SPECIAL FEATURE: FUNCTIONAL DIVERSITY

A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients

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Abstract

Question: Which functional diversity indices have the power to reveal changes in community assembly processes along abiotic stress gradients? Is their power affected by stochastic processes and variations in species richness along stress gradients?

Methods: We used a simple community assembly model to explore the power of functional diversity indices across a wide range of ecological contexts. The model assumes that with declining stress the influence of niche complementarity on species fitness increases while that of environmental filtering decreases. We separately incorporated two trait-independent stochastic processes – mass and priority effects – in simulating species occurrences and abundances along a hypothetical stress gradient. We ran simulations where species richness was constant along the gradient, or increased, decreased or varied randomly with declining stress. We compared observed values for two indices of functional richness – total functional dendrogram length (FD) and convex hull volume (FRic) – with a matrix-swap null model (yielding indices SESFD and SESFRic) to remove any trivial effects of species richness. We also compared two indices that measure both functional richness and functional divergence – Rao quadratic entropy (Rao) and functional dispersion (FDis) – with a null model that randomizes abundances across species but within communities. This converts them to pure measures of functional divergence (SESRao and SESFDis).

Results: When mass effects operated, only SESRao and SESFDis gave reasonable power, irrespective of how species richness varied along the stress gradient. FD, FRic, Rao and FDis had low power when species richness was constant, and variation in species richness greatly influenced their power. SESFRic and SESFD were unaffected by variation in species richness. When priority effects operated, FRic, SESFRic, Rao and FDis had good power and were unaffected by variation in species richness. Variation in species richness greatly affected FD and SESFD. SESRao and SESFDis had low power in the priority effects model but were unaffected by variation in species richness.

Conclusions: Our results demonstrate that a reliable test for changes in assembly processes along stress gradients requires functional diversity indices measuring either functional richness or functional divergence. We recommend using SESFRic as a measure of functional richness and either SESRao or SESFDis (which are very closely related mathematically) as a measure of functional divergence. Used together, these indices of functional richness and functional divergence provide good power to test for increasing niche complementarity with declining stress across a broad range of ecological contexts.

Introduction

Functional diversity indices have the potential to reveal community assembly processes (Mason et al. 2008b, 2012). Vegetation changes along gradients of environmental stress are amongst the most widely observed patterns in plant ecology (e.g. Richardson et al. 2004; Peltzer et al. 2010). Documenting how community assembly processes change along these gradients is crucial for understanding the drivers of observed vegetation change. Functional diversity is not a single, non-divisible concept, but rather is composed of multiple components (Mason et al. 2005), with a large variety of functional diversity indices having been proposed to measure these components (Schleuter et al. 2010; Pavoine et al. 2013). Plant ecologists clearly need guidance on which indices to use. Recent theoretical and practical advances in the measurement of functional diversity have led to an increase in the use of functional diversity indices to detect changes in community assembly processes along ecological gradients (Mason et al. 2011a,b; Pakeman 2011; Spasojevic & Suding 2012). However, these studies are usually restricted to a single ecological context, and so provide little guidance to ecologists on which indices to use. Theoretical models allow us to assess the power of functional diversity indices to detect changes in assembly processes along gradients across a wide range of contexts. This study uses simple theoretical models that embody clearly defined assembly processes to test which functional diversity indices most reliably reveal changes in these processes along gradients of abiotic stress.

Why should functional diversity change along stress gradients?

Stress gradients often represent a shift from below-ground competition for soil nutrients and water to above-ground competition for light with declining stress (e.g. Coomes & Grubb 2000). Competition for light is size-asymmetric (i.e. larger individuals are disproportionately advantaged) whereas below-ground competition is size-symmetric (Schwinning & Weiner 1998; Berntson & Wayne 2000; Cahill & Casper 2000). Competition for light provides more competitive species with an increasing advantage as they outperform (i.e. become taller than) less competitive ones (Grime 1973a,b, 2001; Huston & DeAngelis 1987). Niche differentiation is required for species to co-exist when competition is size-asymmetric, since without niche differentiation even small differences in fitness lead to exclusion of all but the fittest species (Aikio 2004; Kohyama & Takada 2009). Thus, niche differences (i.e. spatial or temporal differentiation in resource use and acquisition) between co-occurring species should increasingly enhance local fitness as light competition becomes more intense, by allowing subordinate species to evade competition with superior competitors (Mason et al. 2011b). This should cause multi-species communities where light competition is intense to have greater functional diversity than those where light is not limiting (Mouchet et al. 2010) for traits linked to spatial or temporal differentiation in resource use and acquisition. There is recent field evidence for this in plant communities (Mason et al. 2012).

Where size-symmetric below-ground competition dominates, species with similar niches are more likely to co-exist, since small differences in competitive ability do not have disproportionate effects on the outcome of competition (Rajaniemi 2003). Co-existence between functionally similar species also results from slower growth rates in stressed communities, which reduce the pace of competition after disturbance (following the dynamic equilibrium theory of Huston (1979) and supported by experimental evidence; Rajaniemi 2003; Wardle & Zackrisson 2005). Consequently, selective pressure for niche differentiation between co-occurring species is less intense in stressed communities. Rather, fitness is enhanced by traits that maximize acquisition and retention of limiting below-ground resources (e.g. Richardson et al. 2005; Lambers et al. 2008; Holdaway et al. 2011).

