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From diversity indices to community assembly processes: a test with simulated data

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Ecological theory suggests that spatial distribution of biodiversity is strongly driven by community assembly processes. Thus the study of diversity patterns combined with null model testing has become increasingly common to infer assembly processes from observed distributions of diversity indices. However, results in both empirical and simulation studies are inconsistent. The aim of our study is to determine with simulated data which facets of biodiversity, if any, may unravel the processes driving its spatial patterns, and to provide practical considerations about the combination of diversity indices that would produce significant and congruent signals when using null models. The study is based on simulated species' assemblages that emerge under various landscape structures in a spatially explicit individual-based model with contrasting, predefined assembly processes. We focus on four assembly processes (species-sorting, mass effect, neutral dynamics and competition colonization trade-off) and investigate the emerging species' distributions with varied diversity indices (alpha, beta and gamma) measured at different spatial scales and for different diversity facets (taxonomic, functional and phylogenetic).

We find that 1) the four assembly processes result in distinct spatial distributions of species under any landscape structure, 2) a broad range of diversity indices allows distinguishing between communities driven by different assembly processes, 3) null models provide congruent results only for a small fraction of diversity indices and 4) only a combination of these diversity indices allows identifying the correct assembly processes.

Our study supports the inference of assembly processes from patterns of diversity only when different types of indices are combined. It highlights the need to combine phylogenetic, functional and taxonomic diversity indices at multiple spatial scales to effectively infer underlying assembly processes from diversity patterns by illustrating how combination of different indices might help disentangling the complex question of coexistence.

The processes behind community assembly have long been a central puzzle in ecology (Diamond 1975, Connor and Simberloff 1979, Leibold et al. 2004). The recently renewed upsurge of interest is motivated by the awareness that accelerating global change does not only threaten single species survival but also community assembly (Díaz and Cabido 2001, Münkemüller et al. 2009). It has been further fueled up by the debate around the neutral theory of biodiversity (Hubbell 2001). Up to now, despite the increasing number of publications proposing new theories (Clark 2009), criticizing theories (Mc Gill 2003) or proposing a reunification of existing theories (Gravel et al. 2006), no broad consensus on a general theory of local community assembly from a pool of regionally available species has been reached (Mc Gill 2010). However, there exists some agreement among ecologists that 1) environmental filtering due to species-sorting along environmental niche axes, 2) competition-colonization trade-offs, 3) neutral dynamics and 4) mass-effects due to short ranged dispersal are among the most important processes ruling community assembly (Leibold et al. 2004, cf. Table 1 for more details and references).

Studying all these processes empirically at large scales is practically unfeasible. Therefore, ecologists commonly apply an 'indirect approach', i.e. they indirectly conclude on driving assembly processes from observed spatial patterns of species, functional or phylogenetic diversity (Gravel et al. 2008, de Bello et al. 2009, Kraft and Ackerly 2010). The reasoning behind is that each assembly or coexistence process should lead to particular diversity patterns. Looking at the diversity patterns should thus allow identifying the underlying processes (Webb et al. 2002, Cottenie 2005). However, when multiple processes are intertwined and play at different spatial scales, assembly dynamics are more complex and it remains challenging to predict biodiversity patterns (Chave et al. 2002, Mouquet and Loreau 2003, Chisholm and Pacala 2010, Pavoine and Bonsall in press).

First applications of the indirect approach built on local species diversity indices (taxonomic alpha diversity). These applications have been expanded in two directions. 1) More facets of biodiversity have been considered: information on functional relatedness (assuming that focal traits are relevant for assembly processes) and phylogenetic relatedness (assuming that trait values of closely related species resemble each other more strongly than those of distantly related species) have been used as proxies for species' niche similarity (Webb et al. 2002, Thuiller et al. 2010, Sokol et al. 2011). 2) Biodiversity has been studied at different spatial scales: alpha (local diversity), beta (turnover between sites) and gamma diversity (regional diversity) were measured along environmental and geographic gradients to help disentangling processes that act at different scales (Silvertown 2006, de Bello et al. 2010, Réjou-Méchain and Hardy 2011, Meynard et al. in press). This approach may contribute to identifying the relationship between community structure and environmental conditions as well as the influence of dispersal and habitat connectivity.

However, studies using these different facets and spatial scales still differ greatly in their outcomes and few general patterns have been identified so far, even when similar ecological systems were studied (Supplementary material Appendix 1, Table A1 for examples and references). For example, neutral dynamics, species-sorting as well as dispersal limitations have all been identified as the most important drivers in different studies of tropical tree diversity. Although some discrepancy between studies may be due to different ecological and environmental conditions, we suggest that the main reasons for the ambiguities lie in conceptual and methodological issues.

In observational research, we never know the underlying 'true' assembly processes and we still lack a consensus about the best combination of diversity indices and statistical randomization tests to infer the processes from observed patterns. As a consequence, until today, it is unknown how well the indirect approach works in general and how well different indices and null models perform. Therefore, here we introduce a conceptual framework that highlights the different assumptions underlying an indirect approach and links these assumptions with the final step of inferring assembly processes from species' distributions. The assumptions are that different assembly processes lead to distinguishable species' distribution patterns (step 1) and that values of diversity indices differ for different spatial distribution patterns (step 2). These first two steps are a prerequisite for inferring underlying assembly processes from distributional patterns by means of diversity indices and randomization tests (step 3). However, it should be noted that these first two steps cannot be tested with field data because they require comparing patterns of communities that differ in their driving assembly processes and for which these driving processes are known. This comparison can only be based on simulated data where processes are known and can be opposed while keeping other factors, such as the size of the species pool, constant. Here, the term species pool is used to describe the set of regionally available species that can reach the local community. This species pool is mainly determined by diversification and adaptation in combination with interspecific interactions over entire regions (Ricklefs 2008). According to our framework, there are at least three reasons that would explain why we find contrasting assembly processes in ecological systems of the same type: the assembly processes truly differ, the same assembly processes result in strong patterns in one case but not in the other (e.g. due to different landscape structure) or applied indices and tests are inconsistent. Up to now, there has been a disconnection between studies testing the three different steps, i.e. between theoretical studies on spatial assembly structure using simulated data (step 1, Tilman 1982, Hubbell 2001, Chave et al. 2002), methodological studies on diversity indices and tests (step 2, Kraft et al. 2007, Cadotte et al. 2010, Mouchet et al. 2010), and studies applying the indirect approach to field data (step 3, Kraft and Ackerly 2010, Meynard et al. in press). By applying step 3 to field data with the aim to identify community assembly processes from diversity indices one assumes that the indirect approach works in principle (i.e. that the assumptions in step 1 and step 2 are fulfilled). However, even though the indirect approach is commonly applied in ecological studies there is a lack of testing of this basic assumption itself. As outlined above, such a test of the utility of the indirect approach requires integrating the three steps of the conceptual framework and thus needs to be based on data where the underlying 'true' assembly processes are known.

