Journal of Vegetation Science **24** (2013) 853–864

SPECIAL FEATURE: FUNCTIONAL DIVERSITY

A family of null models to distinguish between environmental filtering and biotic interactions in functional diversity patterns

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Keywords

Assembly rules; Biotic and abiotic filtering; Limiting similarity; Null models; Simulated communities

Nomenclature

Base de Données Nomenclaturales de la Flore de France (http://bbock.free.fr/botanica/BDNFF.php).

Received 3 April 2012
Accepted 5 November 2012
Co-ordinating Editor: Rasmus Ejrnæs

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Abstract

Questions: Traditional null models used to reveal assembly processes from functional diversity patterns are not tailored for comparing different spatial and evolutionary scales. In this study, we present and explore a family of null models that can help disentangling assembly processes at their appropriate scales and thereby elucidate the ecological drivers of community assembly.

Location: French Alps.

Methods: Our approach gradually constrains null models by: (1) filtering out species not able to survive in the regional conditions in order to reduce the spatial scale, and (2) shuffling species only within lineages of different ages to reduce the evolutionary scale of the analysis. We first tested and validated this approach using simulated communities. We then applied it to study the functional diversity patterns of the leaf–height–seed strategy of plant communities in the French Alps.

Results: Using simulations, we found that reducing the spatial scale correctly detected a signature of competition (functional divergence) even when environmental filtering produced an overlaying signal of functional convergence. However, constraining the evolutionary scale did not change the identified functional diversity patterns. In the case study of alpine plant communities, investigating scale effects revealed that environmental filtering had a strong influence at larger spatial and evolutionary scales and that neutral processes were more important at smaller scales. In contrast to the simulation study results, decreasing the evolutionary scale tended to increase patterns of functional divergence.

Conclusion: We argue that the traditional null model approach can only identify a single main process at a time and suggest to rather use a family of null models to disentangle intertwined assembly processes acting across spatial and evolutionary scales.

Introduction

The effect of biotic interactions on community structure has been predominantly studied at small spatial scales (e.g. Swenson et al. 2006), but new evidence suggests that this effect is also pervasive at large spatial scales (Gotelli et al. 2010). However, it is often difficult to detect signatures of biotic interactions in large-scale diversity patterns due to the overriding selective effect of abiotic processes (Vamosi et al. 2009).

Studies intending to infer processes of community assembly from diversity patterns often focus on niche dissimilarities between co-existing species (Kraft et al. 2007; Münkemüller et al. 2012). The level of species niche overlap in a community can be described via functional diversity indices using a set of functional traits, which reflect species' ecological characteristics (Lavorel & Garnier 2002). Under strong environmental filtering, successful species in a local habitat are more likely to share similar trait values leading to functional convergence

Doi: 10.1111/jvs.12031

(Petchey et al. 2007). Under strong competition, species with overlapping niches are less likely to co-exist leading to functional divergence (MacArthur & Levins 1967). Although theoretical predictions of functional diversity patterns are straightforward when assembly processes are considered in isolation, ecologists face difficulties in elucidating the opposing effects that biotic and abiotic processes have on patterns of functional diversity in communities when these two processes interact with each other.

The traditional approach to studying community assembly rules

The statistical approach to identify the signal of competition vs. environmental filtering is based on the idea that communities assemble through a hierarchy of ecological filters (Diamond 1975; Weiher & Keddy 1995). In the first stage of this hierarchical approach, a 'regional species pool' is defined as the set of species present in the region due to biogeographical and historical processes (Ricklefs 2004). Successive environmental factors (e.g. climate, land use or soil) filter adapted species from this 'regional pool' into a more convergent 'local species pool'. In a second stage, species from the local species pool are filtered by biotic interactions to form the 'observed communities'. When competition for resources predominates, we expect a pattern of functional divergence in the observed community relative to the local species pool.

The detection of significant patterns relies on comparing the observed functional diversity to the diversity expected under a model of random assembly from a selected species pool. Often patterns of competition can only be identified when comparing observed communities to random assemblies from the local species pool, because the regional species pool tends to be functionally too diverse. Therefore, the identification of an appropriate local species pool has been widely discussed but no consensus has yet been reached (Pärtel et al. 2011). Here, we propose to further constrain the traditional null model approach based on the regional pool composed of all species observed in the study (de Bello 2012). Our suggested constraints on this regional species pool take into account two important factors that are responsible for the differences between the regional and the local species pool: the spatial and evolutionary scales.

The effects of spatial and evolutionary scales

The spatial scale of a study can either relate to the extent of the sampling area across which the species pool has been constructed (e.g. habitat, region or continent) or to the resolution (i.e. plot size) of the study. Albeit potentially important, we do not investigate the effect of spatial resolution (Vamosi et al. 2009) in this study. Often a study with a large spatial scale includes a broad range of environmental conditions and thus a species pool with a broad range of trait values (Willis et al. 2010). Large scales thereby reinforce the detection of the effect of environmental gradients, while a small spatial scale is better suited to detect competition (Thuiller et al. 2010; Mouquet et al. 2012). The evolutionary scale is determined by the age of the lineages considered (e.g. which can delimit genera or families). We expect that it is more likely to detect environmental filtering when the evolutionary scale is large, because adaptations related to the bioclimatic niche tend to be conserved within old lineages (Crisp et al. 2009), which could mask the level of functional divergence expected between closely related competing species.