This is consistent with environmental filtering (i.e. when local fitness is enhanced by possession of traits similar to a locally 'optimal' trait value; Mouillot et al. 2007; Mason et al. 2011b). The prevalence of environmental filtering in stressed communities should cause decreased functional diversity (Mouchet et al. 2010). For some stresses, such as nitrogen limitation, fitness could be enhanced by niche differentiation via facilitation (e.g. Walker & Chapin 1986). The hypothesis that functional diversity should decline with stress assumes facilitation effects will be minor compared with the influence of environmental filtering in stressed communities and is based on field evidence from plant communities occurring along a soil phosphorus gradient (Mason et al. 2012). We recognize that factors other than below-ground resource limitation may impose stress on plant communities. We refer to 'stress gradients' in this study, for the sake of brevity.

Using functional diversity indices to detect trait-based assembly processes

Mason et al. (2005) identified three primary components of functional diversity – functional richness, functional evenness and functional divergence. Each component provides independent information on the distribution of species in functional trait space, and a separate index is required to quantify each component (Mouchet et al. 2010). Of the three components, functional richness and functional divergence (or indices that combine them) have most often been linked to community assembly processes

(Mouchet et al. 2010; Mason et al. 2012; Spasojevic & Suding 2012) or ecosystem functioning (Petchey et al. 2004; Mouillot et al. 2011).

The various indices of functional richness aim to measure the volume of niche space occupied by the species within a community (Mouchet et al. 2010). Functional richness should increase when niche complementarity enhances probabilities of species occurrence (Mason et al. 2012). Functional divergence measures the degree to which the abundance of a community is distributed toward the extremities of occupied trait space (Mouchet et al. 2010). Functional divergence should increase when niche complementarity enhances species' relative abundances (Mason et al. 2012). Various indices measure both functional richness and divergence (Mouchet et al. 2010) – FDvar (Mason et al. 2003), Rao quadratic entropy (de Bello et al. 2010) and functional dispersion (Laliberté & Legendre 2010). They should increase when niche complementarity enhances either, or both, species' occurrence probabilities and abundances.

An important property of functional diversity indices is that they be independent of existing diversity measures (Mason et al. 2005; Pavoine et al. 2013). Functional richness increases monotonically with species richness. This means that observed values of functional richness can increase in the absence of any change in assembly processes, simply due to corresponding increases in species richness (Mason et al. 2008b). Comparing observed values for functional richness with those expected from matrix-swap null models that randomize species' occurrences (Manly & Sanderson 2002) can remove any trivial effects of species richness (Mason et al. 2011a; Richardson et al. 2012). This is important for ensuring that changes in functional richness do not lead to spurious conclusions about changes in assembly processes.

Recent studies have used a null model that randomizes abundances across species but within communities to test for trait-based assembly processes in biological communities (Mason et al. 2008a). Comparison of observed values for indices that measure both functional richness and divergence with expected values from this null model effectively converts these indices into pure measures of functional divergence (Mason et al. 2012). This is advantageous, since there is only one existing measure of functional divergence (FDiv; Villeger et al. 2008), and it seems to have only moderate power to detect assembly processes (Mouchet et al. 2010).

Functional diversity, assembly processes and trait-independent stochasticity

Stochastic processes that act independently of species traits, particularly mass and priority effects, may have a strong influence on community assembly. Mass effects occur when source–sink metapopulation dynamics allow species to occur at low abundance in communities where they are unable to maintain a viable population (Kunin 1998; Leibold et al. 2004). This produces a pattern where environmental heterogeneity and spatial distance both have significant, independent effects on species turnover (Cottenie 2005). Potential for mass effects is highest in highly heterogeneous landscapes where communities with different abiotic conditions are separated by very small spatial distances (Kunin 1998). Mass effects disrupt the relationship between traits and occurrence probabilities of species, making it difficult for functional richness indices to detect changes in assembly processes (Mason et al. 2013).

Priority effects occur when assembly order influences the outcome of inter-specific competition (e.g. Ejrnæs et al. 2006). They generally produce patterns where communities in similar environments exhibit persistent differences in species composition (Fukami et al. 2005; Ejrnæs et al. 2006), and seem to be most evident during succession (e.g. Fukami et al. 2005), especially when competition for light has a strong influence on community composition during succession (e.g. Ejrnæs et al. 2006). Priority effects disrupt the relationship between species' traits and both occurrences and abundances, potentially making it difficult for both functional richness and functional divergence indices to detect changes in assembly processes.

Reliable detection of changes in trait-based assembly processes along stress gradients requires a set of functional diversity indices that are robust against trait-independent stochastic assembly processes. Specifically, we need indices that can detect the influence of trait-based processes on either occurrence probabilities or abundances, since trait-independent processes might disrupt the link between species' traits and either occurrence probability or abundance.