Here, we use a comprehensive approach comprising all three steps to test the performance of the indirect approach. We consider the most common indices from different spatial scales (alpha, beta and gamma diversity) and diversity facets (taxonomic, functional and phylogenetic diversity) and consider the assembly processes supposedly most influential (Table 1). We bridge the necessary and so far missing links to evaluate the validity of the approach by the use of simulated data of spatial community structure (Chave et al. 2002, Zurell et al. 2010). The use of simulated data allows testing the approach in the strict sense only within the assumptions of the simulation model and the studied parameter ranges. Results can show whether the approach works at all and illustratively highlight aspects that need to be considered for good performance. Simulated data are generated with a unique mechanistic simulation model that allows for controlling assembly processes simply by choosing species and landscape characteristics adequately. Our comparative analysis follows the steps outlined before (Fig. 1). First, we investigate whether communities based on known different assembly processes show different patterns of species' distribution (step 1). Second, we test whether diversity indices reveal distinct signatures between structurally differing communities (step 2). This step requires analyzing jointly communities with substantially different underlying processes. Based on these analyses we suggest a reduced subset of diversity indices that either alone or in combination provide the necessary information to identify different assembly processes. In a third and final step, we apply the selected subset of diversity indices to our virtual data in a

Table 1. Overview of the four considered community assembly processes with a short description of processes and relevant traits, a reference list and the implementation in the simulation model (Supplementary material Appendix 3, Table A1 for more details).

	Description and spatial prediction	References	Implementation and trait values
Species sorting	Differences in species' response to the environment lead to species-sorting along environmental gradients at moderate to large spatial scales (environmental filtering).	Gause 1934, Mac Arthur and Levins 1967	Species differ in their niche optimum (u_i equidistantly ranges from 0 to 99) but have equal niche width ($\sigma = 5$), maximal relative performance ($h = 1$) and fecundity ($f = 1$).
Trade-off	A competition-colonization trade-off can lead to coexistence when the competitively dominant species has poorer colonizing ability, e.g. due to low fecundity. At small spatial scales one would expect species that coexist to differ in their competition-colonization strategies.	Tilman 1982, 1994	Species show strict negative correlation between maximal relative performance (h_i equidistantly ranges from 1 to 50) and fecundity (f_i equidistantly ranges from 1.96 to 0.04) but have equal niche optima ($u = 50$) and niche width ($\sigma = 100$).
Neutral	Competition of functionally equivalent species leads to a random drift and competitive exclusion and to the random distribution of species along environmental gradients. Speciation and/or immigration maintain coexistence over long time and dispersal limitation results in local species clustering.	Hubbell 2001	Species have equal niche optima ($u = 50$), equal niche width ($\sigma = 100$), maximal relative performance ($h = 1$) and fecundity ($f = 1$).
Mass effect	In heterogeneous environments dispersal leads to source-sink dynamics where species co-occurrences quantitatively depend both on neighboring occupancy and local environmental conditions.	Shmida and Ellner 1984, Mouquet and Loreau 2003	Same species pool as for species-sorting. Mass effect increases for increasingly different environmental conditions in the neighborhood, i.e. is strongest for random landscapes, less strong for auto-correlated landscapes and weakest for gradient landscapes.[1]

[1] The mass effect depends on the connectivity between different habitats. We decided to explore it under different habitat configurations rather than under different dispersal rates, to not further increase the number of simulation scenarios.

more realistic setting with smaller datasets and compare observed values against different null hypotheses. Here, it is sufficient to analyze a dataset containing communities that are all based on the same driving assembly. This final analysis is directly comparable with the procedure one would apply in a field study (step 3).

Methods

We compared the performance of different diversity indices based on a modelling approach (Fig. 2). Landscape and species information build the input for a mechanistic simulation model. The (sampled) data from the output of this model provide the basis for the calculation and analyses of the diversity indices. We describe this approach in three steps following the conceptual framework introduced in Fig. 1.

Species' distribution patterns resulting from assembly processes (step 1)

We started our analyses by generating virtual communities with different structures. We built an individual-based and spatial-explicit mechanistic model that simulated stochastic dynamics of individuals competing for space in heterogeneous environments (Supplementary material Appendix 3 for a full model description). The model is a cellular automaton with one sessile individual, or none, per cell. In this cellular automaton we implemented mortality, offspring production, immigration and competition. Competition was influenced by environmental conditions, which were mapped on the grid with different distributions for different settings.

Community assembly was driven by independent but complementary mechanisms which could be 'turned on and off' independently simply by the choice of the input species pool and the distribution of environmental conditions (Table 1 for assembly processes and related trait values). For species-sorting, the different species were adapted to different optimal environments. This resulted in environmental filtering at the landscape scale with clustered or gradient environmental conditions. However, in random landscapes neighboring sites differed strongly in environmental conditions and thus there was a strong effect of immigration from not well adapted species (Holt et al. 2003, species-sorting in random landscapes is hereafter called 'mass effect', Table 1).

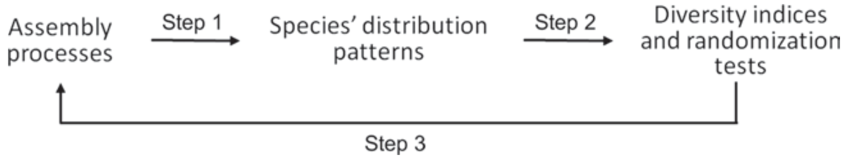

Figure 1. Conceptual framework: three assumptions that need to be fulfilled to go from diversity indices to community assembly processes. Step 1: different community assembly processes result in different spatial distribution patterns. Step 2: values of diversity indices differ for different spatial distribution patterns. Step 3: diversity indices and associated null models can identify non-random assembly processes.