Studies exploring community patterns of functional diversity at both varying evolutionary and spatial scales are rare (e.g. Swenson et al. 2006). One interesting finding is that not only a too large spatial scale but sometimes also a too small spatial scale can hinder the detection of biotic interactions. This may happen because the species pool misses species for which the environmental conditions are suitable but which are excluded by competition from the entire study. This 'dark diversity' (*sensu* Pärtel et al. 2011) may be present in neighbouring areas or lie dormant in the soil seed bank. Including such dark diversity in the local species pool can be critical for detecting biotic interactions (de Bello et al. 2012b).

Here, we explore the interacting effects of gradually changing spatial and evolutionary scales of the species pool on patterns of functional diversity and inferred processes of community assembly. First, we present a simulation study using virtual community data generated with a process-based model that allows fine-tuning of the relative strengths of the different assembly processes present. Second, we present a field case study using plant community plots in the French Alps. We assume the patterns of functional diversity in alpine plant communities will be dominated by strong environmental filtering but biotic interactions are also likely to operate, although quite rarely discerned in such systems (e.g. Spasojevic & Suding 2012). The challenge is thus to remove the large-scale environmental filtering effects from the diversity patterns in order to detect the influence of small-scale processes. Finally, we propose a family of null models to distinguish the respective effects of environmental filtering and competition by manipulating the spatial and evolutionary scales in the statistical analyses, and test our proposed methodology with the virtual community data and the case study.

Methods

Data

Simulation study – Model overview

In a first step, we generated 10 000 independent species pools of 400 species by simulating phylogenies and trait evolution along these phylogenies, with rates of trait evolution (δ) varying over evolutionary time (Pagel 1999). Each species was characterized by a single trait that defined the species-specific niche optimum and a niche breadth that was equal for all species. The phylogenetic signal for these traits, i.e. the trend for closely related species to be more similar than distantly related species, was measured using Blomberg's K (Blomberg et al. 2003).

For each species pool, a single community was initialized with 100 individuals randomly drawn from the species pool. For each simulation step, 100 random individuals were sequentially removed from the communities and replaced by individuals from the species pool (asynchronous updating). The probability of an individual from species *i* entering the community *k*, $P_{all,i,k}$, depended on the specified assembly rules and their relative importance defined by the factors B_{env} (environmental filtering), B_{comp} (competition) and B_{abun} (recruitment) (Table S1).

$$P_{\text{all,i,k}} = \exp\big(B_{\text{env}} \times \log\left(P_{\text{env,i,k}}\right) + B_{\text{comp}} \times \log\big(P_{\text{comp,i,k}}\big) + B_{\text{abun}} \times \log\big(P_{\text{abun,i,k}}\big)\big) \quad (1)$$

$P_{env,i,k}$ modelled the environmental filter: the closer the species trait value (i.e. niche optimum of the species) was to the environmental conditions of the community *k*, the higher was its probability to enter. $P_{comp,i,k}$ modelled the competition filter: the closer the species trait value was to those of the individuals already present, the lower was its probability of entering. In this way, competition between individuals was defined as symmetric. Note that as conspecifics had the same trait values, intra-specific competition was stronger than inter-specific competition. $P_{abun,i,k}$ modelled the recruitment filter: the more abundant the species was in the community, the higher its probability of entering. This term counteracted the high intra-specific competition value generated by the competition filter (see Appendix 1 for details on how the three filters were defined).

The factors B_{abun}, B_{env} and B_{comp} weighted the importance of the three filters in community assembly. In the special case of B_{env} and B_{comp} equalling one, the equation was comparable to a Lotka-Volterra equation with inter- and intra-specific competition and a maximal growth rate dependent on environmental suitability.

We repeated each of the 100 combinations of the parameters B_{env} (five values), B_{comp} (four values) and δ (five values; Table S1) 100 times, leading to a total of 10 000 simulated communities with different assembly rules and different phylogenetic contexts.

Field case study

Study system and site. The study site was the 25-km long Guisane Valley located in the centre of the French Alps (ca. 260 km^2; 44.9° N, 6.5° E). The valley was characterized by contrasting climate conditions, with mean annual temperatures ranging from −2.7 °C to 7.7 °C. As in other valleys of the central Alps, the landscape is a mosaic of coniferous and deciduous forests, shrub heaths, sub-alpine grasslands and alpine meadows. All these habitats were represented in our data set.

Community data and distribution data. We used two databases compiled by the Alpine National Botanic Conservatory. The data used to study community patterns were from a phytosociological survey at the scale of the French Alps, from which we extracted the 95 sites for the Guisane valley (Boulangeat et al. 2012b). Sites were representative of the heterogeneity of the valley climate conditions (Albert et al. 2010). Herbaceous community plots were surveyed by expert botanists in homogeneous vegetation with a size of 100 m^2 on average. Smaller plots had a minimum of 10 m^2 and some forest plots were sampled up to 1000 m^2. The abundance estimates were based on an abundance–dominance scale using cover classes (0.5, 3, 15, 37.5, 62.5 and 87.5%) and then normalized between 0 and 1 to obtain an estimate of the relative abundance of each species. Our community data set included 542 species. The second data set used to include dark diversity into our definition of species pools was a plant occurrences database (presence-only data) covering the French Alps (3 million occurrence points for 2748 species).