Aims and objectives

We aim to explore the power of functional diversity indices to detect shifts in assembly processes along gradients under a wide range of ecological contexts. To achieve this aim we sought to develop a simple assembly model that varies trait convergence in communities along a hypothetical stress gradient, by altering the relative influence of niche complementarity and environmental filtering on species fitness. This model simulates trait values for multiple species pools. It quantifies the effects of environmental filtering and niche complementarity on species fitness, using explicitly defined functions. It varies the relative influence of these assembly processes along the gradient, with niche complementarity becoming more influential as stress declines. It incorporates two forms of stochasticity – mass

and priority effects – to test whether indices are robust against trait-independent processes. It also tests whether variation in species richness affects the power of indices to detect changes in assembly processes along the stress gradient. Our ultimate aim is to select a set of functional diversity indices that will provide a reliable test of the hypothesis that niche complementarity, and hence functional diversity, will increase with declining abiotic stress. To do this we use the following selection criteria:

1. Each index must have reasonable power to detect the increasing influence of niche complementarity with declining stress (henceforth power, for brevity) when either mass effects or priority effects influence community assembly.
2. Power must be high across a range of species richness levels.
3. Variation in species richness along the stress gradient must not affect the power of any index.
4. Collectively, the indices must provide reasonable power across all the contexts examined.

Methods

We begin by outlining the basic assembly model. We then detail how priority and mass effects are built in to incorporate stochasticity. Finally, we list the FD indices we use and explain the two null models examined.

Basic assembly model

The model context is one where the relative influence of niche complementarity and environmental filtering change along a stress gradient, with the influence of environmental filtering being greatest at the most stressed sites. The aim of our study was to examine the ability of functional diversity indices to test the hypothesis that the influence of niche complementarity on community assembly will increase relative to that of environmental filtering with declining abiotic stress. Consequently, we designed our model to produce communities of increasing trait divergence with declining stress by varying the relative influence of environmental filtering and niche complementarity on species fitness. We model the effect of environmental filtering on fitness as a declining quadratic function of the difference between a species' trait value and the locally optimal trait value for a given site:

$$\text{Fitness}_{\text{EF}i} = a(\text{Range}_T - |T_i - T_{\text{opt}}|)^2 \qquad (1)$$

where: Range_T is the range of values for trait T in the species pool, T_i is the trait value for species i, T_{opt} is the locally optimal trait value for the site and a is a scaling factor that

ensures $\text{Fitness}_{\text{EF}i}$ is bound between 0 and 100 when $|T_i - T_{\text{opt}}| \leq \text{Range}_T$. We aimed to avoid negative values for fitness since we used fitness to scale species' abundances (see below) and it is not logical for species to be assigned negative abundances. We used a quadratic function as a simple means of modelling a non-linear decline in fitness with increasing distance of the species' trait value from the optimal trait value.

We model the effect of niche complementarity on fitness as the competitive effect on potential colonizers of species that are already 'present' in the community. In the basic model, species' local fitness determines their selection order. We assume that the species closest to the locally optimal trait value has the highest fitness. Since it colonizes first, we assume its fitness is unaffected by competition from species that colonize subsequently. Competition affects the fitness of all other species. We calculate competition as a declining cubic function of the distance between species in trait space:

$$C_{ij} = b(\text{Range}_T - |T_i - T_j|)^3 \qquad (2)$$

where C_{ij} is the competitive effect of present species j on colonizing species i, and b is a scaling factor that ensures C_{ij} is bound between 0 and 1 when $|T_i - T_{opt}| \leq \text{Range}_T$. We used a cubic function since it is a simple non-linear function and gives a steeper decline in the competitive effect of co-occurring species with increasing trait dissimilarity than does the quadratic function. This in turn provided greater variation in trait convergence along the stress gradient.

The overall effect of competition from the species present on the fitness of potential colonizers is estimated as the sum of C_{ij} values weighted by the fitness of the species present:

$$\text{Fitness}_{\text{NC}i} = 100 - \min\left[\sum_{j=1}^{S} C_{ij} \times \text{Fitness}_j, 100\right] \qquad (3)$$

where Fitness_j is the overall fitness of present species j (see below for calculation of overall fitness). When modelled in this way, competitive effects are additive and the intensity of competition exerted by a species is proportional to its fitness. A potential colonizing species will experience intense competition if it has similar traits to a species that is already present and has high fitness. Overall fitness is calculated as a combination of environmental filtering and niche complementarity effects on fitness:

$$\text{Fitness}_i = c \times \text{Fitness}_{\text{EF}i} + d \times \text{Fitness}_{\text{NC}i} \qquad (4)$$

where $c + d = 1$, so that fitness is always bound between 0 and 100.

In the basic model, species are selected in order of their fitness. The first species selected is the one with the highest $Fitness_{EFi}$ (i.e. with a trait value closest to the local optimum), and its fitness is assumed to be unaffected by competition (i.e. $Fitness_{NCi} = 100$). Fitness for all remaining species is then calculated including both $Fitness_{EFi}$ and the influence of competition from the first species (i.e. as measured by $C_{ij} \times Fitness_j$ in equation 3, with species j being the first colonizing species). The species with the highest fitness is then selected as the second colonizer. The process is repeated until the number of selected species equals the desired local species richness. Fitness of the selected species is then scaled to abundance so that the most abundant species has 10^3 times the abundance of the least abundant species, and differences in abundance between species are proportional to their differences in fitness. This degree of variation in abundances is typical in plant communities. At high levels of d, colonization order has increasing influence on fitness, since late-arriving species will, on average, have lower $Fitness_{NCi}$ than early colonizers.

As demonstrated by de Bello et al. (2011), Albert et al. (2012), Laliberte & Legendre (2010) and de Bello et al. (2012), calculating functional diversity for multiple traits can introduce a variety of complications, and necessitates complex methodological decisions. To avoid such complications, the model uses a single trait to determine both niche complementarity and environmental filtering effects on fitness. There is a good precedent for this based on field studies showing that single traits may simultaneously influence species' occurrences along stress gradients as well as influencing competitive interactions between species at the local community level (Cornwell & Ackerly 2009; Mason et al. 2012). However, we recognize that species' responses to environmental heterogeneity and interspecific competition may be influenced by different traits in many instances (Chesson 2000).