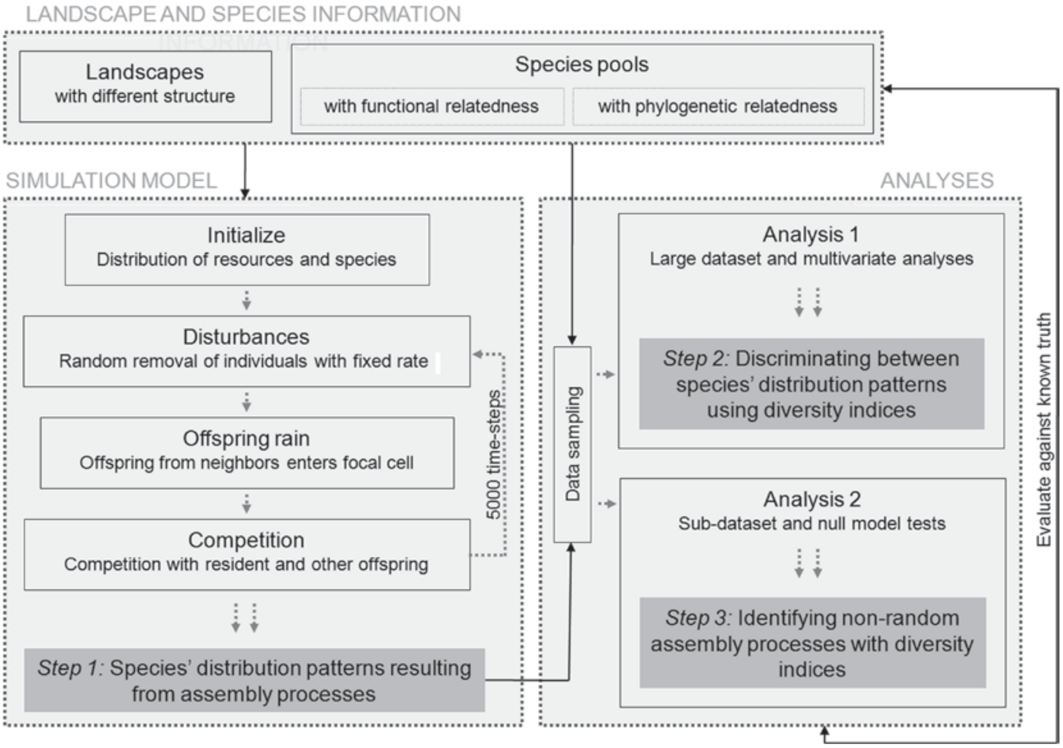

Figure 2. Schematic overview of our modelling approach: the combinations of different landscapes (i.e. spatial structure of the environment) and different species pools (i.e. trait distribution and phylogenetic relatedness) are the input for the spatially-explicit and individual-based simulation model. This input influences the outcome of the modelled processes in the simulation model and ultimately spatial patterns of species' distributions (step 1, see also Fig. 1). Based on datasets sampled from both the input information (landscapes and species-pools) and the emerging spatial distribution patterns we calculated a range of diversity indices and investigated the power of these indices to discriminate between spatial distribution patterns of species (step 2, see also Fig. 1) and, in combination with null model tests, to identify non-random community assembly processes (step 3, see also Fig. 1).

For the competition-colonization trade-off, all species were equally adapted to environmental conditions but differed in maximal performance and fecundity, with both traits being negatively correlated in the species-pool. For neutral dynamics, all species were equal (Table 1).

We run 9 simulation scenarios (each repeated 10 times giving rise to 90 runs). For the different scenarios, we combined three different species pools with different distributions of trait values (neutral, competition-colonisation trade-off, or species-sorting, Table 1) with three different landscape structures (random, gradient or auto-correlated environment, Supplementary material Appendix 4 for used algorithms and Fig. 3 upper row).

We simulated phylogenetic relatedness of species in three steps. We first created phylogenetic trees with random splitting of branches over evolutionary time (with a branching rate of 0.02 and 50 leaves; package geiger, software R, R Development Core Team 2011). In a second step, we let six 'auxiliary traits' evolve such that changes in trait values over evolutionary time were directly related to branch lengths in the trees (Brownian motion model with root value of zero and variance of 1, package ape). Finally, these auxiliary traits were used to connect the leaves of the trees with the species from the pool and their predefined traits (i.e. niche optimum, niche width, maximal relative performance, fecundity, Table 1). This was done such that the rank order of the first axis of a principal component analysis (PCA) on all six auxiliary traits was the same as the rank order of the predefined traits. This approach generated phylogenies with strong phylogenetic signal for all species pools but (by definition) for neutral communities (Supplementary material Appendix 3, Table A2). The auxiliary traits and the first axis of the PCA were only used to generate this strong phylogenetic signal and only the predefined traits were used afterwards. Phylogenetic signal is the tendency of closely related species to be more similar than distantly related species and can be measured by Blomberg's K (Blomberg et al. 2003).

At the end of the simulation runs we observed the resulting species' distributions. As a first step we visually described spatial clustering and relations of species' distributions with environmental conditions across the whole landscape and reported the percentage of unoccupied space as well as the number of species that survived.

Different diversity indices resulting from different spatial distribution patterns (step 2)

For the second step of the conceptual framework (Fig. 1, 2) we sampled datasets from the model output, calculated diversity indices and tested whether these indices differed for different types of communities. Datasets were sampled by uniformly placing 400 simulated 'sampling sites' on the landscape grids. Each sampling site had an extent of 100 grid

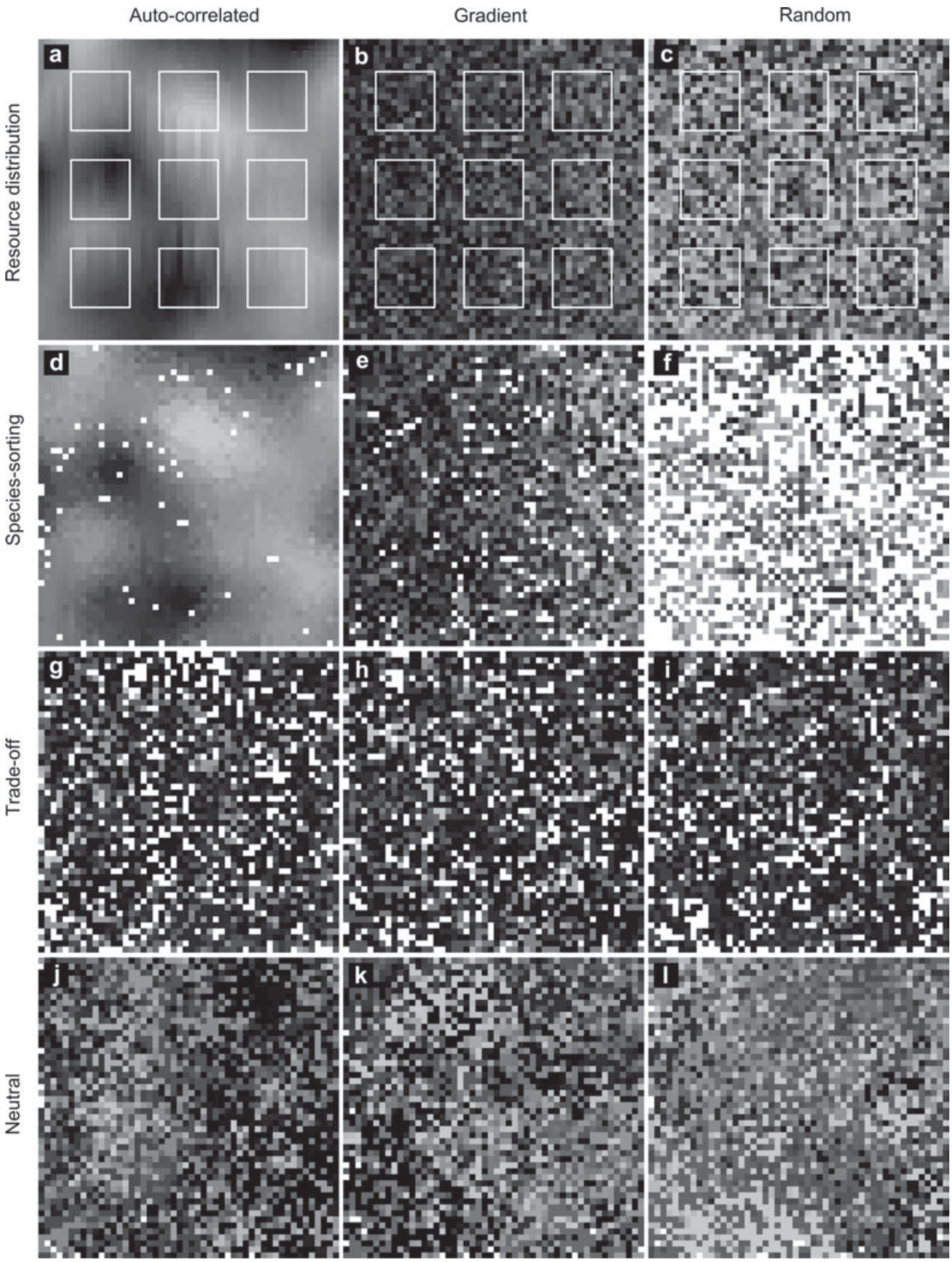

Figure 3. Simulated spatial patterns in landscape cut-outs (50 × 50 cells) with auto-correlated, gradient and random environmental structure. The upper row shows spatial distributions of environmental conditions (grey shades refer to environmental conditions, larger open white squares mark the sampled sites). The three lower rows show distributions of individuals from the different species (different grey shades for different species) for exemplary runs of the simulation model with a species-sorting, a trade-off and a neutral species pool; the species-sorting species pool in the random landscape produces mass effects (panel f). The more similar grey shades are the more functionally similar are species. White cells are unoccupied.