Functional traits. We used the functional trait database ANDROSACE (see Appendix 2 for details). We chose three functional traits: specific leaf area, height and seed mass to describe species' ecological strategies according to the leaf–height–seed scheme (LHS; Westoby 1998). These traits are strongly related to the fundamental processes of plant life, i.e. dispersal, establishment and persistence (Weiher et al.1999), and their combination has been proved to capture well the existing variation in plant ecological strategies (Lavergne et al. 2003). Specific leaf area (SLA, i.e. light intercepting area per leaf dry mass) reflects the trade-off between resource acquisition and conservation. Height at maturity is related to competitive ability and avoidance of environmental stress (Körner 2003). Seed mass strongly influences dispersal and is related to establishment ability (Pakeman et al. 2008). We calculated functional diversity on the basis of these three traits assuming that they capture essential aspects of the niche. Given this assumption, functional diversity of a community should be a good proxy for the amount of niche overlap in the community. In our study case, the three traits described above presented a low to moderate phylogenetic signal (K ranging from 0.08 to 0.44, see Table S2) and were linked to the main environmental gradient in the study area (see Fig. S2). Due to missing data in the trait database, we excluded 169 species characterized by less than two trait values. However, the remaining species still accounted for more than 80% of the total abundance of each community (Pakeman & Quested 2007). Finally, our data set represented a total of 95 communities and 373 species.

Phylogeny. A genus-level phylogeny of alpine plants was built using the workflow proposed in Roquet et al. (2013) with DNA sequences downloaded from Genbank (see Appendix 2 for details). The tips of the phylogenetic tree were resolved with polytomies to obtain a species-level phylogeny.

Statistical analyses

Functional diversity indices

We used Rao's quadratic diversity (Rao 1982), expressed as $D^{\mathrm{R}} = \sum_i \sum_j d_{\mathrm{ij}} f_{\mathrm{i}} f_{\mathrm{j}}$, with *d*ij being a measure of the functional distance between the species *i* and *j*, and *fi* being the relative abundance of species *i* in the community (Ricotta 2005).

For the simulated study, the functional distance between species was calculated as the Euclidean distance between their trait values. For the field study case, the three continuous traits were log-transformed to conform to normality and then standardized (i.e. centred and divided by their SD). The functional distance matrix was calculated for each species pool based on the Euclidean distances. We applied the R-function *quasieuclid* to ensure the Euclidean properties of our distance matrices despite the missing data (package *ade4;* Pavoine & Dolédec 2005; R Foundation for Statistical Computing, Vienna, AT).

Null model algorithms

Randomization schemes. The spatial scale of the null models could be adapted by randomizing either 'within the regional species pool' (large spatial scale) or 'within the local species pool' (small spatial scale). We thus decreased the spatial scale of the species pool by reducing it to the pool of species with similar environmental preferences to those conditions that prevailed within each community (as introduced by Peres-Neto et al. 2001). For each community, the randomization algorithm replaced each observed species with a species from the regional pool. In the 'suitability-based randomization' (SB-R), the probability of a species being selected depended on the probability of it occurring in the community given the environmental conditions ('suitability index'). In addition, we applied the 'equiprobable randomization' traditional approach (i.e. all species have an equal probability of being selected; EQ-R).

Similarly, evolutionary scale of the null models could be adapted by randomizing either 'across all lineages' (large evolutionary scale) or 'within lineages' (small evolutionary scale). We used the partial randomization scheme proposed in Hardy & Senterre (2007). For a given age, we defined the associated lineages across the phylogeny and only permuted the species within these lineages. This procedure could be repeated for several ages, thus making it possible to pinpoint shifting points of lineage age between convergent and divergent communities ('intra-lineages randomization', IL-R, vs. 'across-lineage randomization', AL-R, where the entire tree is randomized). We tested 19 age values regularly spaced along the tree. Note that IL-R could be easily combined with SB-R to study interacting effects of reduced spatial and evolutionary scales on functional diversity patterns (Table 1).

We analysed all simulated and real communities using these 40 different randomization schemes: one combining EQ-R and AL-R (non-constrained null model), one combining SB-R and AL-R, 19 combining EQ-R and IL-R, and 19 combining SB-R and IL-R.

Suitability indices. In order to perform SB-R, suitability indices were estimated for each species in each community. We defined suitability as a species' probability of occurring in the community given the environmental conditions. For each simulated community *k* and each species *I*, the suitability index was given as $\mathrm{P}_{\mathrm{env,i,k}}$ (Equation 1, Appendix 1).

For the field data, we built a species distribution model (Guisan & Thuiller 2005) in order to estimate species' abiotic niches, and thereby their probability of occurrence according to a set of climatic and topographic variables for each species independently (see Appendix 2 for details). Based on the species distribution models, we extracted the probability of presence (suitability indices) for the 373 plant species of the community data in each of the 95 communities.

Species pools. For the simulation study, the 'true' species pools were known and could be used directly for the different null models. For the field study, we constructed a *'Reduced species pool'* (R-SP) from the species present in the 95 community plots. We further construct an *'Extended species pool'* (E-SP) by adding 350 supplementary species (characterized by at least two trait values). These species were known to be present in the Guisane valley according to the plant occurrences database but were not present in our sampled community data set. The rationale behind this strategy was to include potential dark diversity, i.e. species able to both survive the environmental conditions of the Guisane and disperse into the communities under study (Table 1). Based on the species distribution models mentioned above, we extracted the probability of presence (suitability indices) for these 350 plant species in each of the 95 communities.

