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# Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients

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## Summary

1. The physiological tolerance hypothesis proposes that plant species richness is highest in warm and/or wet climates because a wider range of functional strategies can persist under such conditions. Functional diversity metrics, combined with statistical modelling, offer new ways to test whether diversity–environment relationships are consistent with this hypothesis.

2. In a classic study by R.H. Whittaker (*Ecological Monographs*, 1960), herb species richness declined from mesic (cool, moist, northerly) slopes to xeric (hot, dry, southerly) slopes. Building on this data set, we measured four plant functional traits (plant height, specific leaf area, leaf water content and foliar C:N) and used them to calculate three functional diversity metrics (functional richness, evenness and dispersion). We then used a structural equation model to ask whether ‘functional diversity’ (modelled as the joint responses of richness, evenness and dispersion) could explain the observed relationship of topographic climate gradients to species richness. We then repeated our model examining the functional diversity of each of the four traits individually.

3. Consistent with the physiological tolerance hypothesis, we found that functional diversity was higher in more favourable climatic conditions (mesic slopes) and that multivariate functional diversity mediated the relationship of the topographic climate gradient to plant species richness. We found similar patterns for models focusing on individual trait functional diversity of leaf water content and foliar C:N.

4. *Synthesis.* Our results provide trait-based support for the physiological tolerance hypothesis, suggesting that benign climates support more species because they allow for a wider range of functional strategies.

**Key-words:** determinants of plant community diversity and structure, plant functional traits, R.H. Whittaker, Siskiyou-Klamath, species richness, structural equation modelling, topographic microclimate

## Introduction

Species richness is higher not only in the tropics, but also more generally where the climate is warm and moist rather than cold or arid (e.g. Hawkins, Porter & Diniz 2003; Kissling, Field & Bohning-Gaese 2008). One of the leading hypotheses to explain this pattern (along with the ‘faster speciation’ (Fisher 1960) and ‘more individuals’ hypotheses (Rohde 1992)) is the ‘physiological tolerance hypothesis’ (Currie *et al.* 2004). According to this hypothesis, environments with abundant water and solar energy permit a wider

range of functional strategies; in turn, higher numbers of species are able to tolerate such benign environments, whereas only smaller subsets of species can tolerate the more demanding conditions of cold and/or aridity. Many correlative studies of species richness appear to support this hypothesis (Hawkins, Porter & Diniz 2003; Normand *et al.* 2009; Kessler *et al.* 2011). Kleidon & Mooney (2000) linked this hypothesis explicitly to plant functional traits by simulating plant ‘species’ as random sets of functional traits related to water uptake and growth. They found that more ‘species’ could persist in warm and wet than in cold or dry environments and that this model could broadly reproduce observed global climate–richness relationships.

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The physiological tolerance hypothesis is closely related to the concept of environmental filtering in community assembly (e.g. Cornwell & Ackerly 2009; Weiher *et al.* 2011). Environmental filtering suggests that species present in the regional pool can only join a local community if they possess the functional traits required to overcome site-specific environmental challenges ('filters'), such as drought, cold or nutrient scarcity (Weiher & Keddy 1995). The physiological tolerance hypothesis is a specific application of environmental filtering, standing out in two ways from the broader concept of filtering. First, it focuses on species richness, whereas most studies of environmental filtering are concerned with community composition (e.g. Cornwell & Ackerly 2009; Spasojevic & Suding 2012). Secondly, it focuses on temperature and water as sources of stress for plants and makes a specific directional prediction: that species richness and functional diversity will be lower in climates that are cold, arid or both.

Trait-based ecology (Lavorel & Garnier 2002; McGill *et al.* 2006; Petchey & Gaston 2006) offers new tools for understanding many aspects of community assembly, including metrics of functional diversity that describe the distribution of species traits within and among communities (Mouchet *et al.* 2010; Schleuter *et al.* 2010). Importantly for the physiological tolerance hypothesis, functional diversity metrics have been proposed as indicators of the distribution of niche space in communities (McGill *et al.* 2006). One approach for integrating multiple metrics of functional diversity in hypothesis tests is through the use of latent variables in structural equation modelling (SEM; Grace 2006). Latent variables in SEMs represent general attributes, such as the functional diversity of a community, which cannot be perfectly measured with a single indicator variable. However, their influence can be estimated from the convergent behaviour of several observable metrics, such as functional richness, evenness and dispersion in this case (see McCune & Grace 2002 Chapter 30, and Materials and methods, for more information on latent variables).