cells (10 × 10 grid cells). Distances between sampling sites were 5 grid cells (Fig. 3). The datasets containing the species by site matrices were completed with information on average environmental conditions, Euclidean distances between sites, species' trait values and phylogenetic relatedness. We added small random errors to the trait values to simulate uncertainty (normally distributed with mean zero and a coefficient of variation of 10%). This was done first because phylogenetic data include a random error as well and second to allow some variation for calculating functional diversity within neutral communities.

Our comprehensive analysis was based on the only approach that allows calculating indices for different facets and scales of diversity while taking into account species abundances: the Rao index of diversity (Rao 1982). We considered additive as well as proportional partitioning of gamma diversity into alpha and beta components and applied the appropriate corrections (de Bello et al. 2010). Additionally, we included correlations between diversity indices (Petchey et al. 2007) and environmental and physical distances (Legendre et al. 2009). Overall, we calculated 42 diversity indices and took the average over sampling sites for each simulation run to get one final value per diversity index and simulation run (Table 2).

We investigated whether the different community assembly processes revealed distinct signatures across the diversity indices with a classification tree type of model. This analysis was performed over all 90 simulations with the 42 diversity indices as independent variables and the 9 different scenarios as the response variable. Because the 42 diversity indices were inevitably correlated we could not use traditional classification tree techniques, but used a bootstrap aggregation of trees called Random Forest (Breiman 2001) combined with a conditional importance measure (Strobl et al. 2008). The advantage of random forest over traditional regression-tree type of models is that it runs efficiently on large datasets and can handle large numbers of explanatory variables without

Table 2. Overview of diversity indices at different spatial scales and for different diversity facets. Abbreviations for the diversity indices: a, b, g for alpha, beta, gamma diversity; t, f, p for taxonomic, functional, phylogenetic diversity; r for correlation, geo for geographic and env for environmental distance. NS stands for species number. Beta diversity was described both, via the proportion of gamma not yet explained by alpha where 100% indicates no common species shared between pairs of sites (abbreviated by ‘prop’) and by the difference of gamma and alpha diversity (abbreviated by ‘add’). Dissimilarity matrices for functional and phylogenetic diversity metrics were either based on the full set of present species or only on the nearest neighbor (abbreviated by ‘mntd’). The last column of the table (step 3) indicates whether (1) or not (0) this index was used in the final null model analyses.

Short description	Spatial scale	Diversity facet	Abbreviation	Step 3
Diversity metrics				
Simpson[1]	alpha	taxonomic	at	1
Mean number of species	alpha	taxonomic	at_NS	0
Rao	alpha	functional	af	1
Rao	alpha	phylogenetic	ap	0
Mean nearest neighbour distance	alpha	functional	af_mntd	1
Mean nearest neighbour distance	alpha	phylogenetic	ap_mntd	0
gt − at	beta	taxonomic	bt_add	1
gt(NS) − at(NS)	beta	taxonomic	bt_add,NS	0
(gt − at) × 100/gt	beta	taxonomic	bt_prop	1
(gt(NS) − at(NS)) × 100/gt(NS)	beta	taxonomic	bt_prop,NS	0
gf − af	beta	functional	bf_add	1
(gf − af) × 100/gf	beta	functional	bf_prop	1
gp − ap	beta	phylogenetic	bp_add	0
(gp − ap) × 100/gp	beta	phylogenetic	bp_prop	0
Simpson[1]	gamma	taxonomic	gt	1
Number of species	gamma	taxonomic	gt_NS	0
Rao	gamma	functional	gf	1
Rao	gamma	phylogenetic	gp	0
Correlation coefficients				
Spearman	alpha	taxonomic – taxonomic	r_at_Ns _at	1
Spearman	alpha	taxonomic – functional	r_at_af	0
Spearman	alpha	taxonomic – functional	r_at_NS_af	0
Spearman	alpha	taxonomic – phylogenetic	r_at_ap	0
Spearman	alpha	taxonomic – phylogenetic	r_at_ap_mntd	0
Spearman	alpha	taxonomic – phylogenetic	r_at_NS_ap	0
Spearman	alpha	taxonomic – phylogenetic	r_at_NS_ap_mntd	0
Spearman	alpha	functional – phylogenetic	r_af_ap	0
Spearman	alpha	functional – phylogenetic	r_af_ap_mntd	0
Spearman	alpha	phylogenetic – phylogenetic	r_ap_ap_mntd	0
Spearman	alpha	taxonomic – environment	r_at_env	0
Spearman	alpha	taxonomic – environment	r_at_NS_env	0
Spearman	alpha	functional – environment	r_af_env	0
Spearman	alpha	phylogenetic – environment	r_ap_env	0
Spearman	alpha	phylogenetic – environment	r_ap_mntd_env	0
Mantel Pearson	beta	taxonomic – phylogenetic	r_bt_bp	0
Mantel Pearson	beta	functional – phylogenetic	r_bf_bp	0
Mantel Pearson	beta	functional – taxonomic	r_bf_bt	1
Mantel Pearson	beta	taxonomic – environment	r_bt_env	1
Mantel Pearson	beta	taxonomic – geo. distance	r_bt_geo	1
Mantel Pearson	beta	functional – environment	r_bf_env	1
Mantel Pearson	beta	functional – geo. distance	r_bf_geo	1
Mantel Pearson	beta	phylogenetic – environment	r_bp_env	1
Mantel Pearson	beta	phylogenetic – geo. distance	r_bp_geo	1

[1] number of species weighted by abundances.

variable deletion (Breiman 2001). Random Forest is an algorithm that builds on repeated construction of classification trees based on randomly drawn variables and samples with replacements. Each tree is then validated on the cases withheld from fitting (out-of-bag validation). *M* trees are 'grown' and all are used for prediction, weighted by their validation performance. The importance of each variable over the set of trees is estimated through randomizations. It informs about how different the independent variables are for different classes of the response variable.