Outputs of null models

For each simulated community, we calculated the rank of the observed diversity value in the distribution of 500 randomized values of each of the null models. High (low) rank values indicated higher (lower) than expected diversity under the null expectation. We chose a significance level of 5% (0.025 and 0.975 significant threshold). We then studied the distribution of ranks across communities in relation to the parameters of the simulation model and the null models.

In the communities of the Guisane valley, the 40 different randomization schemes for each of the two species pools (R-SP, E-SP) resulted in a total of 80 null models. For each null model, we used 1000 repetitions and reported the ranks of observed values in the null distributions. We controlled for the size of the sample space for the evolutionary constrained null model, i.e. the number of possible random communities that could be generated by the null model. This was done for each evolutionary scale and each community.

The number of possible random communities r_{ij}, for a community *i* and an evolutionary scale *j* defining lineages *L* was calculated as: $\log(r_{\mathrm{ij}}) = \sum_{L}\left[\log(n_{\mathrm{L}}!) - \sum_{k}\log(n_{\mathrm{L,i,k}}!)\right]$ with n_L the number of species in the lineage *L* and $n_{L,i,k}$, the number of species of the lineage *L* in the abundance class k of the community *i.*

All analyses were carried out using the software R 2.14, with the following packages: ade4, adephylo, ape, geiger, picante, spadicoR and randomForest.

Results

Simulation study

Influence of the suitability-based randomizations (spatial scale)

The null models built using both the traditional equi-probable randomization (EQ-R) and the suitability-based randomization (SB-R) correctly detected environmental filtering and competition processes when they acted in isolation (Fig. 1, upper right corner for competition, Benv = 0 and Bcomp = 10; and lower left corner for environmental filtering, Benv = 2 and Bcomp = 0). When the communities were randomly assembled (Benv = Bcomp = 0), EQ-R correctly detected neutral assembly (random diversity pattern), while SB-R wrongly indicated competition (significant divergence; Fig. 1, upper left corner). When both competition and environmental filtering were strong (Benv = 2 and Bcomp = 10), EQ-R was able to detect environmental filtering (significant convergence) but the additional use of SB-R also allowed detection of competition (Fig. 1, lower right corner); only when applied together did the two randomization schemes successfully disentangled the interplay of competition and environmental filtering. In the case of moderate environmental filtering (Benv = 0.5), EQ-R and SB-R successfully identified environmental filtering and competition if competition was also moderate (Bcomp = 1). When competition was stronger (Bcomp = 5), SB-R correctly identified competition but environmental filtering was too weak to be detected by EQ-R.

Influence of intra-lineage randomizations (evolutionary scale)

Overall, the intra-lineage randomizations (IL-R) did not better detect ecological processes than the across-lineage randomizations (AL-R). The median of the distribution of ranks was more or less constant regardless of the chosen age value for IL-R randomizations (Fig. 2, cutting at the root corresponds to AL-R) for all ecological processes.

The phylogenetic signal of trait distribution in the phylogeny only weakly influenced the outcome of IL-R and in an unexpected direction (Fig. 2). Even with a strong phylogenetic signal, the IL-R randomization scheme did not substantially increase the rank values (Table 2).

Field case study

For the restricted species pool (R-SP), a decrease of the spatial scale (i.e. use of SB-R, compared to EQ-R) only slightly shifted the ranks towards less convergent functional diversity patterns (mean rank increase of 0.09; Fig. 3, top left), showing that environmental filtering was less pervasive at smaller spatial scale, but still overwhelming. This trend was consistent across communities (98% of the communities ranks increased; Table 2).

For the sake of simplicity, we have only displayed the outcome of one IL-R null model and chose an intermediate evolutionary scale in Fig. 3 (roughly corresponding to lineages at the family or order taxonomic level). The reduction of evolutionary scales tended to increase the ranks but provided more variable results between communities than the reduction of spatial scale (Table 2). Finally, the combined reduction of spatial and evolutionary scales (using both SB-R and IL-R) most strongly increased the ranks (mean rank increase of 0.16; Fig. 3). Fifteen out of the 18 communities presenting a significant environmental filter-

