functional diversity. To reduce the number of candidate species for determining PFGs, we propose restricting

the classification procedure to these representative species.

Given that hybrid-DVMs may create new situations from those observed locally, the dominance criteria have to account for potential dominance, which can be estimated using the largest possible number of observations of species abundance in communities where the species occurs, even beyond the study area.

Selecting ecological characteristics for species classification

The rationale of the approach is to select a minimum set of traits or features which capture the functional divergence between species and the mechanisms modeled in hybrid-DVMs, and combine species-level responses to environmental gradients and mechanisms of community assembly (Fig. 2).

Functional ecologists have identified the key traits involved in individual plant responses to various environmental disturbances (McIntyre *et al.*, 1999; Cornelissen *et al.*, 2003). Relevant traits are called 'response traits' (Lavorel & Garnier, 2002) and mostly relate to 'vital attributes', which are key life-history characteristics determining the species sequence along vegetation succession (Noble & Slatyer, 1980). They include three groups of traits (Fig. 2, left). One group relates to plant colonization following disturbance. Two main strategies are considered: either species' persistence during the disturbance (e.g., seed dormancy, defenses against

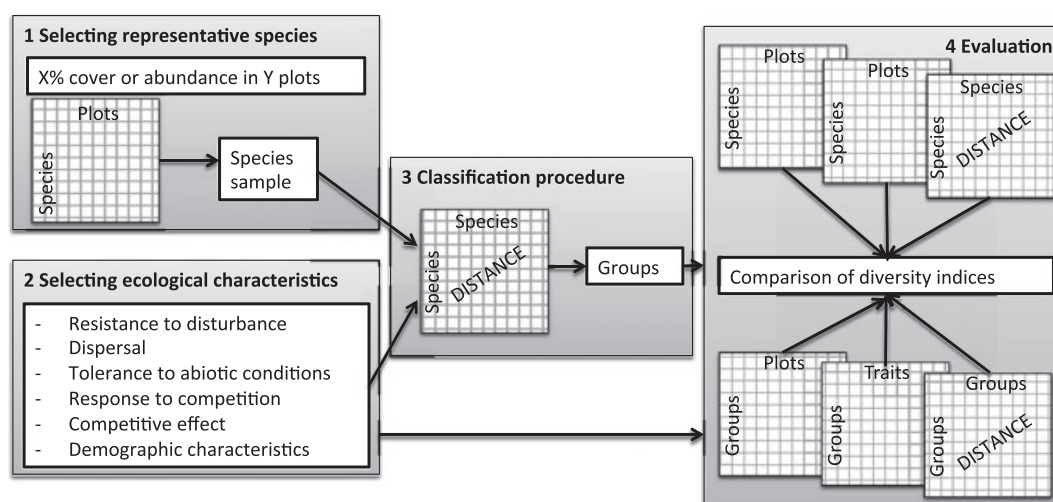


Fig. 1 Iterative steps to build Plant Functional Groups from a regional flora. The first step is the selection of a subset of the flora, which represents the dominant species, relevant to the modeling the vegetation dynamics. The second step is the selection of a limited number of key traits not only to represent the vegetation structure and ecosystem functions but also biodiversity. The third step is a classification to determine emergent groups. The fourth step aims to attribute the groups' trait values and producing diversity indices for the final evaluation.