Varying assembly processes along the gradient

Values for c and d vary along the hypothetical stress gradient. We simulated species' abundances for ten points (termed sites henceforth) along the stress gradient. At the most stressed site, $c = 0.91$ and $d = 0.09$, so that 91% of overall fitness is determined by environmental filtering and 9% is determined by niche complementarity. Moving from the most stressed to least stressed end of the gradient, we decreased c and increased d by intervals of 0.09, so that at the least stressed site $c = 0.1$ and $d = 0.9$, with 10% of overall fitness due to environmental filtering and 90% due to niche complementarity. In this way, fitness, and hence abundance, is largely determined by proximity to the locally optimal trait value at the most stressed site. At the least stressed site, for all but the species with the highest

abundance value, abundance is largely determined by having complementary traits to species that are already present.

Generating regional species pools and locally optimal trait values

Values for a single trait were simulated for 130 indigenous New Zealand herbaceous and woody angiosperm, gymnosperm and fern species following a Brownian motion model of evolution with mean of 0 and SD of 1 (Blomberg et al. 2003). These species form the pool of potential colonizers for our simulated communities. We chose to examine only a single trait, since identifying ecological mechanisms driving variation in functional diversity often requires each trait to be analysed separately (Mason et al. 2011b). We used Phylomatic (http://www.phylodiversity. net/phylomatic/) to construct a hypothesized phylogenetic tree for our species, and used the New Zealand Plant Phylogeny Database (http://plantphylogeny.landcareresearch. co.nz/WebForms/Home.aspx) to manually graft species that were not available in Phylomatic. Branch lengths were computed following Grafen (1989) using the 'compute.brlen' in R package 'ape' (Paradis et al. 2004; R Foundation for Statistical Computing, Vienna, AT, Australia). There may be some potential for characteristics of our phylogeny or the model of trait evolution to alter results. However, it seems that aspects like phylogenetic tree shape generally have only subtle effects on the likelihood of detecting assembly processes (Kraft et al. 2007). Also, a recent study using the same simulation model as used here has shown that the strength of trait conservatism used in generating species pools via trait evolution models does not affect the relationship between species turnover and functional traits along environmental gradients (Mason & Pavoine 2012).

Locally optimal trait values for each site were spaced evenly along the central 60% of the gradient of total traits present in the species pool. The intention here was to ensure that functional diversity values at the extremes of the stress gradient were not affected by limitations in the trait values present in the species pool. There is a risk that functional diversity values might be artificially constrained if the optimal trait values at the ends of the stress gradient are too close to the edge of the trait space occupied by the species pool. Altering locally optimal trait values is consistent with multiple observations that the trait values of locally dominant species vary monotonically along stress gradients (Peltzer et al. 2010).

Under this basic model, species' abundances are a deterministic function of their traits and the traits of co-occurring species. This is quite unrealistic, since stochastic processes that act independently of traits also

influence abundance in plant communities. Consequently, we do not use the basic model to test whether functional diversity indices can detect changes in assembly processes. Rather, we employ two extensions that incorporate different types of stochasticity.

Mass effects model

This is a simple extension of the basic model where, for each site, the species present are randomly selected from the species pool (e.g. if we wanted a community of ten species, we would randomly select ten species from the regional species pool). The basic model then calculates the fitness and abundance of the selected species. Under this model, species' occurrences are completely unrelated to their traits, but abundance is a deterministic function of the traits of the species present. This is an extreme form of mass effects. This model tests whether functional diversity indices can detect changes in trait-based assembly processes in communities where these processes have weak effects on species' occurrences (i.e. neither biotic nor abiotic filtering excludes species from local communities), but a strong effect on species' abundances. The assumption that mass effects are not influenced by the traits linked to environmental filtering and niche complementarity is perhaps an oversimplification (Münkemüller et al. 2012). However, seed production and dispersal are the traits most likely to drive mass effects, since high propagule pressure is the key factor in maintaining sink populations (Mouquet et al. 2004). Further, there is evidence that traits linked to regenerative strategy vary independently of those linked to resource use and acquisition (Grime et al. 1997; Díaz et al. 2004), so this assumption may be more or less realistic.

Priority effects model

This model randomizes the order of species' colonization, whereas species' traits determine colonization order in the basic model. In this model, colonization order affects the degree of competition experienced by each species, with early-colonizing species, on average, experiencing less intense competition. Species fitness is calculated as in the basic model, but competitive effects on fitness are based on this randomized colonization order. The desired number of species is then selected based on species fitness (so when generating communities of ten species, the ten fittest species are selected). Since colonization order may have a strong influence on the level of competition a species experiences, the priority effects model incorporates stochasticity in the relationship between traits and both species' occurrences and abundances. This stochasticity is highest in the least stressed sites where the influence of competition on

fitness is strongest. This is consistent with evidence that priority effects are stronger in high productivity environments where size-asymmetric competition for light is more intense (Ejrnæs et al. 2006). This model tests whether functional diversity indices can detect changes in trait-based assembly process in communities where priority effects disrupt the effect of these processes on both occurrences and abundances.