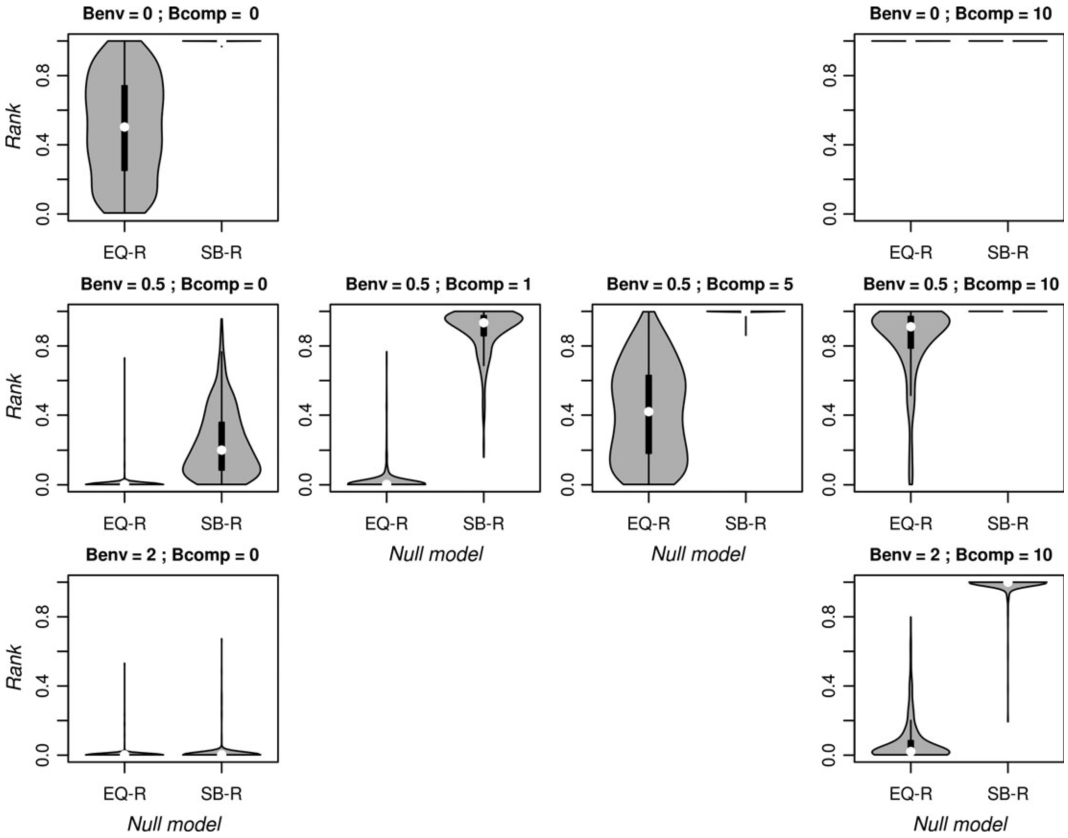

Fig. 1. Comparison of the outcomes of the 'equiprobable randomisation' (EQ-R) and the 'suitability-based randomisation' (SB-R) null models for the simulated community data. Each subplot presents the distribution of the ranks in a violin plot (Hintze & Nelson 1998) generated for a specific combination of environmental filtering (Benv) and competition (Bcomp). Community assembly is random in the upper-left corner, driven by competition only in the upper-right corner (Bcomp > 0), driven by environmental filtering only in the lower-left corner (Benv > 0), and driven by the interplay of these processes in the lower-right corner). A rank value higher than 0.975 indicates a diversity value higher than expected under the null model, while a rank value lower than 0.025 indicate a diversity value lower than expected under the null model

ing signal (convergence) at large spatial and evolutionary scale (EQ-R: AL-R) presented no signal (neutral pattern) at a small spatial and evolutionary scale (SB-R: IL-R).

For the extended species pool, we observed the same trends: the ranks obtained using the combination of SB-R and IL-R increased strongly compared to the use of a non-constrained null model (91% of the communities ranks increased; Table 2), showing that environmental filtering was less pervasive at the small rather than the large spatial and evolutionary scale. Moreover, 22 out of the 28 communities with a significant environmental filtering signal at large spatial and evolutionary scale (EQ-R: AL-R) showed no signal at a small spatial and evolutionary scale (SB-R: IL-R).

With an increasingly smaller evolutionary scale, the outcome of the null models (either EQ-R: IC or IL-R: SB-R) tended to detect a less convergent diversity pattern (i.e. the mean rank value increased; Fig. S4). This showed that the trend described above for a constraint on an intermediate evolutionary scale can be generalized: when the evolutionary scale was smaller, the environmental filtering was less pervasive, although the proportion of communities becoming significantly divergent remains negligible. This was true whatever species pool was considered. Furthermore, we note that the choice of cutting age for IL-R heavily impacted the sample space of the null model. At the chosen intermediate and larger evolutionary scale, the number of possible random communities remained largely superior to the number of used randomizations. However, for smaller evolutionary scales, the sample space of the null model decrease dramatically for some communities, indicating lower power of the null model.

Finally, regardless of the evolutionary and spatial scale considered, the communities appeared more convergent (i.e. ranks decreased; Fig. S3) when using the extended species pool (E-SP) as opposed to the reduced species pool

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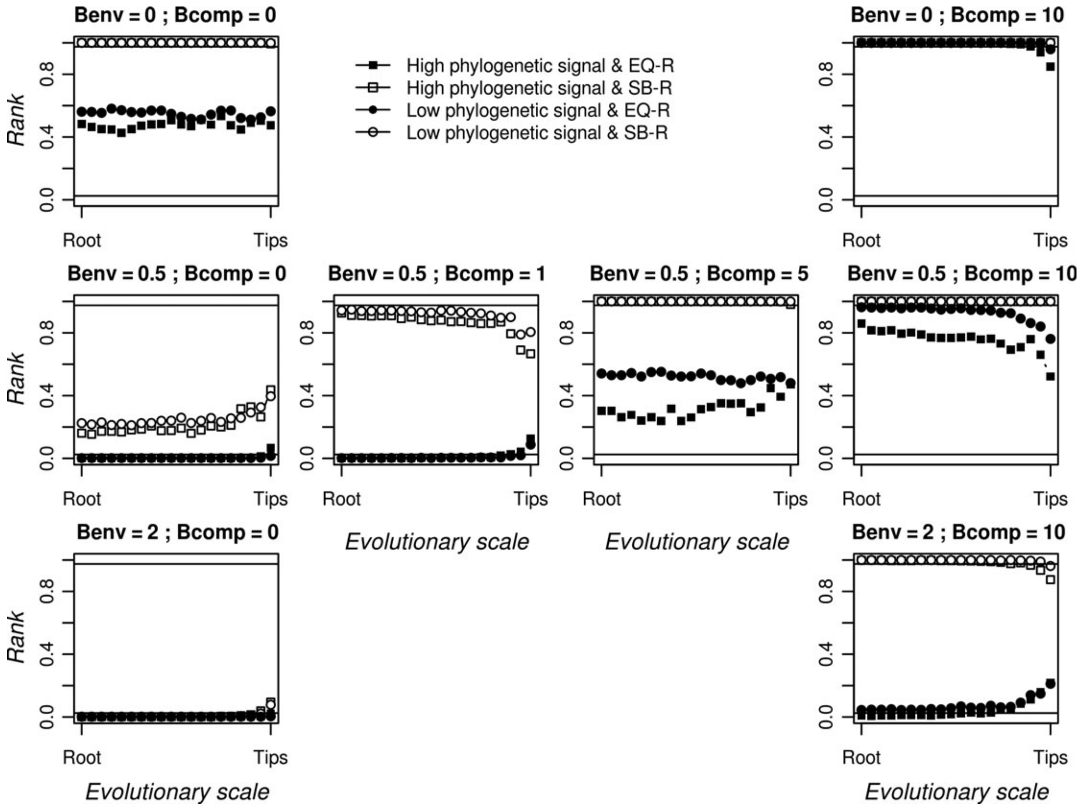