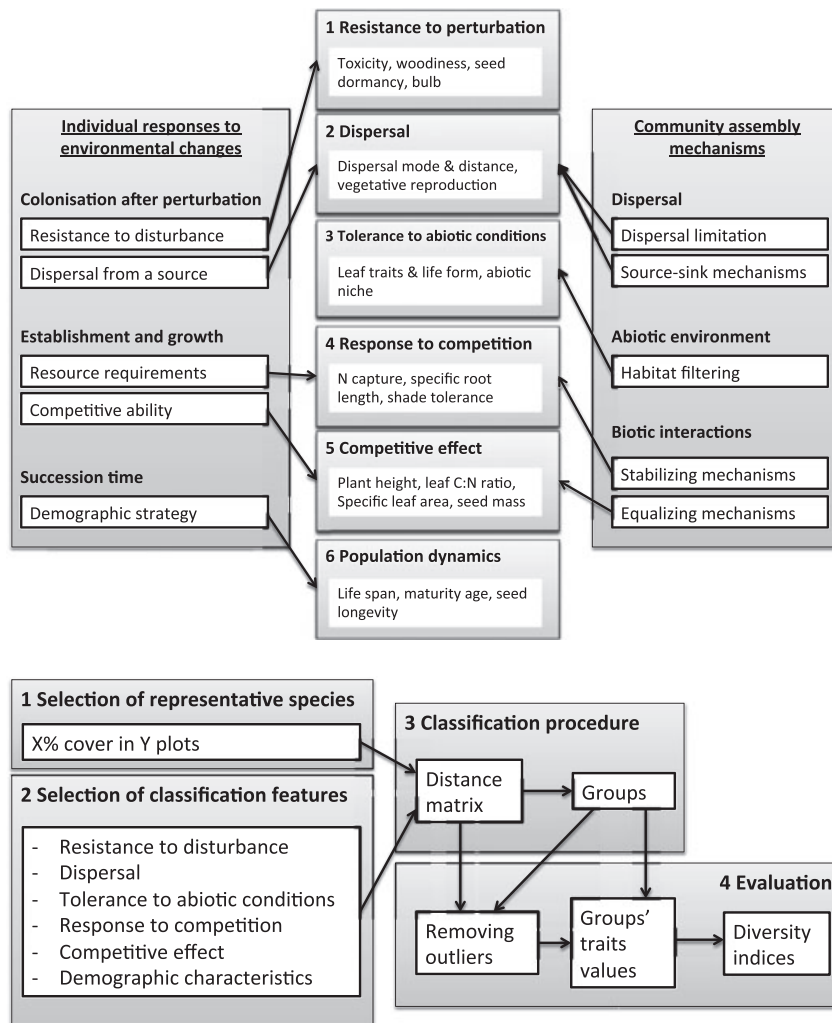


Fig. 2 The six types of mechanisms for the selection of classification features. Two theoretical frameworks are presented on the sides and are related to the six categories. Left: theoretical background from functional ecology; Right: theoretical background from community ecology; Middle: examples of traits or species characteristics are given for each category.

herbivores or fire) or colonization from a source (e.g., dispersal ability, vegetative reproduction). The second group concerns the species' ability to establish and grow, and relates to niche requirements and competitive ability (e.g., plant height or leaf traits) (Fig. 2, left). The third group concerns life-history traits influencing species position along ecological successions (e.g., maturity age, longevity) (Fig. 2, left).

To move from species-level responses to community composition and biodiversity, relevant traits must also capture community assembly mechanisms (Suding *et al.*, 2008). In doing so, we directly refer to the coexistence mechanisms implemented in hybrid-DVMs. Three types of mechanisms are commonly distinguished in community assembly theory, namely dispersal, abiotic filtering, and biotic interactions (Soberon,

2007) (Fig. 2, right). First, dispersal characteristics, although often considered in functional ecology (Pausas *et al.*, 2004; Herauld, 2007), are not included in the PFT classifications for DVMs. Dispersal mechanisms are usually involved in parts of hybrid-DVMs to reflect the spatial dynamics (e.g., dispersal limitation and source-sink mechanisms, Pulliam, 2000) and need to be represented by traits related to species dispersal distances. Second, PFGs need to explicitly merge species with similar abiotic niches, which account for the main abiotic forces of the ecosystem studied (e.g., climatic and soil variables). Although climate tolerance is closely related to some vegetative traits including in PFT classification (e.g., leaf size, leaf phenology, and life form) (Harrison *et al.*, 2010), species may also be grouped according to their abiotic niche similarity (e.g.,

Laurent *et al.*, 2004). Finally, the interest of involving multiple species or groups of species is to model biotic interactions. For instance, competition for light is often accounted in DVMs (Table 1). More generally speaking, competition for resources involves two types of mechanisms (Chesson, 2000). The equalizing mechanism implies a hierarchy of species according to their competitive effect (e.g., measured by leaf traits of plant height, Fig. 2) and results in the dominance of the best competitor. The stabilizing mechanism counterbalances the established hierarchy through niche differentiation (e.g., measured by specific root length or shade tolerance, Fig. 2) and can be considered as a response to competition. These two mechanisms are the basis for maintaining species diversity (Chesson, 2000) and have been shown to contribute to functional diversity (Navas & Violle, 2009).

By combining individual responses to environmental change and community assembly, we have identified six different features that need to be homogeneous within PFGs (Fig. 2): (1) resistance to disturbance, (2) dispersal, (3) tolerance to abiotic conditions, (4) response to competition, (5) competitive effect, and (6) demographic characteristics.

Classification procedure

Once traits and species have been selected, the aim is to reduce the number of modeling entities by defining emergent groups of species (Lavorel *et al.*, 1997; Pillar, 1999; Herault & Honnay, 2007). This issue is usually tackled using a clustering algorithm, for instance agglomerative hierarchical clustering based on a distance matrix (Pillar, 1999; Herault, 2007; Mouchet *et al.*, 2008). If the plant traits are continuous, categorical and/or ordinal, the appropriate measure is the Gower distance, which mixes categorical and quantitative traits (Pavoine *et al.*, 2005; Podani & Schmera, 2006). The agglomerative hierarchical clustering algorithm is based on the distance matrix and provides a dendrogram that is then pruned to form the groups. The choice of the number of groups can be validated using several metrics (Halkidi *et al.*, 2001).

Assessing PFGs' ability to represent biodiversity

The aim here is to evaluate how well the PFG delimitation can capture and predict biodiversity patterns using hybrid-DVMs. In addition to taxonomic diversity (TD), functional diversity (FD) is crucial as it directly relates to ecosystem functioning (Hooper *et al.*, 2005). Two FD dimensions could be considered. First, functional divergence (FDiv, Mason *et al.*, 2005) is expected to influence ecosystem processes through complemen-

tary resource use (Tilman *et al.*, 1997). Second, the functional identity of dominant species has been shown to be the most relevant determinant for some biogeochemical processes (Diaz *et al.*, 2007; Mokany *et al.*, 2008). It can be measured using the community weighted mean (CWM), which represents the expected trait value for a random community biomass sample (Garnier *et al.*, 2004).

Many elements are simplified for the purposes of clarification, including trait selection and the choice of a limited number of groups. It is therefore important to evaluate the amount of information lost during the process by comparing species-based to PFG-based functional metrics at community level. In other words, if PFG-based functional metrics are able to significantly explain species-based metrics, then the PFG classification is robust and can be used for biodiversity modeling. Species-based and PFG-based diversity measures can be compared using the classification traits, which provide information on the robustness of the clustering, and using independent traits (not used for the classification process) providing cross-validation of the trait selection procedure, and testing the robustness of newly built PFGs in capturing the main ecosystem features.