Identifying non-random assembly processes with diversity indices (step 3)

The aim of the third step is to identify a set of different diversity indices able to distinguish between the assembly processes (Fig. 1, step 3). The main difference compared to step 2 is that the analysis is not based on the pooled data of all different assemblies and thus does not contrast patterns of diversity indices for different assembly processes. Instead, we independently test for deviations from random species distributions for each diversity index and each dataset. Ultimately, a combination of indices that show different significant deviations from random expectations for different assembly processes can be used to identify not only non-random but also specific assembly processes.

We split the 90 large datasets randomly into 5 parts to obtain 450 smaller sub-datasets containing fewer sites (5×90 simulation runs) and used only those diversity indices that performed well in the Random Forest model (20 best indices). For each sub-dataset and each test we randomized the data 1000 times and determined the quantiles of observed diversity indices. When the quantiles of the observed value were below 5 or above 95% we called this significant decrease or increase, respectively (we performed one-sided tests as we had hypotheses about the directions of deviations from random expectations for most indices). For the null model, we chose two commonly used randomization algorithms (Helmus et al. 2007, Mouchet et al. 2010). Different null models may yield different results because implicitly defined null hypothesis differ from the explicitly defined null hypothesis one wishes to test (Gotelli and Graves 1996). Here, our explicit null hypothesis was that the abundance structure within each sampling site does not differ from a random one. Our first null model was based on permuting the elements of the species by sites matrix within each site by reshuffling species abundances independently for each site (hereafter called 'species within sites' null model, see null model 2s in Hardy 2008). Besides the spatial distribution of species, this model breaks down implicitly the inter-site abundance distributions for each species (Helmus et al. 2007, Hardy 2008). The second null model was based on permuting the elements of the species by sites matrix among sites independently for each species (hereafter called 'sites within species' null model, see null model 3i in Hardy 2008). This model implicitly breaks down the original local species diversities per site (Hardy 2008).

Results

Species distribution patterns resulting from assembly processes (step 1)

Different assembly processes resulted in distinct spatial distributions of species (Fig. 3d–l). The percentage of unoccupied cells varied greatly among communities. On average in all landscapes 15% of cells were unoccupied in communities based on competition-colonisation trade-offs while in neutral communities 0.1–0.2% of cells were unoccupied. For species-sorting 2% of cells were unoccupied in the auto-correlated landscapes and 11% in the gradient landscapes. In simulations with strong mass-effects 46% of cells were unoccupied. The 50 species from the species pool were present in almost all simulations at the final time-step. Species richness was slightly reduced only for species-sorting in the auto-correlated landscape (on average 47 species).

Species' distributions with species-sorting in the auto-correlated and gradient landscapes mirrored the distributions of environmental conditions (Fig. 3d, e). However, species' distributions with strong mass effects, neutral dynamics or trade-offs were unrelated to environmental conditions (Fig. 3d–f, i–l).

Different diversity indices resulting from different spatial distribution patterns (step 2)

Taxonomic alpha diversity was highest for mass effects, lower for species-sorting and neutral communities and lowest for trade-off communities (Fig. 4a). This pattern was partly reversed for functional diversity where species-sorting generated much lower alpha diversity than mass effects, neutral dynamics or trade-offs (Fig. 4b) and blurred for phylogenetic alpha diversity (Fig. 4c). All facets of beta diversity were lowest for trade-off communities. Taxonomic beta diversity was high for all other assembly processes. Functional and phylogenetic beta diversities were intermediate for mass effects and high for species-sorting and neutral dynamics (Fig. 4d, e, f). Consistently, correlations of all facets of beta diversity and environmental distance were high for species-sorting and much lower for all other assembly processes (Fig. 4g, h, i). Clustering and distance decay were strong for neutral communities (Fig. 3) and resulted in positive correlations of all facets of beta diversity and geographic distance (Supplementary material Appendix 3, Fig. A5). For all other assembly types there was no strong distance decay (Fig. 4j, k, l) with the exception of species-sorting in the gradient landscape (Supplementary material Appendix 3, Fig. A5).

The random forest model correctly identified the landscape structure and species pool for 84 out of the 90 simulations. The assembly processes were always adequately identified, errors occurred only for the landscape structures. Random landscapes with trade-off communities were three times misidentified as gradient landscapes, and one auto-correlated landscape was misidentified as a gradient landscape. Auto-correlated and random landscapes with neutral communities were each once misidentified as random landscapes and auto-correlated landscapes, respectively.