Functional diversity indices and null models

We examined two indices of functional richness – the FD of Petchey & Gaston (2002) and the FRic of Villeger et al. (2008), which is derived from the convex hull volume of Cornwell et al. (2006). For a single trait, FRic is simply the range of trait values spanned by the species present. To ensure values for each simulated community for both these measures were bound between 0 and 1, they were expressed as a proportion of the values for the entire species pool. We used FDiv as a measure of functional divergence. For functional evenness (i.e. evenness in the distribution of abundance in functional trait space; Mason et al. 2005) we used the FEve of Villeger et al. (2008). We examined two mathematically quite similar indices that are a combination of both functional evenness and functional divergence – FDis (Laliberte & Legendre 2010) and Rao quadratic entropy (referred to as Rao henceforth; Rao 1982; Pavoine & Doledec 2005; de Bello et al. 2010). Although there is some debate about the appropriate dissimilarity measure to use in calculating Rao (de Bello et al. 2012), we use Gower distance, as recommended by Pavoine et al. (2009).

We compared FRic and FD values relative to random expectation under a matrix-swap null model (Manly & Sanderson 2002) using the standardized effect size (SES) of Gotelli & McCabe (2002). These indices are termed SES-FRic and SESFD henceforth. FDis and Rao were compared with values obtained when abundances were randomized across species but within plots (after Mason et al. 2008a). These indices, termed SESFDis and SESRao, are pure measures of functional divergence, since the functional richnesses of the observed and randomized communities are always identical. We also compared FDiv to this null model. We used 10^4 randomizations in all null-model analyses, to ensure accurate estimates of SES values. We did not randomize abundances between communities because it is unclear how SES values derived in this way relate to the three primary components of functional diversity. Observed FEve was not compared with either null model since it is independent of species richness, and it is unclear how SES values generated when randomizing species' abundances within communities should be interpreted.

Under the mass effects model, functional richness indices (FD, FRic, SESFD and SESFRic) should have no power to detect changes in assembly process, since species' occurrences are unrelated to their traits. Similarly, indices that are partially influenced by functional richness (FDis and Rao) might also have low power in the mass effects model. However, indices of functional divergence (FDiv, SESFDis and SESRao) should have good power since they are only influenced by how abundance is distributed in occupied trait space. Under the priority effects model, the effect of traits on species' occurrences is also disrupted, but much less severely than is the mass effects model, so functional richness indices should have good power to detect changes in assembly processes. Priority effects also disrupt the relationship between traits and relative abundances, which might influence the power of functional divergence indices, and indices that are partially influenced by functional divergence (FDis and Rao).

Simulation framework

The same simulation framework was applied to the mass effects and priority effects models. In each case, it began with the generation of trait values for the species pool. Then communities were assembled for each of the ten sites occurring along the hypothetical stress gradient. Functional diversity values were calculated for each of the sites, along with Pearson correlation and Spearman rank correlation coefficients between each functional diversity index and the influence of niche complementarity on fitness (as indicated by the coefficient d). Significant positive correlations (i.e. two-tailed $P < 0.05$) between functional diversity indices and d indicate that they are able to detect the increasing influence of niche complementarity on community assembly with declining stress. Both these correlation coefficients gave similar power for all indices, so we only present the results for Pearson r here. We also examined log-linear, quadratic and exponential relationships between functional diversity indices and d. In no instance did these relationships yield greater power (according to Akaike's information criterion; Burnham & Anderson 2002) than Pearson r.

We generated trait values for 100 hypothetical regional species pools (i.e. 100 separate simulations of trait values for the 130 species in our phylogenetic tree), and simulated communities at five levels of local species richness: 5, 10, 15, 20 and 25. For example, with a local species richness level of 5, each of the ten simulated local communities (one community for each point along the stress gradient), contains five species. For each species richness level, we recorded the proportion of significant correlations (termed power henceforth) obtained between each index and the

influence of niche complementarity on fitness (as indicated by the coefficient d). We tested whether the power of indices was affected by variation in species richness along the gradient, by simulating communities of varying species richness. To examine power with increasing species richness, communities containing five species were simulated for the two most stressed sites (i.e. sites with the lowest d values). Communities with ten species were simulated for the two next most stressed sites, and so on until communities with 25 species were simulated for the two least stressed sites (i.e. the two sites with the highest d values). This provides an indication of power when species richness increases with the influence of niche complementarity (d). We repeated this process in reverse to estimate power when species richness declined with d. We also examined power when species richness varied randomly with d. Where significant negative correlations were obtained, these were recorded as 'negative power', so that power was bound between -1 and 1.

Results

For the priority effects models, FRic, FDis, Rao and SESFRic had power of >0.95 for all levels of species richness (Fig. 1a). Thus, these indices had at least a 95% chance of detecting an increase in niche complementarity with decreasing stress. FD and SESFD had power of >0.9 for the two lowest levels of local species richness (i.e. five and ten species), but not the three highest (i.e. 15, 20 and 25 species). All other indices had low power in comparison.

For the mass effects model, SESFDis and SESRao had power of ≥ 0.8 at all levels of local species richness (Fig. 1b). The power of FDis and Rao increased with species richness, being ~0.8 for the two highest levels of local species richness (i.e. 20 and 25 species). All other indices had very low power.

Variation in species richness along the stress gradient did not markedly affect the power of FRic, FDis, Rao, SESFRic, SESRao and SESFDis in the priority effects model (Fig. 2a). In contrast, power for FD was much higher when species richness increased and much lower when it decreased with declining stress. Power for SESFD showed the opposite pattern, being much higher when species richness decreased and much lower when it increased with declining stress.