Case study: flora in the Ecrins national park, France

We applied the PFG construction framework to flora in the Ecrins National Park to represent the whole vegetation with limited number of plant functional groups that could be further modeled.

Vegetation database

The Ecrins National Park ('Ecrins' hereafter), in the French Alps (Fig. 3), is characterized by mountainous to alpine ecosystems (700–4000 m a.s.l.) and contains over 2000 plant species (Kerguelen, 1993). The National Alpine Botanical Conservatory (CBNA) provided the vegetation-plot database of flora in the surrounding region, including 11 628 community plots and 1579 species sampled between 1980 and 2009 (Fig. 3 and see Boulangeat *et al.*, 2012). Within each community plot, species cover (in its strata) was recorded in six classes (1, less than 1%; 2, 1–5%; 3, 5–25%; 4, 25–50%; 5, 50–75%; 6, up to 75%) (Braun-Blanquet, 1946). We converted these values to relative abundance using mean cover class percentages.

Application of the method

Selecting representative species. We derived species dominance from community plots over the whole region

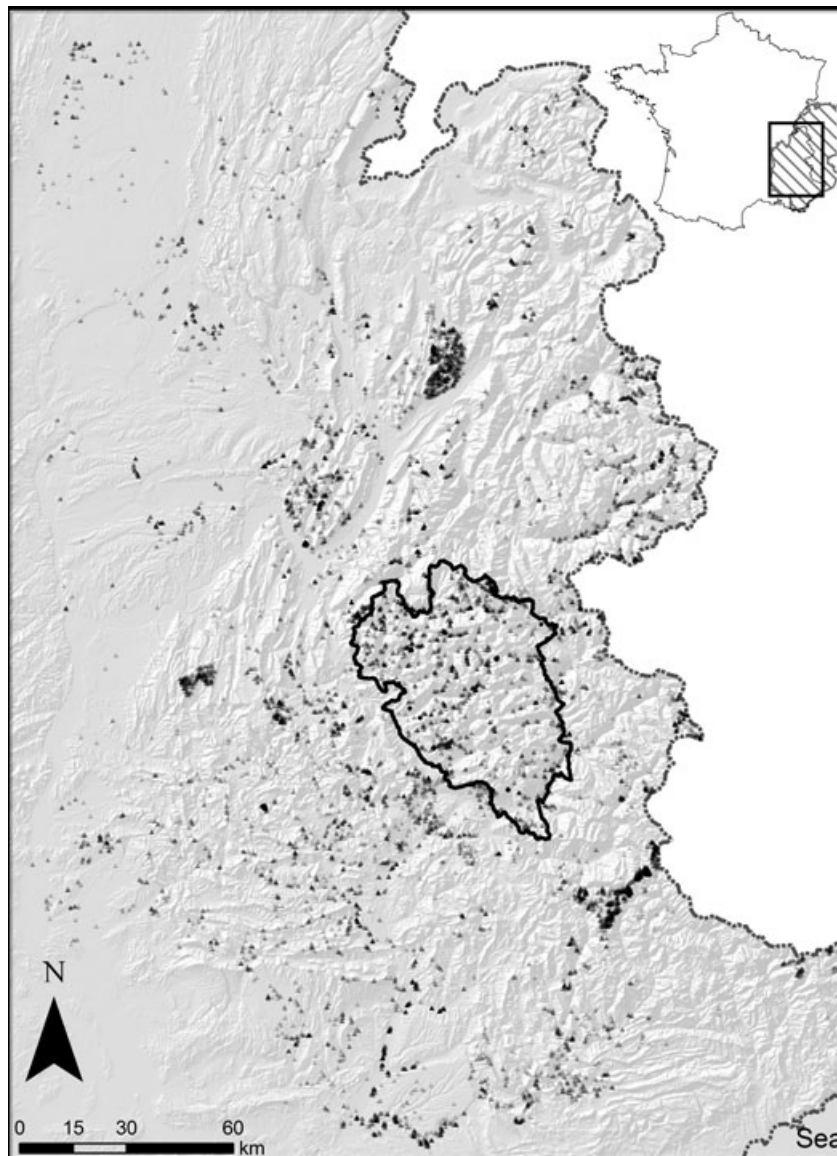


Fig. 3 Study area. The study area is located in the southeast of France in the French part of the Alpine Arc. Gray strips in the inlay indicate the Alpine Convention area. The Ecrins national park, delimited with a bold line, is situated along the Italian border, in the south-east of France, close to the Mediterranean sea. Community plots that have been surveyed in the region are represented by triangles. The hillshade background represents the elevation.

surrounding the Ecrins (11 628 plots) (Fig. 3). To select potential dominant species situated in high productivity plots with multiple strata, we selected species with a cover class above 25% (cover classes 4–6) in at least three community plots. We additionally selected species with maximum relative abundance of over 20% and median relative abundance of over 1% to account for dominant species in low productivity plots (e.g., scree, sparse grassland). From this pool of dominant species we selected the one with a minimum of 10

observations within the Ecrins. Finally, we retained 412 representative species representing together at least 70% abundance in 80% of the community plots within the Ecrins.

Selecting ecological characteristics for species classification. We chose species features to represent the six previously identified categories (Fig. 2).