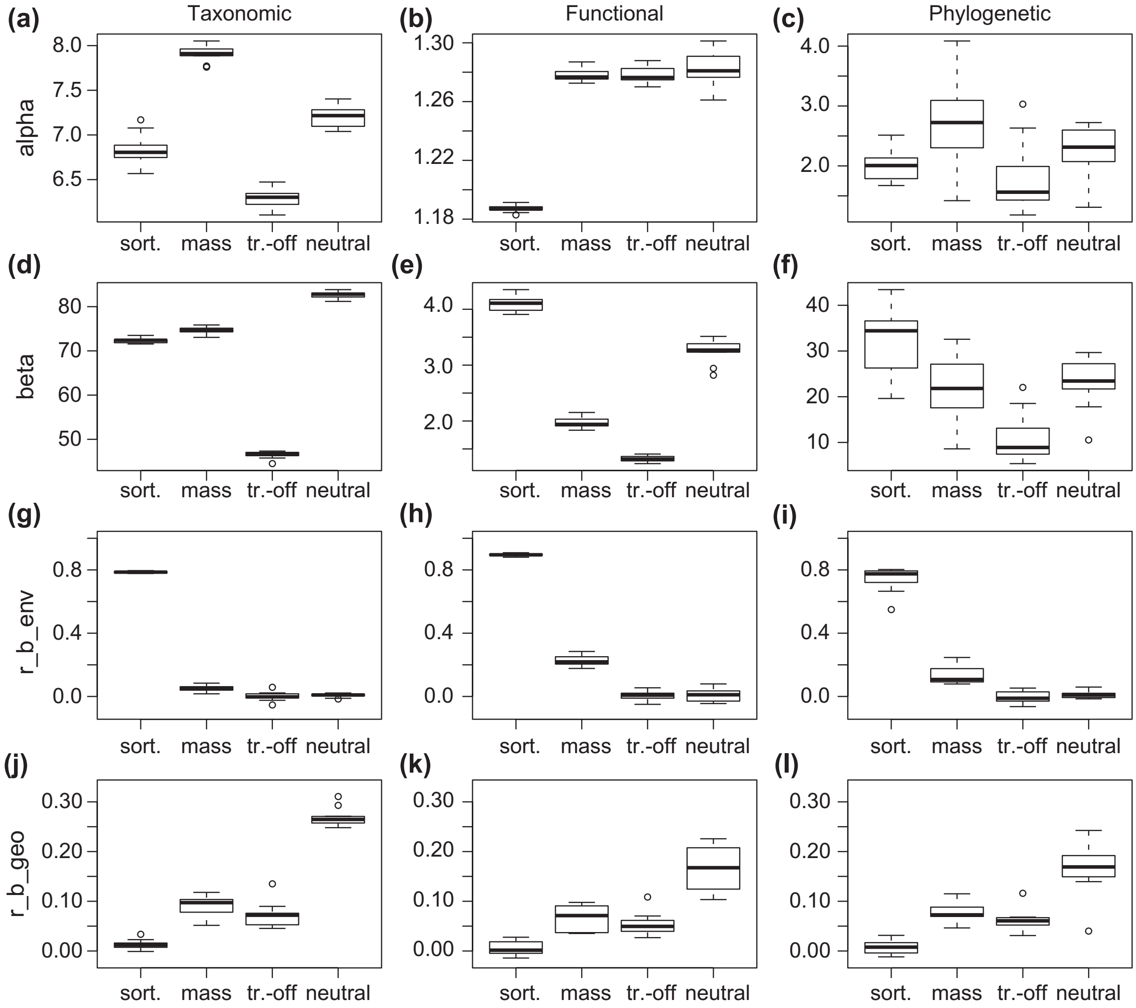

Figure 4. Different facets and spatial scales of diversity patterns. Taxonomic, functional and phylogenetic facets are combined with indices for alpha (Rao index), beta (proportional), correlations of beta with environmental distance, r_b_env, and beta with geographic distance, r_b_geo. Abbreviations and diversity indices are explained in Table 2. Four different assembly types were investigated: neutral, species-sorting (sort.), mass effect (mass) and trade-off (tr.-off) assemblies (under random landscape with species-sorting species pools for mass effects and auto-correlated landscapes with associated species pools for all other assembly types).

In sum, misidentifications only occurred for those assembly processes where species distributions were not related to the resource distribution in the landscape and thus were to be expected. In the random forest analysis, the first eight most important diversity indices contributed to 66% of the overall explained variance (Fig. 5). These indices were taxonomic and functional beta diversity and their correlations with environmental distance (and one taxonomic alpha and gamma diversity, Fig. 5). Further twelve indices from different facets and spatial scales of diversity explained an additional 32% of the overall explained variance. To summarize, the analysis revealed that taxonomic and functional beta diversity indices made the strongest contributions to the random forest model.

Identifying non-random assembly processes with diversity indices (step 3)

For the null model analyses we selected 17 of the 20 most important diversity indices from the bootstrap aggregated trees model accounting for 83% of the overall explained variance (three indices were disregarded because they cannot be randomized with the selected null models, Table 3). The 'species within sites' null model and the 'sites within species' null model gave largely congruent results for functional beta diversity and for correlations of taxonomic, functional or phylogenetic beta diversity with geographic or environmental distance (Fig. 6). Under species-sorting, functional beta diversity, the correlation of all facets of beta diversity with environmental distance, and the correlation of functional and taxonomic beta diversity, were significantly increased while functional alpha diversity was significantly decreased compared to random expectations. In gradient landscapes, there was an additional positive increase of the relation between beta diversity and geographic distance. Communities ruled by mass effects showed a significantly increased correlation between functional beta diversity and environmental distance and significantly decreased functional beta diversity. In trade-off communities, functional beta diversity was significantly decreased. Finally, in neutral communities, the correlation between taxonomic beta

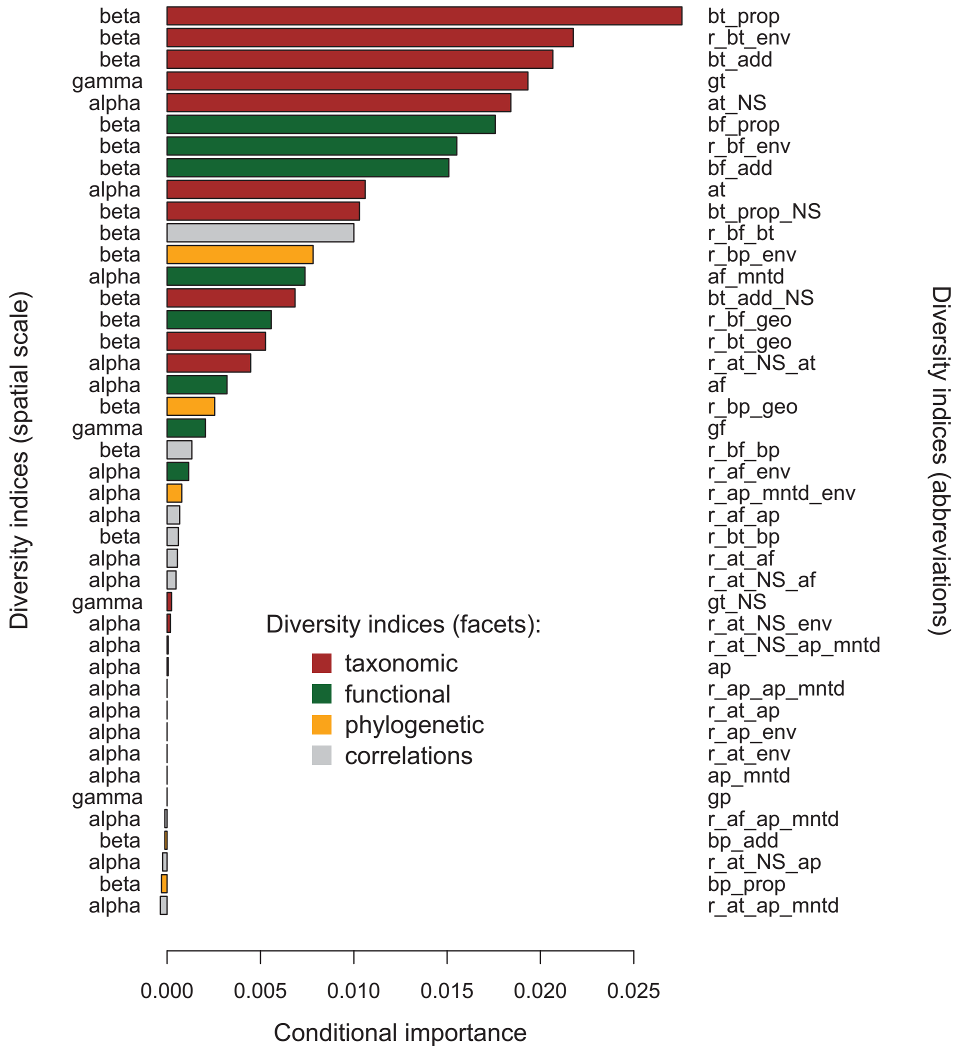

Figure 5. Estimated conditional variable importance based on the Random Forest model. Variable importance indicates the overall explanatory effect size (main and interaction effects) of diversity metrics on the response. We used conditional estimates to account for collinearity between the diversity metrics. Abbreviations and diversity indices are explained in Table 2. For example, the correlation between taxonomic beta diversity and environmental distance (r_bt_env) was the most important diversity metric to differentiate between community assembly rules.

diversity and geographic distance was greater than expected by chance. Additionally, in gradient landscapes the correlation between taxonomic beta diversity and environmental distance as well as the correlation between phylogenetic beta and geographic distance was significantly increased. In random landscapes all facets of beta diversity were positively correlated with geographic distance. All other studied indices did either show no significant results or showed results that were incongruent between the null models. To summarize, each of our simulated assembly processes was identified by a single diversity index or a combination of indices. Only functional beta (and partly alpha) diversity and correlations between beta diversity and environmental or geographic distance provided matching results for the two different null models.