Fig. 2. Comparisons of the outcomes of the 'intra-lineages randomisation' (IL-R) as functions of the evolutionary scale. Each subplot contains the median of the distribution of ranks of communities generated for a specific combination of environmental filtering (Benv > 0) and competition (Bcomp > 0). A rank value close to 'Root' indicates a 'close-to-root' age value while an age value close to 'Tips' indicates a 'close-to-tips' age value. Specifically the randomizations at age 'Root' are 'across-clades randomisation' (AC-R), i.e. all tips are shuffled among each other. Closed (open) symbols indicates the coupling with EQ-R (SB-R); square (circle) symbols indicate the distribution of ranks for communities whose phylogeny was generated by a δ parameter of 0.1 (10) and thus high (low) phylogenetic signal.

(R-SP); however, the differences between these species pools were small.

Discussion

Detecting biotic interactions: scale matters

A primary result of our simulation study was that null models constraining the spatial scale help in detecting biotic interactions, even if these were overlaid with strong environmental filtering. These constrained null models reflected well the 'local species pool' (Zobel 1997). In contrast, reducing the evolutionary scale using intra-lineage randomization did not improve the detection of biotic interactions, even when the niche phylogenetic signal was high. The field case study provided complementary insights. The combined use of constraints for the spatial (SB-R) and the evolutionary (IL-R) scale increased divergence in the functional diversity pattern and thus identified a potential effect of competition. The inconsistency between the field and simulation studies about the importance of evolutionary scaling likely resulted from the fact that in the simulation study species niches were fully known and described by the functional patterns. The evolutionary scaling did not add any further information. In the field case study, the phylogenetic relationships were likely to capture species' niche dimensions not well represented by the measured traits, such as the nitrogen fixing ability of Fabaceae species. If measured traits do not fully represent species' niches, evolutionary constrained null models can be beneficial as they can buffer the lack of information on niche-relevant species traits in the functional analysis (Carboni et al. 2013).

Interpretation of diversity patterns from field data

Alpine communities are highly constrained by steep climate gradients (in particular temperature and radiation; de Bello et al. 2012a). The challenge is thus to go beyond

Table 1. Overview of the different null models with null hypotheses associated with their tests.

	Name	Description	Associated Hypothesis	References
Randomization				
Large scale	Across-lineages randomization (AL-R)	Species abundance values are shuffled across the entire phylogeny	All species in the phylogeny are functionally equivalent	
Reduction of evolutionary scale	Intra-lineages randomization (IL - R)	Species abundance values are shuffled within pre-defined lineages (defined by age)	Species within lineages are functionally equivalent	Hardy & Senterre 2007
Large scale	Equi-probable randomization (EQ - R)*	Probability of being attributed to an abundance value is equal for all species	All species of the regional species pool are functionally equivalent	
Reduction of spatial scale	Suitability-based randomization (SB - R)	Probability of a species being attributed to an abundance value is proportional to the abiotic suitability of the site considered	Species of the local species pool are functionally equivalent	Peres-Neto et al. 2001
Species pools				
	Reduced species pool (R – SP)	Species pool composed of the species present in at least one of sites studied	The species in the data set fully describe the species pool	
	Geographical extended species pool (GE – SP)	Species pool extended to species present in the study area according to independent data	Dark diversity is missing and needs to be included in the species pool	Pärtel et al. 2011

*If evolutionary scales and spatial scales are independently varied, AL-R equals EQ-R. However, as they can be varied in combination (cf. Fig. 3, last column), we need to differentiate between AL-R and EQ-R.

Table 2. Summary of the change in ranks for the communities of the field case study when reducing spatial and evolutionary scales: at small spatial scale and large evolutionary scale (SB-R), at large spatial and small evolutionary scale (IL-R) and at small spatial and evolutionary scales (SB-R: IL-R). The reduced species pool (R-SP, first three rows) and the extended species pool (E-SP, last three rows). We used a 5% error rate to establish the significance threshold for switching ranks (0.025 and 0.975). For a graphical representation, see Fig 3.