1. *Resistance to disturbance:* In the Ecrins, the main disturbance being grazing by domestic stock, we used

a palatability index based on pastoral values (Jougle, 1999).

2. *Dispersal*: was represented by distances classes, extracted from Vittoz & Engler (2007) and additional determination following the same protocol. This classification is based on the most efficient dispersal mode, plant height, habitat, seed mass and dispersal attributes (e.g., wings, pappi). It identifies seven classes that discriminate a log-increase of dispersal distances.
3. *Tolerance to abiotic conditions*: We conducted a Principal Component Analysis (PCA) on 19 BIOCLIM variables (biologically meaningful variables derived from temperature and rainfall values, see Supporting Information Table S3) (Hutchinson *et al.*, 2009) at 250 m resolution in the Ecrins. Pairwise similarities of species abiotic niches were estimated from the overlap of their observed distributions (D-metric, Schoener, 1970) projected into the first PCA plan (Broennimann *et al.*, 2012).
4. *Response to competition*: Because competition for light is the species interaction commonly modeled in DVMs (Table 1), we chose to depict response to competition by shade tolerance. We used an ecological indicator value for species light requirements (Landolt *et al.*, 2010), adapted to the study region.
5. *Competitive effect*: Following the same idea of species interactions modeled by competition for light, species' competitive ability was represented by plant height. This trait is also interesting as it is a good proxy for individual biomass (Moles *et al.*, 2009) thus partly representing ecosystem productivity (De Bello *et al.*, 2010b).
6. *Demographic characteristics*: Given the limited amount of available data and uncertainty related to species demography (e.g., longevity), we used a pre-classification based on Raunkiaer's life forms (Raunkiaer, 1934) that represent the main differences in demographic traits such as individual longevity, age at maturity, and fecundity (Chapin III *et al.*, 1996; Lavorel *et al.*, 1997; Lavorel & Garnier, 2002). For instance, in our data set, known maturity ages were clearly different for phanerophytes (11.57 ± 5.68 years), chamaephytes (4.36 ± 2.48 years), and other species (2.77 ± 0.80 years). As the herbaceous species were mostly hemicryptophytes (261 species), with few geophytes (34 species) and therophytes (17 species), we only distinguished three classes, namely phanerophyte, chamaephyte, and herbaceous species. The advantage of using life forms is also to capture a wide range of plant traits related to ecosystem functioning. For instance, the simple distinction between woody and non-woody

species is related litter decomposition and litter production (Dorrepaal, 2007).

Classification procedure. For each life form group (phanerophyte, chamaephyte, and herbaceous), we built a distance matrix using Gower's formula (Gower, 1971). Dominant species with missing data were removed, which restricted the set to 290 species representing together at least 70% abundance in 60% of the Ecrins' community plots. The total pairwise distance between species x and species y was as follows:

$$D(x, y) = (1/5) \cdot (|H_x - H_y| / (H_{\max} - H_{\min}) + |L_x - L_y| / N_L + |D_x - D_y| / N_D + |P_x - P_y| / N_p + (1 - O(x, y))) \quad (1)$$

where H is plant height (squared-transformed), L light class, D dispersal class (exponentially transformed), P palatability class, O climatic overlap (Schoener's D metric), and N_t the number of classes for trait t . We used the Unweighted Pair Group Method with Arithmetic Mean clustering algorithm (UPGMA, Kaufman & Rousseeuw, 1990), as it has been shown to distort the distance matrix less than other methods (Mouchet *et al.*, 2008). We used the Dunn index, the R-squared (Halkidi *et al.*, 2001), the index of Calinski & Harabasz (Calinski & Harabasz, 1974), and the average silhouette (Kaufman & Rousseeuw, 1990) to choose the number of groups.

The classification identified height phanerophyte groups (P1–P8), six chamaephyte groups (C1–C6), and 10 herbaceous groups (H1–H10) (see Supporting Information Figure S1 and Table S1). Phanerophyte groups separated pioneer trees (e.g., *Larix decidua* P4, and *Betula alba* P8) from climax trees for various types of climate (e.g., external alps P5, internal alps P6), intermediate forests (e.g., *Pinus cembra* P1, *Populus tremula* P2) and subordinate trees (e.g., *Acer opalus* P7, *Fraxinus excelsior* P3).

Chamaephyte groups distinguished between shrubs (e.g., *Alnus alnobetula* C4), dwarf shrubs (e.g., *Vaccinium myrtillus* C6, *Calluna vulgaris* C5), cushion plants (e.g., *Silene acaulis* C3), and other chamaephytes (e.g., *Teucrium chamaedrys* C1, *Cerastium uniflorum* C2). Some of these groups were found in mountainous to subalpine ecosystems (C1, C4, C5) and other modeled alpine ecosystems (C2, C3, C6).