Discussion

Diversity indices and null models have been widely used to infer different community assembly processes from species' distribution patterns (Webb et al. 2002, Mouillot et al. 2007, Kraft and Ackerly 2010). However, inconsistent results from field studies (Mc Gill 2003, Volkov et al. 2003, Supplementary material Appendix 3, Table A1) and first validation tests with virtual data (Chave et al. 2002, Kraft et al. 2007, Chisholm and Pacala 2010, Réjou-Méchain and Hardy 2011) have seriously challenged this approach. Following the conceptual framework that we have outlined in the introduction (Fig. 1) we could show that – at least for the ecological system simulated here – it is possible to infer community assembly processes from patterns of diversity. First, simulated species-sorting, mass effect, neutral and trade-off dynamics produced clearly distinct spatial patterns of species' distributions (Fig. 3, 4; step 1, Fig. 1). Second, a broad range of species' diversity indices calculated from samples of these species' distributions differed among the different assemblies (Fig. 4; step 2, Fig. 1). Third, using null models, a small number of diversity indices from different facets and spatial scales combined allowed identifying the correct assembly processes (Fig. 6; step 3, Fig. 1).

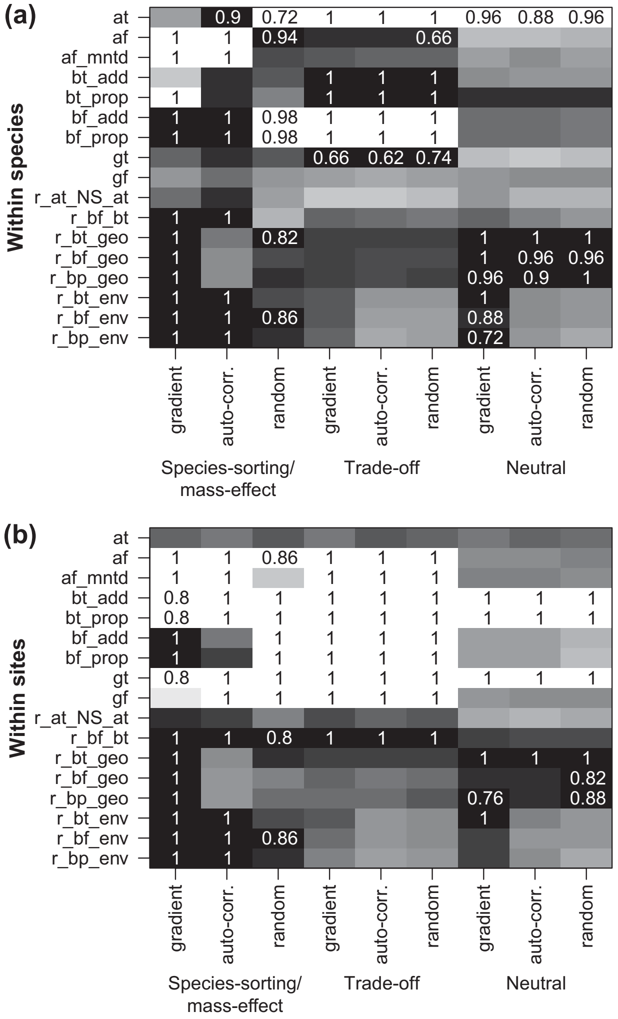

Figure 6. Power of the selected diversity indices and two different null models to identify non-random communities. Plot (a) shows results for the 'sites within species' and plot (b) for the 'species within sites' null model. Three different summary statistics for the 50 datasets per scenario are presented (which show only slightly different results): 1) average quantiles of observed values in the distribution of randomized values are given by grey shade with white indicating low and black indicating high values; 2) if these average quantiles are significant, i.e. above 0.95 or below 0.05, numbers are plotted; 3) these plotted numbers give the rate of datasets which gave the same significance as the overall mean. Abbreviations and diversity indices are explained in Table 2. For example, the indices for functional beta diversity (bf_add and bf_prop) identify significant signals for trade-off communities and species-sorting communities but not for communities with neutral dynamics. For the 'sites within species' null model and trade-off as well as mass effect communities (species-sorting species pool in a random landscape) the mean quantile of observed values in the randomized values is 0 (black squares), significantly below random expectations (thus values are plotted) and in all 50 datasets significantly below random expectations (rate equals 1). For species sorting (without mass effect), the mean quantile of observed values in the randomized values is 1 (black squares), significantly above random expectations (thus values are plotted) and in all 50 datasets significantly above random expectations (rate equals 1). For neutral communities, observed values are not distinguishable from random expectations (intermediate grey shades and no numbers plotted).

Assembly processes

Compared to alpha diversity indices observed under other assembly processes, species-sorting produced a combination of moderate taxonomic but decreased functional alpha diversity. This pattern is the result of the combination of close packing on the niche axis (i.e. species have slightly different niche optima and small niche widths) and the locally very similar environments. This combination favours the coexistence of different but functionally related species in local communities (Mizera and Meszena 2003). The same mechanisms result in the strong positive relation of community turnover (all facets) with environmental turnover. In contrast, under mass effects there are more locally maladapted species, with their presence being influenced by the neighbouring community composition (Shmida and Ellner 1984, Mouquet and Loreau 2003, Leibold et al. 2004). In our simulations, this is reflected by a strong accordance of taxonomic and functional alpha diversity and low functional beta diversity. The relationship between functional turnover and environmental turnover is however still strong. Trade-offs between competition and colonization lead to low taxonomic alpha diversity but to large functional alpha diversity because only species from considerably different parts of the trade-off space can coexist locally. The strongest difference compared to other assembly processes is the reduced taxonomic beta diversity (step 2, Fig. 1) and, compared to null expectations, the reduced functional beta diversity (step 3, Fig. 1). The low beta diversity shows that the trait space for successful coexistence through trade-offs is very limited. Neutral dynamics produce strong clustering and distance decays for taxonomic diversity due to dispersal limitation (Chave et al. 2002). Observed smaller effects of functional and phylogenetic clustering are an artefact produced by taxonomic clustering as species are functionally neutral.

We found that distinguishing the assembly processes based on single diversity indices can lead to inadequate interpretations (de Bello et al. 2009, Kraft and Ackerly 2010). For example, neutral dynamics produce spatial clustering. If by chance this spatial clustering matches environmental heterogeneity, resulting positive correlations of environmental and species turnover become indistinguishable from species-sorting (Fig. 6). However, our results indicate that significant patterns in functional beta diversity are in most cases able to rule out neutral mechanisms and could be used as a firm and repeatable tests of neutral assembly (Fig. 6). When additionally taking the significantly reduced functional alpha diversity and higher correlation of functional and taxonomic beta diversity of species-sorting assemblies into account one may be able to disentangle the assembly processes. Our study suggests that the situation is clearer for trade-offs and mass effects. However, results for assemblies with mass effects would probably be less clear if we had additionally varied dispersal distances in our simulations (Chave et al. 2002, Mouquet and Loreau 2003).

In this work the aim was not to test specific hypotheses regarding the theoretical multifaceted response of the 42 different diversity indices to the different combinations of species pools and landscape configurations. Deriving these predictions would have implicated a strong focus on theoretical aspects (step 1 of the conceptual framework), would have been partly specific to the model used here and goes beyond the scope of this paper. However, such predictions have already been published elsewhere for single diversity indices (Webb et al. 2002) and for pairwise combinations of diversity indices (Pavoine and Bonsall in press).