	Percentage of communities increasing rank	Mean increase in rank	SD of rank increase	Number of communities switching from convergent to non-convergent	Number of communities switching from non-convergent to convergent/total number of communities
R-SP					
EQ-R to SB-R	98%	0.09	0.06	9/18	0/77
EQ-R to IL-R	79%	0.08	0.13	7/18	1/77
EQ-R to SB-R: IL-R	89%	0.16	0.16	15/18	0/77
E-SP					
EQ-R to SB-R	100%	0.12	0.09	18/28	0/67
EQ-R to IL-R	80%	0.07	0.11	14/28	2/67
EQ-R to SB-R: IL-R	91%	0.19	0.18	22/28	1/67

environmental filtering to detect the additional influence of small-scale processes on community assembly. It was thus logical to observe environmental filtering as the dominant assembly process when an equi-probable null model approach was applied (EQ-R). Reducing the spatial scale of the analysis by adding habitat suitability constraints (SB-R) reduced functional convergence, indicating that the environmental factors considered in the suitability index were originally driving the patterns of convergence. The functional convergence remaining might be due to further small-scale processes (e.g. micro-environmental conditions not included in the suitability index or other biotic interactions favouring the co-existence of similar species). Overall, we did not detect significant functional divergence in alpine plant communities, at any studied evolutionary or spatial scale. This result may have several explanations.

First, competitive interactions between plant species do not necessarily lead to trait divergence (e.g. Laliberté et al. 2013). Besides niche differentiation, the sharing of com-

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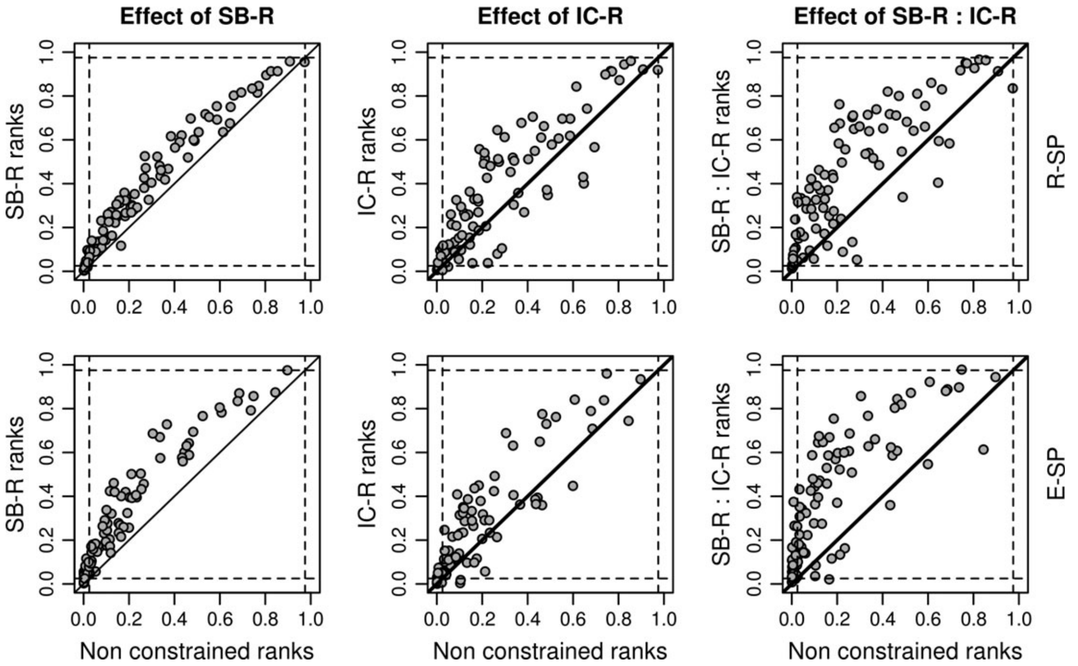

Fig. 3. Comparison of the outcomes of the different constrained null models for the case study according to the scales of the analysis. Results at large spatial and evolutionary scales (EQ-R: AC-R) are compared against the results: at fine spatial scale and large evolutionary scale (SB-R, first column), at large spatial scales and small evolutionary (IL-R, second column), and at fine spatial and evolutionary scales (SB-R: IL-R, third column). The first row presents results for the reduced species pool (R-SP) and the second row presents results for the extended species pool (E-SP). The dotted lines represent the significance threshold of the rank values (0.025 and 0.975). The thick lines separate the communities whose ranks increased from these whose ranks decreased with the use of the constrained null model vs. the non-constrained null model. For a numerical summary, see Table 2

mon traits that enhance competitive ability can also lead to the co-existence of species (Mayfield & Levine 2010). Second, our selection of key traits might not be appropriate to evaluate niche overlap. This is somehow unlikely, given that the use of these functional traits have been widely advocated for herbaceous ecosystems (Grime 2006). However, we neglect the intra-specific trait variability along the gradients of the Guisane valley (Albert et al. 2010). As competition is essentially an individual-level process, the use of aggregated species-level trait values could mask the functional divergence between competing neighbours (Clark et al. 2011). Third, other biotic interactions and local ecological processes, such as the removal of palatable species by grazers (de Bello et al. 2006) or local land use such as fertilization selecting for species with high SLA (Quétier et al. 2007; Gerhold et al. 2013), might influence diversity patterns towards convergence.

Overall, we conclude that characterizing species by their position in the LHS plant ecology strategy scheme mainly revealed the effect of environmental filtering at large spatial and evolutionary scales. Neutral processes and not niche-based competition seemed to drive community assembly at small spatial and evolutionary scales. These results are congruent with other studies suggesting that biotic interactions do not play an important role in the functional structuring of sub-arctic–alpine communities (Mitchell et al. 2009; but see Spasojevic & Suding 2012).