Among the 10 herbaceous groups, one represented understorey species (*Prenanthes purpurea* H4). Two other groups represented mountainous to subalpine herbaceous, separated by their dispersal abilities either over short (*Cacalia alliariae* H6) or long distances (*Arrhenatherum elatius* H3). Four groups were mostly found in subalpine ecosystems and differed in terms

Table 2 Correlations between species-based and PFG-based diversity metrics. The number of species involved in the comparison varies according to the availability of trait data. $N = 1902$ plots corresponds to all community plots in the Ecrins national park. $N = 1128$ plots corresponds to the well-represented plots, where dominant species represent at least 70% of the abundance. Three different Community Weighted Means are computed for plant height (CWM_H), mowing tolerance (CWM_M) and seed mass (CWM_S). Three different functional divergence measures are proposed, with varying trait combinations. FD_C (classification traits): plant height, Raunkiaer life form, and dispersal distance class. FD_I (independent traits): Mowing tolerance, woodiness, dispersal vector, and seed mass. FD_{LHS}: plant height, seed mass, leaf traits (Leaf area, Specific Leaf Area, Leaf Dry Matter Content). TD is a measure of taxonomic diversity (Simpson index)

Species-based diversity measure	PFG-based diversity measure	Correlation $N = 1902$ plots	Correlation $N = 1128$ plots	Number of species
Classification traits				
CWM _H	CWM _H	0.96	0.99	959
FD _C	FD _C	0.77	0.90	982
Independent traits				
CWM _M	CWM _M	0.65	0.74	974
CWM _S	CWM _S	0.55	0.62	657
FD _I	FD _I	0.55	0.71	963
FD _{LHS}	FD _{LHS}	0.68	0.75	647
TD	TD	0.52	0.76	1579

of their dispersal abilities, palatability or climatic preferences (H2, H5, H7, and H10). Finally, three groups formed alpine meadows with different grazing tolerance, ranging from high (e.g., *Nardus stricta* H9, *Festuca quadriflora* H1) to low palatability (*Cirsium spinosissimum* H8).

Assessing PFGs' ability to represent biodiversity. We tested the resulting PFGs' ability to represent plant diversity by comparing species-based measurements (also including rare species originally excluded from the classification procedure) to PFG-based measurements of diversity. Using the representative species associated to each PFG we built PFG communities, with each PFG having cover class equal to the highest cover class of contributing species in each plot, followed by a standardization to estimate the PFGs' relative abundance. Concerning functional diversity, we selected several sets of traits reasonably represented in our database (i.e., involving at least 647 species, see Table 2).

The seven supplementary traits (woodiness, mowing tolerance, dispersal vector, seed mass, leaf area, specific leaf area, and leaf dry matter content) were extracted from the database ANDROSACE (Thuiller *et al.* unpublished, see Supporting Information Table S3). We attributed trait values to each PFG after removing outlier species (i.e., with mean distances to other species of the group falling outside of the 95% left-handed confidence interval) (see Supporting Information Figure S2 and Table S2).

We computed different measures of biodiversity at community scale for the 1902 Ecrins community plots sampled, and for the 1128 correctly represented ones (i.e., where PFGs represent at least 70% of plot abun-

dance). First, we computed the Community Weighted Mean (CWM) for plant height and two independent traits (i.e., not used to build PFGs), namely seed mass and mowing tolerance. Second, we used Rao Quadratic entropy as a common framework for taxonomic diversity and functional divergence (De Bello *et al.*, 2010a). We computed functional divergence for classification traits and for independent traits. In addition, we computed functional divergence using traits of the LHS scheme of ecological strategies, as proposed by Westoby (1998), because they are intended to represent the main inter-specific differences in ecological strategies.

Generally speaking, we observed strong correlations between species-based and PFG-based indices, which suggest that the main biodiversity patterns are adequately captured by our PFG classification (Table 2 and Fig. 4). Note that both functional identity (CWM) and functional divergence (FDiv) are preserved after the reduction of the overall vegetation to 24 PFGs. For classification traits, functional diversity indices (CWM_H and FDiv_C) there was a significant correlation between species-based and PFG-based implementations (Table 2), proving that there was a sufficient number of groups to represent the properties of the vegetation. Correlations for indices involving independent traits (CWM_M, CWM_S, and FDiv_I) were also strong and demonstrated that the few selected species characteristics were capable of capturing trait syndromes. Moreover, the functional divergence of the LHS scheme (FDiv_{LHS}) was well captured, showing that the main plant strategies were comprehensively summarized by the 24 PFGs. However, the associated graph showed that plots with low FDiv_{LHS} were not well classified (Fig. 4d). The robustness of the classification was also illustrated