Diversity indices and null models

Overall we found that no single diversity index alone but only a combination of indices from different spatial scales and facets of diversity could identify and differentiate between assembly processes. In our simulated communities, a combination of functional beta diversity, functional alpha diversity and the correlations of community turnover (all facets) with environmental turnover and distance performed best in disentangling assembly processes. This small set of diversity indices performed well in both the direct comparison of observed species distributions (Fig. 1, step 2) and the comparison of observed species distributions with null model expectations (Fig. 1, step 3). All other indices having different signatures with the different assembly processes do not show consistent results under the different null models. The reason for this is twofold. First, more opposing results are to be expected when comparing two patterns generated by different assembly processes than when comparing two patterns generated by an assembly process and a random process. For example, species-sorting assemblies show significantly increased beta diversity, trade-off communities show significantly decreased beta diversity and randomized beta diversity shows intermediate values. Second, the different null models do not only break down patterns related to the underlying assembly processes but also other patterns as they also test implicit null hypotheses. The 'species within sites' model implicitly breaks down the inter-site abundance distributions for each species (Helmus et al. 2007, Hardy 2008) which can explain the significantly reduced taxonomic beta diversities found in our study (Fig. 6). The 'sites within species' model implicitly breaks down the original local species diversities per site (Hardy 2008) which can explain the significantly reduced local alpha diversities (Fig. 6).

We started with a large set of 42 indices from different spatial scales and facets of diversity. Our analysis selected those that captured community turnover (beta diversity), and among them those relating community turnover to either environmental or geographic distance. One reason for this is clearly the high amount of information contained in these diversity indices. These indices are also less sensitive to the above-discussed problems of null models.

Back to reality

An empirical test of all steps of our conceptual framework (Fig. 1) in the stricter sense would be impossible because it would require prior knowledge about the driving community assembly processes (Fig. 1, steps 1 and 2). Approximate tests might be performed in some particular situations where we may have strong hypotheses about the main drivers of community assembly. We call these tests approximate as they do not allow for strict testing because they are either based on correlational relationships, which do not permit causal interpretation, or they involve experiments under controlled conditions, which do not allow for generalization to large scales, large species pools and uncontrolled complex natural conditions. Such empirical approximations can include 1) microcosm experiments (Bell 2010), 2) experimental studies in which assembly processes are estimated directly via independent measures (Adler et al. 2007) or 3) communities for which strong hypotheses exist, for example dominance of competition vs facilitation along stress gradients (Callaway and Walker 1997). All these empirical approximations have some limits to generate generalizations. The fact that we can never be certain about the underlying processes is one of them. Similarly, we cannot be sure that results can be extrapolated from experimental microcosms to natural conditions.

Although the assumptions (Fig. 1, steps 1 and 2) of the indirect approach (step 3) cannot be tested for each empirical application, we have shown here that they hold – at least for ecological systems similar to the one simulated here. Besides this test of the method, our simulations provide some further insights into how applications of the indirect approach can be optimized. For example, our results on the importance of beta diversity highlight the advantage of a sampling design, which allows contrasting diversity patterns along constant vs sharply changing environmental gradients. By selecting sites with similar environmental conditions but contrasting geographic distances, one could try to estimate the effect of dispersal while controlling for the effect of environmental filtering using variance-partitioning techniques (Legendre et al. 2005). Note that the opposite view could also be used, i.e. using nearby sites along strong environmental gradients. However, in reality it may be difficult to choose sites that are similar in terms of environmental conditions at distant geographic distances and sites that are very dissimilar at close geographic distances, as the environmental variables are themselves often auto-correlated in space. Therefore, often it becomes difficult to determine which part of the spatial structure could be attributed to environmental filtering or to dispersal limitations (for a discussion of this topic see Meynard et al. in press).

The simulation approach has the advantage over these empirical approaches of clearly providing a test of diversity indices under different but explicit assumptions. The robustness of such conclusions will obviously depend on the realism of the initial assumptions regarding community assembly processes. However, this is the only way we can unequivocally manipulate all relevant initial conditions. Creating virtual data is fraught with difficulties. Our choice of assembly processes, species pools and landscape structures for the individual-based model represents only one possible implementation and is influenced by arbitrary decisions. For example, our finding that functional diversity indices perform better than phylogenetic diversity indices is surely due to our choices to include only traits that are important for species coexistence and not to account for biases or stronger measurement errors. Phylogenetic indices may well outperform functional indices when relevant traits are unknown or unavailable (Cadotte et al. 2010).

Generally, we would expect that more and interacting assembly processes influence field data and that therefore data and patterns will be burdened with additional noise.

This will make it more difficult to distinguish between assembly processes that already produce very similar patterns in our relatively simple simulations. Therefore, we advise that conclusions should only rely on significant patterns in null model tests rather than on non-significant ones. For example, one could argue that species-sorting and neutral communities differ because neutral communities show non-significant functional and phylogenetic turnover with environmental turnover. However, if data are noisier the same result may, by chance, emerge for species-sorting communities. Second, conclusions should only rely on patterns congruent among null models testing the same central hypothesis because all null models additionally test further implicit hypotheses. For studied systems that differ too much from the simulated data here, it might be necessary to adapt the simulation model to the focal system and directly test for the best combination of diversity indices and expected uncertainties. Furthermore a similar approach could be conducted with more complex evolutionary models of trait evolution (e.g. repeated convergences, stabilizing selection) to explore whether emerging patterns of phylogenetic diversity may change. For instance, repeated convergences of ecological characteristics among lineages coupled with strong species-sorting could result in phylogenetic over-dispersion in local communities.

Conclusions

Metacommunity theory has been postulated as a new paradigm that helps to bridge the gap between local community-level processes and large-scale biodiversity (Leibold et al. 2004). In this context, our study supports the potential for inference of assembly processes from biodiversity patterns by exemplarily demonstrating with virtual data how some diversity indices can provide important insights into the understanding of what generates diversity at larger spatial scales. It highlights the need to combine phylogenetic, functional and taxonomic diversity indices at multiple spatial scales as partial analysis of only one diversity facet or scale will remain contentious. Further, it calls for only using those diversity indices that produce significant signals and congruent results among different null models. Based on our simulated scenarios and the associated assumptions, we suggest functional beta diversity, functional alpha diversity and the correlations of community turnover (all facets) with environmental turnover and distance decay as an appropriate combination of indices.

We believe that as more and more large-scale datasets become available, unraveling processes from large-scale patterns becomes a key tool to study questions like the anticipation of global change effects (Gotelli et al. 2010). If we were to better understand the main processes underlying community changes in degrading and changing habitats and implications of invasions we would be able to implement models of species and diversity dynamics more confidently. Here, we propose advances towards this direction and demonstrate the usefulness of virtual ecologist approach sensu Zurell et al. (2010) for the study of community assembly processes. We advocate that this multilevel approach can readily be adapted to a diverse set of ecological communities.

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Supplementary material (Appendix E7259 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.