For the mass effects model, the power of SESFD, SESFRic, SESRao and SESFDis was unaffected by variation in species richness along the stress gradient (Fig. 2b). However, variation in species richness strongly affected the power of FD, FRic, FDis and Rao. In the case of FD and FRic, power was negative when species richness declined with declining stress.
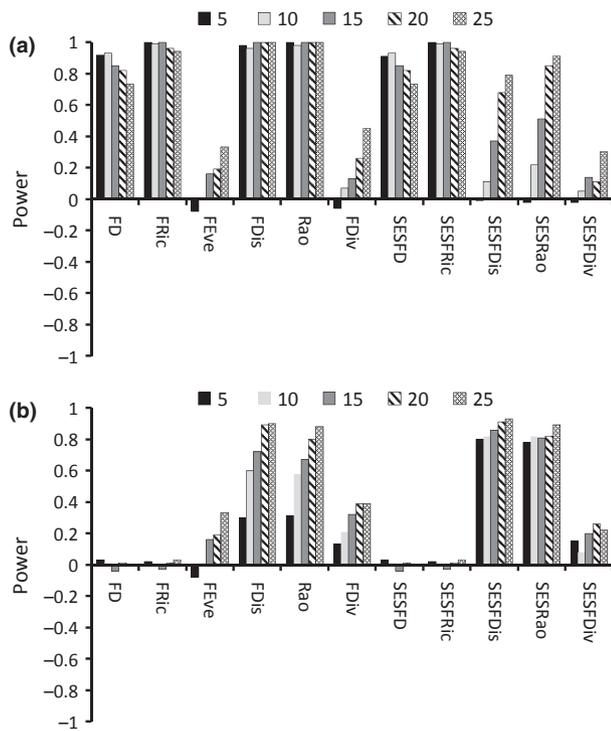
Fig. 1. Power of functional diversity indices to detect the increasing influence of niche complementarity with declining stress when: (**a**) priority effects disrupt the relationship between species traits and abundances, and (**b**) mass effects disrupt the relationship between species traits and occurrences. Numbers associated with different types of bar shading indicate species richness of local communities. FD is the sum dendrogram branch length, FRic is convex hull volume, FEve is functional evenness, FDis is functional dispersion, Rao is quadratic entropy and FDiv is functional divergence. SESFD and SESFRic are, respectively, observed FD and FRic expressed relative to a matrix-swap null model. SESRao, SESFDis and SESFDiv are, respectively, observed Rao, FDis and FDiv expressed relative to a null model randomizing abundances across species, but within communities.

Fig. 2. Power of functional diversity indices to detect the increasing influence of niche complementarity with declining stress with species richness increasing, decreasing or varying randomly as stress declines. In (**a**) priority effects disrupt the relationship between species' traits and abundances, while in (**b**) mass effects disrupt the relationship between species' traits and occurrences. FD is the sum dendrogram branch length, FRic is convex hull volume, FEve is functional evenness, FDis is functional dispersion, Rao is quadratic entropy and FDiv is functional divergence. SESFD and SESFRic are, respectively, observed FD and FRic expressed relative to a matrix-swap null model. SESRao, SESFDis and SESFDiv are, respectively, observed Rao, FDis and FDiv expressed relative to a null model randomizing abundances across species, but within communities.

Discussion

We are aware of only one simulation study examining the power of a broad range of functional diversity indices to detect community assembly processes (Mouchet et al. 2010). Their study did not consider how null models and variation in species richness affected power. Nor did it determine which indices maintained power in the face of trait-independent, stochastic processes. Similarly, we are only aware of a single study using simulated data to test if null models altered the conclusions drawn from functional diversity patterns (de Bello 2012). However, that study considered a much narrower range of contexts than we have.

Our results extend these existing studies in several key ways. They show that the power of functional diversity indices to detect chan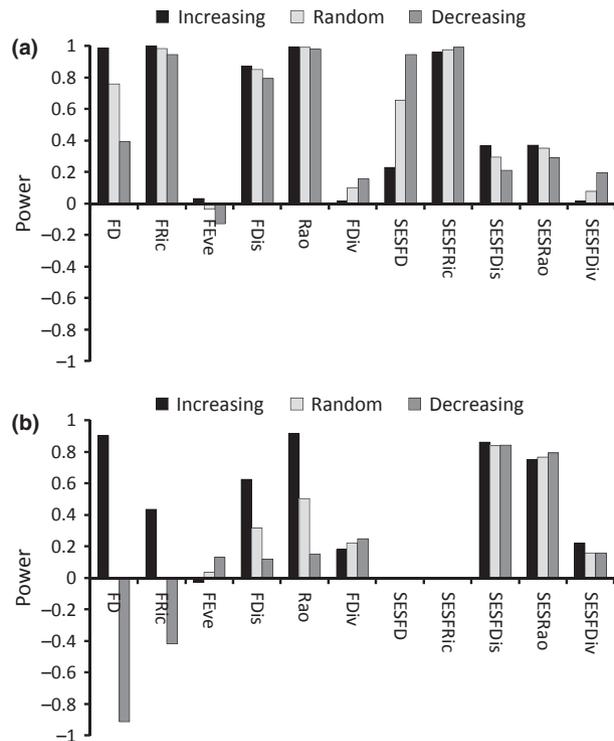ges in assembly processes is highly context-dependent. Thus, any study examining changes in assembly processes along gradients should employ several, complementary functional diversity indices. They demonstrate that different types of stochasticity have contrasting effects on the power of functional diversity to detect changes in assembly processes, with our two assembly models giving highly divergent results. They show that stochastic processes alter the dependence of indices on species richness. They also reveal that we need to compare observed functional diversity values to null models (using standardized effect size, SES) to ensure that we draw the right conclusions about assembly processes.