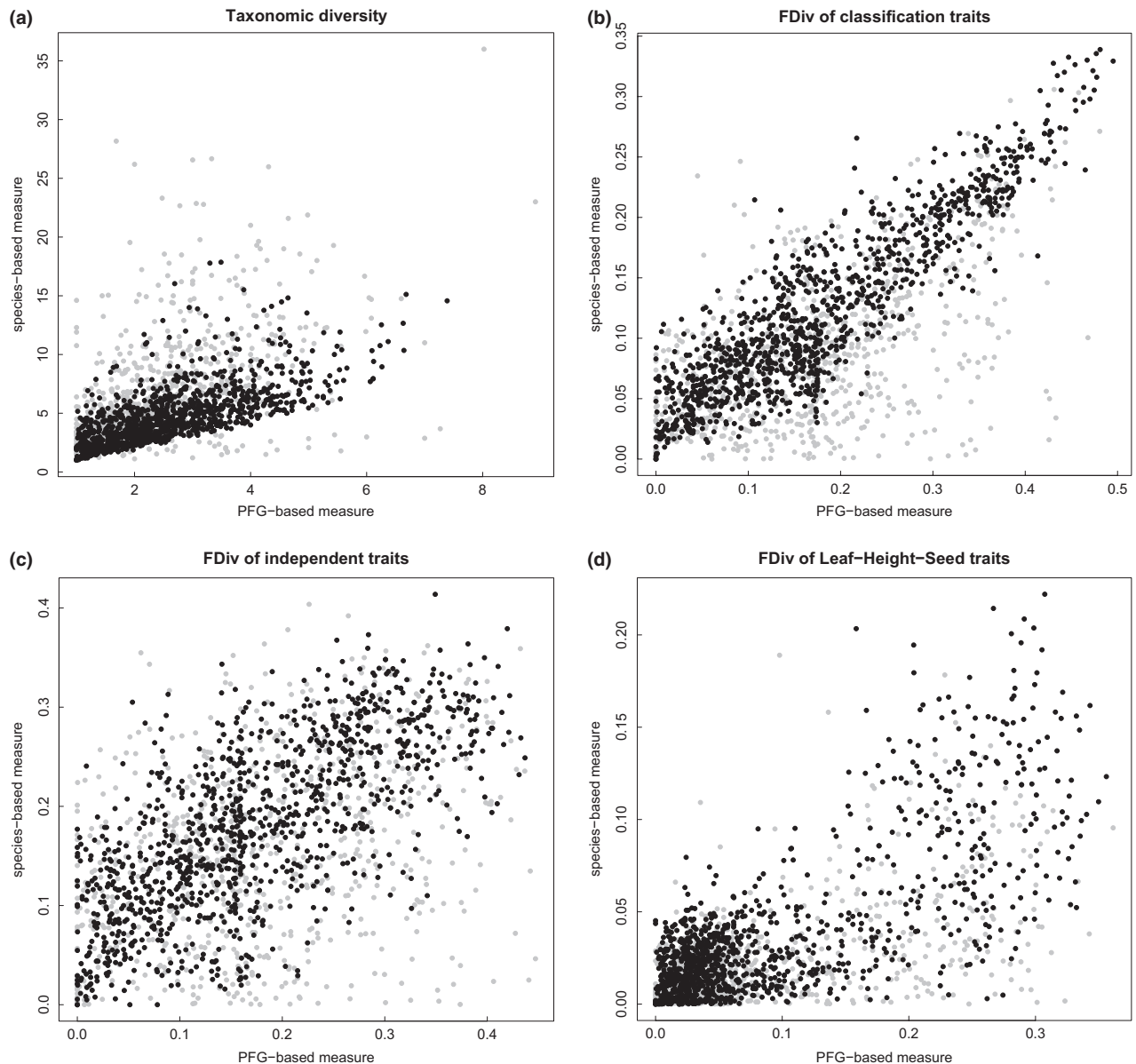


Fig. 4 Comparisons of species-based and plant functional groups (PFG)-based measurements of diversity. The following graphs show the relationship between species-based and PFG-based measurements of diversity. Results for all 1902 plots are shown as gray dots and results for the 1128 well-represented plots are shown as black dots. Four different indices are presented. (a) Taxonomic diversity. (b) Functional diversity of classification traits, including plant height, Raunkiaer life form, and dispersal distance class. (c) Functional diversity of independent traits, including mowing tolerance, woodiness, dispersal vector, and seed mass. (d) Functional diversity of Leaf-Height-Seed traits, including plant height, seed mass, and three leaf traits (Leaf area, Specific Leaf Area, Leaf Dry Matter Content).

by the limited impact of missing data and thus of dominant species. With only 70% of the species identified as representative (290 out of 412), the main diversity trends were preserved, even taking into account plots with missing representative species (Table 2). Finally, although designed to represent functional diversity, the PFGs also captured much taxonomic diversity, in particular when all the dominant species from all plots were represented (Pearson correlation = 0.76, Table 2).

Discussion

A comprehensive framework for the selection of key classification features

Previous studies have highlighted the need to move from life form-based classification to emergent group classification based on functional traits (Epstein *et al.*, 2001; Jeltsch *et al.*, 2008; Harrison *et al.*, 2010; Kattge

et al., 2011). Here, we propose a framework to include the minimum set of relevant traits with which PFG can represent the overall plant diversity (including herbaceous ecosystems), and can be used in dynamic models of vegetation at regional scale. In the example from our study, the selected traits made it possible to use 24 PFGs to depict functional identity and divergence in species assemblages, which make them suitable for assessing biodiversity. In addition, the 24 PFGs may be involved in hybrid-DVMs because they represent the main mechanisms of these models (competition for resources, tolerance to abiotic conditions, and dispersal). They consequently offer the possibility to model the spatial and temporal dynamics of biodiversity patterns at regional scale that no approach can currently provide. The main limitation to including more species and improving trait selection remains data availability, although considerable efforts have been made to compile global plant trait databases (Kattge *et al.*, 2011).

Representing diversity using a limited number of entities

The comparison between species-based and PFG-based functional diversity indices shows that although some information is lost, the variation of functional diversity between plots remains similar (Table 2). Previous studies have already showed that CWM is well described even when only the species that produce the largest proportion of the biomass are used (Garnier *et al.*, 2004; Pakeman & Quested, 2007) because these species are expected to be the determinant of ecosystem properties (Grime, 1998). Concerning taxonomic diversity, the biomass ratio hypothesis suggests that dominant species are structuring the communities, and may facilitate the establishment of subordinate species (Grime, 1998). A strong association may therefore exist between dominant and subordinate species, allowing dominant species to reflect the diversity of the entire community. However, ignoring less abundant species might make it difficult to represent the dynamics of the vegetation in certain situations. For instance, some very special habitats such as scree slopes, or peat bogs with mostly rare species might be poorly modeled.