Our work builds on a classic study, in which Whittaker (1960) observed that herb species richness in the Siskiyou Mts. (Oregon, USA) declined from mesic (cool, moist northerly) slopes to xeric (hot, dry southerly) slopes. Whittaker (1960) argued that mesic slopes were more 'favourable' for herb species than xeric slopes, but admitted difficulty in defining 'favourability' independently of the flora. Reanalysing

Whittaker's data, Grace, Harrison and Damschen (2011; Fig. 1a) reaffirmed the existence of the topoclimatic gradient in richness and showed that unlike other richness gradients in the data (elevation, soil), it could not be explained by variation in herb or tree abundances. Grace, Harrison and Damschen (2011) interpreted the topographic richness gradient as being caused by 'filtering'; as moisture decreases along the gradient, species drop out as their tolerances are exceeded (Gough, Grace & Taylor 1994); however, this mechanism was not explicitly tested.

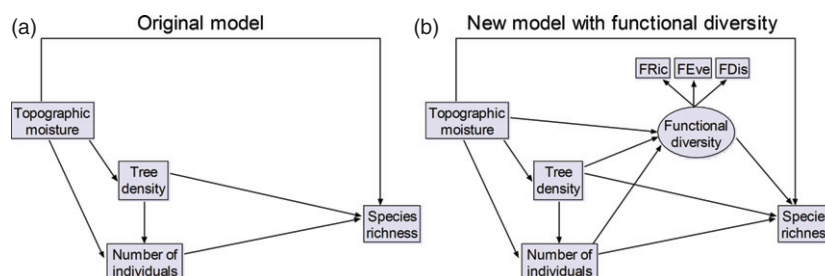
We tested the physiological tolerance hypothesis using the same data and a new SEM (Fig. 1b), in which topoclimate affects species richness via functional diversity. Functional diversity is calculated from plant height, specific leaf area (SLA), leaf water content (LWC) and foliar carbon-to-nitrogen ratio (C:N) and modelled as a latent variable (see Materials and methods). Our intent in using a latent variable is to model functional diversity as a general entity, similar to the intent behind modelling animal body size as a general property in ecology and evolution (Grace 2006; Chapter 4). In accordance with Whittaker (1960) and other authors (Kleidon & Mooney 2000; Currie *et al.* 2004), we predicted that the effect of topoclimate on species richness is mediated by higher functional diversity in more benign (mesic) environments.

## Materials and methods

### STUDY SITE AND DATA SET

This study was based on data collected in the Siskiyou Mountains of southern Oregon. The data used in this study were collected by Whittaker (1960) from 396 20 × 50 m (1000 m<sup>2</sup>) plots from June to August 1949–1951. Details on study site and the original data set can be found in Whittaker (1960), Damschen, Harrison and Grace (2010), Harrison, Damschen and Grace (2010) and Grace, Harrison and Damschen (2011). This data set includes counts of all tree species for the whole 1000 m<sup>2</sup> plot; a list of herb species present in the whole plot; and counts of herb individuals by species within 25, 1 m<sup>2</sup> subplots along the 50 m centre line of the plot. Number of herb individuals (density) for each plot was determined using the herb abundances in the 25, 1 m<sup>2</sup> subplots. Tree density was obtained from the count of total tree individuals in the whole 1000 m<sup>2</sup> plot.

Plots were distributed across different soil types, elevations and what Whittaker (1960) called the 'topographic moisture gradient' (henceforth 'topoclimate'), which was demonstrated to have a strong



**Fig. 1.** (a) General form of structural equation model evaluated for herb species richness in Whittaker's (1960) data from Grace, Harrison and Damschen (2011) modified to control for the effects of soil and elevation. (b) Updated model including the role of functional diversity (represented by all functional traits combined) in influencing species richness. Path coefficients are standardized prediction coefficients (Grace & Bollen 2005).

influence on community composition (Whittaker 1960; Damschen, Harrison & Grace 2010). Topoclimate was measured on a qualitative scale from 1 to 10, where a score of 1 was a mesic (cool, moist, northerly) site along a ravine with flowing water; 2–4 were relatively mesic north to north-east slopes; 5–7 were intermediate; and 8–10 meant xeric (hot, dry, south to south-west) slopes. In a few cases, Whittaker used gradient lengths other than 10 and also assigned multiple gradient scores to a single site. We standardized his scores and averaged multiple site values in accordance with Damschen, Harrison and Grace (2010). Previous analyses have found these scores to be correlated with January insolation (Damschen, Harrison & Grace 2010; Grace, Harrison & Damschen 2011). Here, we reversed the original scoring system, so that that increasing numeric values corresponded to increasingly mesic sites.