Below we discuss what our results for functional diversity patterns tell us about shifts in assembly processes in our two models. We specifically outline when and how null models improve our ability to detect shifts in assembly processes along gradients. We finish by suggesting a set of

functional diversity indices that should be appropriate for a wide range of ecological contexts. In doing this we provide some guidance about what presence or lack of significant variation in these indices along stress gradients may reveal about community assembly processes.

Null models, stochasticity and power to detect shifting assembly processes

In the mass effects model, SESRao and SESFDis were the only measures to give reasonable power (≥ 0.8) for all levels of species richness. SESRao and SESFDis values were partially contingent on the random selection of species from the species pool. This explains why we obtained only moderate power. This result for SESRao and SESFDis reveals the increasing influence of niche complementarity on species' abundances with declining stress. That SESRao and SESFDis had greater power than observed Rao and FDis shows that use of an appropriate null model to obtain standardized effect size (SES) improved our ability to detect changes in assembly processes along the stress gradient. FD, FRic, SESFD and SESFRic had power of ~0 for all levels of species richness. This is to be expected since trait-based assembly processes do not influence species' occurrence probabilities under this model, so that functional richness varies at random along the stress gradient.

In the priority effects model, FRic and SESFRic reliably detected an increase in functional richness with declining stress for all levels of species richness. FDis and Rao had higher power than SESFDis and SESRao, especially at lowest levels of species richness. FDis and Rao are sensitive to changes in functional richness, but SESFDis and SESRao are not. This suggests that the power of FDis and Rao was largely due to increases in functional richness with declining stress. These results reveal the increasing influence of niche complementarity on species' occurrences (via increases in functional richness) with declining stress. The comparatively low power of SESFDis and SESRao also indicates that priority effects disrupted the influence of trait-based assembly processes on species' abundances. These results also show that the null models we used to produce SES values provided no increase in power under the priority effects model.

Null models, stochasticity and dependence of power on species richness

In the mass effects model, FD and FRic led to completely different conclusions according to whether species richness increased or decreased with declining stress. Using these indices we would conclude, incorrectly, that the influence of niche complementarity on species' occurrences increases with declining stress in the former case and

decreases in the latter. However, when expressing observed values for these indices relative to those expected from a matrix-swap null model (i.e. SESFD and SESFRic), we would conclude, correctly, that the influence of niche complementarity on occurrences does not change with stress, irrespective of how species richness varies along the gradient. The power of FDis and Rao was also greatly affected by variation in species richness, being much higher when species richness increased with declining stress, which would affect conclusions about assembly processes. This is due to their sensitivity to functional richness, which is itself influenced by species richness, but not assembly processes in this model. Power of SESRao and SESFDis was unaffected by variation in species richness along the gradient. These results show that using null models to generate SES values helped remove the influence of species richness on functional diversity. This is important to prevent drawing spurious conclusions about assembly processes when species richness varies greatly between communities.

In the priority effects model, variation in species richness along the stress gradient did not affect the power of FRic, FDis and Rao. Thus, there was no evidence that variation in species richness would lead to spurious conclusions under this model. Consequently, there was no need to use null models to remove the influence of species richness.

Recommended indices and interpretation of significant correlations

Our results permit us to identify a set of indices that give reasonable power to detect changes in assembly processes across the range of contexts examined. They also allow us to suggest interpretations for presence or lack of significant correlations between these indices and stress gradients. The recommended indices and interpretations of correlations between them and stress gradients are summarized in Table 1.

Our results indicate that when priority effects influence species composition, but mass effects are weak, SESFRic will have good power to detect increasing niche complementarity in the priority effects model. SESFRic was also robust against variation in species richness in both our assembly models, and thus satisfies all our criteria. When using multiple traits, SESFD might also be an appropriate index. Its sensitivity to variation in species richness may have been partly due to saturation of observed FD values at high species richness, which itself could arise from our using only a single trait. Here we have presented a basic matrix-swap null model where swapping of species' occurrences between any pair of sites is permitted. Instances where sites are separated by large geographical distances

Table 1. Recommended indices and interpretations of significant correlations between indices and stress gradients.