Classifying species into groups is justified by functional redundancy (Walker, 1992), but although we assumed that dominant species represent all the relevant characteristics of the vegetation and that emergent groups are clearly distinct, it is more likely that species are positioned along a functional continuum (Westoby *et al.*, 2002). Therefore, some species may have characteristics that are shared by several groups or continuous traits that overlap between two groups. New methods need to be developed to optimize the number of

groups. For instance, they could include fuzzy classification methods (e.g., Pillar & Sosinski, 2003) and optimize correlations of functional diversity measures (with species-level based measures) in addition to traditional indices measuring homogeneity within, and heterogeneity between groups.

Future directions

The validity of plant functional classifications has been tested in the literature using experimental (e.g., Bret-Harte *et al.*, 2008; Keith *et al.*, 2008), empirical (e.g., McIntyre & Lavorel, 2001; Pausas *et al.*, 2004), and theoretical approaches (e.g., Bradstock *et al.*, 1998; Bond *et al.*, 2005). However, neither these studies nor our own account for vegetation dynamics. Additional work is needed to test the validity of these groups in a dynamic context, for instance retrieving the observed diversity and vegetation structure using a hybrid-DVM. We also suggest that our approach is tested in other regions of the world, in different biomes (Mediterranean, sub-tropical) where different ecological mechanisms are structuring the vegetation (e.g., fires rather than grazing).

Acknowledgements

The research leading to these results received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement no. 281422. IB was funded by the French 'Agence Nationale de la Recherche' with the project SCION (ANR-08-PEXT-03) and by the European Commission's FP6 ECOCHANGE project (GOCE-CT-2007-036866). We would also like to thank the Ecrins National Park (especially Cédric Dentant and Richard Bonnet), for their valuable input and insightful comments on our work. Thanks also to Version Original for checking and correcting the English language in this article.

References

- Albert CH, Thuiller W, Lavorel S, Davies ID, Garbolino E (2008) Land-use change and subalpine tree dynamics: colonization of Larix decidua in French subalpine grasslands. *Journal of Applied Ecology*, **45**, 659–669.
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.
- Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.
- Boulangeat I, Lavergne S, Van Es J, Garraud L, Thuiller W (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *Journal of Biogeography*, **39**, 204–214.
- Bradstock RA, Bedward M, Kenny BJ, Scott J (1998) Spatially-explicit simulation of the effect of prescribed burning on fire regimes and plant extinctions in shrublands typical of south-eastern Australia. *Biological Conservation*, **86**, 83–95.
- Braun-Blanquet J (1946) Über den Deckungswert der Arten in den Pflanzengesellschaften der Ordnung Vaccinio-Piceetalia. *Jahresbericht der Naturforschenden Gesellschaft Graubündens*, **130**, 115–119.
- Bret-Harte MS, Mack MC, Goldsmith GR *et al.* (2008) Plant functional types do not predict biomass responses to removal and fertilization in Alaskan tussock tundra. *Journal of Ecology*, **96**, 713–726.