Detecting biotic interactions: (not) a matter of species pool

In our field case study, extending the species pool did not have a marked effect on the detection of competition. This result suggests that the analysis was robust to the inclusion of dark diversity. However, we cannot be sure that all of the dark diversity was included, as local competition could have excluded species from the entire Guisane valley.

Constraining species pools allows a reduction of the evolutionary scale but also increases the risk of Type II errors as less random combinations of species can be drawn from the species pool to construct the null expectation of the diversity pattern (Gotelli & Ulrich 2012). In our study, the effect of this risk is striking when using IL-R, as the sample space significantly decreases when the cutting age becomes very close to the tips (Fig. 4). When using IL-R, the sample space should therefore be evaluated beforehand to evaluate the power of the null model.

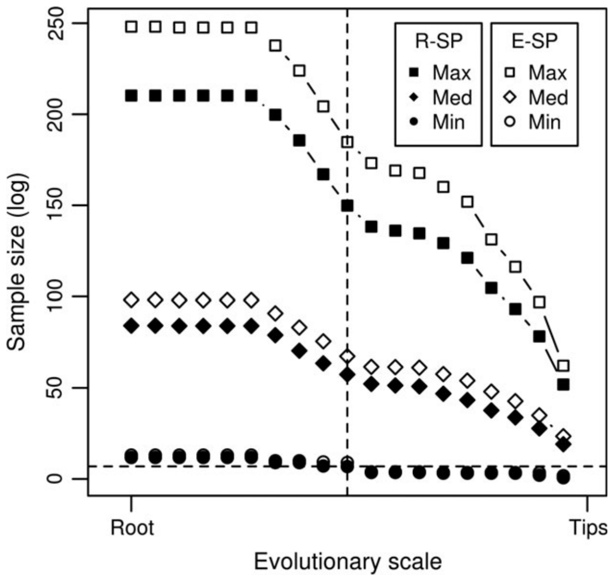

Fig. 4. Sample space of 'intra-lineage randomization' (IL-R) as a function of the evolutionary scale. Sample space was estimated as the number of different random communities the IL-R null model can generate for an 'observed' community and at varying evolutionary scales. We displayed the median (diamond), maximum (square) and minimum (circle) over communities for each species pool (R-SP, filled symbols; E-SP, open symbols). The horizontal dotted line indicates the threshold of 1000 random possibilities. The *x*-axis represents the age value used as a parameter for the IL-R and the vertical dotted line indicates the evolutionary scale used to generate Fig. 3.

Species distribution models as a new tool for diversity pattern analysis

Our study highlights the potential of species distribution models to refine the species pool concept by defining a pool of species adapted to local environmental conditions based on suitability estimates (introduced in Boulangeat et al. 2012a). One potential drawback is that suitability-based randomization (SB-R) might lead to false positives when using flawed suitability information. This situation occurred in our simulation study, where the species suitability indices were based on a trait unrelated to species' niches in the random community assembly scenario. As a result, the test wrongly identified divergence and thus competition as a major assembly process. This result calls for caution in real-life situations where the habitat zsuitability is assessed from the observed distribution of species, and may reflect other processes than environmental filtering. Such an approach should then be preceded by a cautious selection of relevant abiotic variables driving species distributions, niche differentiation and thus environmental filtering.

Perspectives for diversity pattern analyses

Detecting the influence of biotic interactions in observed diversity patterns is a challenging task because of the pervasive environmental heterogeneity in large-scale ecological data sets (Cavender-Bares et al. 2009; Thuiller et al. 2010). Using a family of null models allows changing of the spatial and evolutionary scales of the analysis. Caution should however be taken: we showed the negative impact of flawed input data on the output of constrained null models and the importance of evaluating the sampling space when constraining null models. Finally, the combined interpretation of the different null model outcomes enables uncovering of fine-scale functional divergence patterns within large-scale convergence patterns.

Acknowledgements

The research leading to these results received funding from the European Research Council under the European Community's Seventh Framework Programme FP7/2007–2013, Grant Agreement no. 281 422 (TEEMBIO). TM was funded by the ANR-BiodivERsA project CONNECT (ANR-11-EBID-002), as part of the ERA-Net BiodivERsA 2010 call. FB acknowledges support from the grant GACR P505/12/1296. The field research was conducted on the long-term research site Zone Atelier Alpes, a member of the ILTER-Europe network. ZAA publication n° 24. The computations presented in this paper were performed using the CIMENT infrastructure (https://ciment.ujf-grenoble.fr), supported by the Rhône-Alpes region (GRANT CPER07_13 CIRA: www.ci-ra.org).

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Supporting information

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

Appendix S1. Simulation model details.

Appendix S2. Field data details (phylogeny, trait database).

Figure S1. Simulation model illustration.

Figure S2. Relationships between the field case study functional traits and the environment.

Figure S3. Comparison of null models outcome between R-SP and GE-SP.

Figure S4. Influence of varying age values on IL-R outcome on the field data.

Figures S5–7. Complementary analyses on IL-R outcome on the field data.

Table S1. Simulation model parameters.

Table S2. Phylogenetic signal of the field case study functional traits.

Table S3. Phylogeny branch length calibration data.

Table S4. Summary of the comparison of null models outcome between R-SP and GE-SP.

Doi: 10.1111/jvs.12031