SESFRic	SESRao/SESFDis	Interpretation
+	NS	Increasing influence of NC on *occurrences*, but not abundances, with declining stress
NS	+	Increasing influence of NC on *abundances*, but not occurrences, with declining stress
+	+	Increasing influence of NC on both *occurrences* and *abundances*, with declining stress
NS	NS	No change in influence of NC on either occurrences or abundances, with declining stress

SESFRic is the standardized effect size for the FRic of Villeger et al. (2008) obtained using a matrix-swap null model to randomize occurrences. SESRao and SESFDis are standardized effect size for (Rao) quadratic entropy and functional dispersion (FDis) obtained using a null model randomizing abundances across species but within communities. NC refers to niche complementarity. + indicates a significant positive correlation between functional diversity and declining stress. SESRao/SESFDis indicates that these indices are interchangeable due to their similar behaviour.

may require application of spatial constraints (e.g. Rox-burgh & Matsuki 1999) so that the null model incorporates dispersal limitation effects (e.g. as proposed by Mason et al. (2007)). However, in testing for changes in assembly processes along ecological gradients we advise against using environmentally constrained matrix-swap null models (e.g. Peres-Neto et al. 2001). This is because environmental constraints on species' occurrences are relevant in testing for shifts in assembly processes along gradients, and thus should not be included in null models randomizing species' occurrences. In making these suggestions, we are none-the-less aware that null models randomizing species' occurrences have for decades been the subject of intense debate (e.g. Connor & Simberloff 1979; Diamond & Gilpin 1982; Harvey et al. 1983; Gotelli 2000; Manly & Sanderson 2002; Hardy 2008). In the end, the appropriate null model always depends on the question and the context in which it is posed.

SESRao or SESFDis should both have good power to detect changes in assembly processes when mass effects have a strong influence in species' occurrences. Mathematically, these indices are very similar and consequently can be used interchangeably. They were the only indices giving reasonable power to detect the increased influence of niche complementarity on abundances in the mass effects model. Either of these indices is required to avoid spurious acceptance of the null hypothesis of no change in trait-based assembly processes when mass effects strongly influence species' occurrences. While SESRao and SESFDis had low power in the priority effects model, they were robust against variation in species richness along the stress gradient. Thus, variation in species richness will not cause these indices to yield spurious conclusions when stochastic processes disrupt the relationship between species' traits and abundances. The other index of functional divergence we used, FDiv, had low power across all of the contexts we examined. Pavoine & Bonsall (2010) showed several instances where FDiv values did not vary between communities that did actually have different functional divergence (see their Appendix A), which may explain the low power we observed for this index.

We do not recommend directly using observed Rao and FDis values, for three reasons. First, variation in species richness strongly affected the power of both indices in the mass effects model. Second, it is difficult to interpret correlations between these indices and stress gradients since they measure both functional richness and functional divergence. This means we cannot use them to disentangle the effects of niche complementarity on occurrences from its effects on abundances. Finally, they provide no benefit for detecting changes in assembly processes if appropriate indices of functional richness and functional divergence are available. We have identified SESFRic as an appropriate index of functional richness and SESRao or SESFDis as appropriate measures of functional divergence. However, it is possible that Rao and FDis values, calculated using occurrences rather than proportional abundances and compared to a matrix-swap null model, could also reveal the effects of assembly processes on species' occurrences.

In no instance did FEve provide good power to detect changes in assembly processes. Previous studies have found little evidence for change in functional evenness in plant communities along ecological gradients (e.g. Mason et al. 2012). It is possible that limited evidence for functional evenness as an indicator of local assembly processes could be due to limitations of FEeve (see Pavoine & Bonsall 2010; Appendix A). It is also possible that variation in functional evenness is simply not associated with changes in assembly processes. We require indices of functional evenness that more closely approximate the concept (as presented by Mason et al. (2005)) before we can verify this.

We recognize that the modelling approach we have employed is highly simplified, and may not fully reflect processes that occur in real plant communities. We also recognize that many processes, other than mass and priority effects, might prevent relationships between functional diversity from emerging. Our intention was to build a model where changes in trait-based assembly processes are clearly defined, and to use this model in selecting indices for testing the hypothesis that these processes change along stress gradients. Our study has successfully done this. However, it would indeed be interesting to test whether

different types of assembly models give similar results. Our work could most fruitfully be extended using two quite different approaches. First, individual-based models would provide useful insights since competitive interactions occur between individuals (e.g. Huston & Smith 1987). This might provide a more realistic examination of how niche complementarity and environmental filtering influence the distribution of species and abundance of local communities in trait space. Second, models that simulate meta-community processes would provide a more realistic examination of trait-independent stochastic processes (e.g. Münkemüller et al. 2012). Metacommunity models incorporate both priority and mass effects. They thus provide a suitable avenue for exploring the power of functional diversity indices to detect changes in trait-based assembly processes in the face of stochasticity.

Another potential extension of our modelling framework would be to consider whether functional diversity indices might be able to reveal how interactions between disturbance and stress influence community assembly. There is emerging evidence that below-ground resource availability strongly moderates the impact of disturbance on taxonomic diversity in plant communities (e.g. Haddad et al. 2008). However, it remains unclear what assembly processes are responsible for this. Simple assembly models might be helpful in predicting expected patterns of functional diversity given hypothesized changes in assembly processes for different combinations of stress intensity and disturbance frequency.

Conclusions

Indices of functional richness and functional divergence had the highest power to detect changes in assembly processes along our hypothetical stress gradient. However, the power of these indices was highly context-dependent. Use of appropriate null models increased power and removed the influence of species richness on index values when mass effects predominated. We recommend convex hull volume expressed relative to a matrix-swap null model (e.g. SESFRic) to detect the influence of trait-based assembly processes on species' occurrences. Both Rao quadratic entropy and functional dispersion expressed relative to a null model randomizing abundances across species but within communities (e.g. SES-Rao or SESFDis) reliably detect the influence of assembly processes on species' abundances. We must always exercise caution in deriving general predictions from a single simulation study. However, we can at least be certain that use of these complementary indices together will provide a reliable test for changes in assembly processes along stress gradients for the range of contexts we have studied.

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