- Broennimann O, Fitzpatrick MC, Pearman PB *et al.* (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, **21**, 481–497.
- Calinski RB, Harabasz J (1974) A dendrite method for cluster analysis. *Communications in Statistics*, **3**, 1–27.
- Calow P (1987) Towards a definition of functional ecology. *Functional Ecology*, **1**, 57–61.
- Chapin III FS, Bret-Harte MS, Hobbie SE, Zhong H (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, **7**, 347–358.
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.
- Cornelissen JHC, Lavorel S, Garnier E *et al.* (2003) Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–308.
- Daly C, Bachelet D, Lenihan JM, Neilson RP, Parton W, Ojima D (2000) Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications*, **10**, 449–469.
- De Bello F, Lavergne S, Meynard CN, Leps J, Thuiller W (2010a) The partitioning of diversity: showing Theseus a way out of the labyrinth. *Journal of Vegetation Science*, **21**, 992–1000.
- De Bello F, Lavorel S, Diaz S *et al.* (2010b) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, **19**, 2873–2893.
- Diaz S, Lavorel S, De Bello F, Quetier F, Grigulis K, Robson M (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 20684–20689.
- Dorrepaa E (2007) Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? *Journal of Ecology*, **95**, 1167–1180.
- Epstein HE, Chapin FS, Walker MD, Starfield AM (2001) Analyzing the functional type concept in arctic plants using a dynamic vegetation model. *Oikos*, **95**, 239–252.
- Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S, Haxeltine A (1996) An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochemical Cycles*, **10**, 603–628.
- Gallien L, Munkemüller T, Albert CH, Boulangeat I, Thuiller W (2010) Predicting potential distributions of invasive species: where to go from here? *Diversity and Distributions*, **16**, 331–342.
- Garnier E, Cortez J, Billès G *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Gower JC (1971) General coefficient of similarity and some of its properties. *Biometrics*, **27**, 857.
- Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Halkidi M, Batistakis Y, Vazirgiannis M (2001) On clustering validation techniques. *Journal of Intelligent Information Systems*, **17**, 107–145.
- Harrison SP, Prentice IC, Barboni D, Kohfeld KE, Ni J, Sutra JP (2010) Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science*, **21**, 300–317.
- Herauld B (2007) Reconciling niche and neutrality through the Emergent Group approach. *Perspectives in Plant Ecology Evolution and Systematics*, **9**, 71–78.
- Herauld B, Honnay O (2007) Using life-history traits to achieve a functional classification of habitats. *Applied Vegetation Science*, **10**, 73–80.
- Hooper DU, Chapin FS, Ewel JJ *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Hutchinson M, Xu T, Houlder D, Nix H, McMahon J (2009) *ANUCLIM 6.0 User's Guide*. Fenner School of Environment and Society, Australian National University, Canberra.
- Jeltsch F, Moloney KA, Schurr F, Köchy M, Schwager M (2008) The state of plant population modelling in light of environmental change. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 171–189.
- Jouglet JP (1999) *Les végétations des alpages des Alpes françaises du Sud: guide technique pour la reconnaissance et la gestion des milieux pâturés d'altitude*. Cemagref, Antony, France.
- Kattge J, Diaz S, Lavorel S *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.
- Kaufman L, Rousseeuw PJ (1990) *Finding Groups in Data: An Introduction to Cluster Analysis*. Wiley, New York.
- Keith DA, Akcakaya HR, Thuiller W *et al.* (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560–563.
- Kerguelen M (1993) *Index synonymique de la flore de France*. Muséum National d'Histoire Naturelle, Paris.
- Landolt E, Bäumler B, Erhardt A *et al.* (2010) *Flora Indicativa. Ecological Indicator Values and Biological Attributes of the Flora of Switzerland and the Alp*. Haupt Verlag, Berne.
- Laurent JM, Bar-Hen A, Francois L, Ghislain M, Cheddadi R (2004) Refining vegetation simulation models: from plant functional types to bioclimatic affinity groups of plants. *Journal of Vegetation Science*, **15**, 739–746.
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant trait: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution*, **12**, 471–478.
- Lavorel S, Touzard B, Lebreton JD, Clement B (1998) Identifying functional groups for response to disturbance in an abandoned pasture. *Acta Oecologica-International Journal of Ecology*, **19**, 227–240.
- Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ (2006) TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling*, **199**, 409–420.
- Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112–118.
- McIntyre S, Lavorel S (2001) Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of Ecology*, **89**, 209–226.
- McIntyre S, Lavorel S, Landsberg J, Forbes TDA (1999) Disturbance response in vegetation towards a global perspective on functional traits. *Journal of Vegetation Science*, **10**, 621–630.
- Mokany K, Ash J, Roxburgh S (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.
- Moles AT, Warton DI, Warman L *et al.* (2009) Global patterns in plant height. *Journal of Ecology*, **97**, 923–932.
- Mouchet M, Guilhaumon F, Villeger S, Mason NWH, Tomasini JA, Mouillot D (2008) Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos*, **117**, 794–800.
- Navas ML, Violle C (2009) Plant traits related to competition: how do they shape the functional diversity of communities? *Community Ecology*, **10**, 131–137.
- Noble IR, Slatyer RO (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Plant Ecology*, **43**, 5–21.
- Pakeman RJ, Quested HM (2007) Sampling plant functional traits: what proportion of the species need to be measured? *Applied Vegetation Science*, **10**, 91–96.
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.
- Pausas JG, Lavorel S (2003) A hierarchical deductive approach for functional types in disturbed ecosystems. *Journal of Vegetation Science*, **14**, 409–416.
- Pausas JG, Bradstock RA, Keith DA, Keeley JE, Network GF (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*, **85**, 1085–1100.
- Pavoine S, Ollier S, Pontier D (2005) Measuring diversity from dissimilarities with Rao's quadratic entropy: are any dissimilarities suitable? *Theoretical Population Biology*, **67**, 231–239.
- Pereira HM, Leadley PW, Proenca V *et al.* (2010) Scenarios for Global Biodiversity in the 21st Century. *Science*, **330**, 1496–1501.
- Pillar VD (1999) On the identification of optimal plant functional types. *Journal of Vegetation Science*, **10**, 631–640.
- Pillar VD, Sosinski EE (2003) An improved method for searching plant functional types by numerical analysis. *Journal of Vegetation Science*, **14**, 323–332.
- Podani J, Schmera D (2006) On dendrogram-based measures of functional diversity. *Oikos*, **115**, 179–185.
- Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- Raunkiaer C (1934) Nonsynchronous spatial overlap of lizards in patchy habitats. Clarendon Press, Oxford, UK.
- Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, **51**, 408–418.

- Sitch S, Smith B, Prentice IC *et al.* (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.
- Soberon J (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.
- Suding KN, Lavorel S, Chapin III FS *et al.* (2008) Scaling environmental change from traits to communities to ecosystems: the challenge of intermediate-level complexity. *Global Change Biology*, **14**, 1125–1140.
- Thuiller W, Albert C, Araujo MB *et al.* (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology Evolution and Systematics*, **9**, 137–152.
- Thuiller W, Lafourcade B, Engler R, Araujo MB (2009) BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.
- Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.
- Verheyen K, Honnay O, Motzkin G, Hermy M, Foster DR (2003) Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology*, **91**, 563–577.
- Vittoz P, Engler R (2007) Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica*, **117**, 109–124.
- Walker BH (1992) Biodiversity and ecological redundancy. *Conservation Biology*, **6**, 18–23.
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby M, Falster DS, Moles AT (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology System*, **33**, 125–159.
- Whittaker RH (1965) Dominance and diversity in land plant communities. *Science*, **147**, 250–260.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Evaluation of the optimal number of groups.

Figure S2. Effect of removing outlier species.

Table S1. Species in each group.

Table S2. The resulting PFGs and their classification trait values.

Table S3. BIOCLIM description of variables.

Table S4. Databases used for species traits or characteristics. As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.