#### TRAITS AND FUNCTIONAL DIVERSITY

Functional diversity metrics for the understorey herbs were derived from measures of plant height, SLA, LWC and foliar C:N collected as per Cornelissen *et al.* (2003) from Whittaker's study region in June and July 2009. These traits were chosen as they are expected to differ in their contribution to specific assembly processes (Westoby *et al.* 2002; Spasojevic & Suding 2012) and thus may indicate different mechanisms by which functional diversity may lead to increased species richness (see below for explanation). Plant height was measured as length from ground level to the highest photosynthetically active tissue. For leaf traits (SLA and LWC), we collected one or two leaves from each of five mature and non-senesced individuals, fully hydrated the leaves in water tubes, weighed them to obtain a fresh mass, photographed them and measured their areas using image analysis software. We dried the leaves for 72 h at 60 °C, weighed them and calculated SLA as area/dry mass ( $\text{cm}^2 \text{g}^{-1}$ ) and LWC as the ratio of fresh mass to dry mass (Garnier *et al.* 2001). Foliar C:N was determined via gas combustion (Siegel, Hauck & Kurtz 1982) at the University of Georgia Stable Isotope/Soil Biology Laboratory (Athens, GA, USA).

Plant height is allometrically related to overall plant size (biomass, rooting depth, lateral spread) as well as to competitive interactions for light (Aan, Hallik & Kull 2006). High specific leaf area is associated with lower leaf life span and higher tissue N (Reich, Walters & Ellsworth 1997) and with an allocation strategy including fast relative growth rate (Westoby *et al.* 2002). High leaf water content is associated with a slower relative growth rate (Garnier & Laurent 1994; Vile, Shipley & Garnier 2006) and tolerance to low water availability (Farooq *et al.* 2009). Low leaf carbon-to-nitrogen ratio (C:N) is associated with higher efficiency of N use (Hobbie 1992; Aerts & Chapin 2000).

We calculated functional richness, functional evenness and functional dispersion (see Mouchet *et al.* 2010; Schleuter *et al.* 2010 for reviews of these metrics) for all traits in combination and each trait individually using the FD package (Laliberté & Legendre 2010) in R (R Development Core Team 2010). Functional richness measures the ranges of trait values in a community, and when considering all traits together, it is calculated as the minimum convex hull volume that includes all the species considered (Cornwell, Schilck & Ackerly 2006). For individual traits, functional richness is calculated as the difference between the maximum and minimum functional values present in the community (Mason *et al.* 2005). Functional evenness measures the degree to which the biomass of a community is distributed evenly in trait space and is calculated as the abundance-weighted evenness in the distribution of species in a functional trait space (Mason *et al.* 2005; Villeger, Mason & Moullot 2008). Functional

dispersion, which indicates the degree of trait dissimilarity among species, is calculated as the abundance-weighted mean distance of each species in multidimensional trait space to the centroid of all species and is statistically independent of species richness (Laliberté & Legendre 2010). All plots with trait coverage of <80% of the species present were dropped, resulting in  $n = 248$  of the original 396.

#### STATISTICAL ANALYSIS

We tested all variables for normality, and number of herb individuals, number of trees, functional dispersion and functional evenness, which statistically violated this assumption based on a Shapiro–Wilk goodness-of-fit test (Brown & Hettmansperger 1996), were natural log-transformed. To aid in interpretation of the results, we first explored univariate relationships between each functional diversity metric and herb density, tree density, topography and species richness. As several quadratic relationships were found by Grace, Harrison and Damschen (2011), we tested for both linear and nonlinear (quadratic) relationships for each response measure and selected the best fit using Akaike Information Criteria (Burnham & Anderson 2004). We used SEM to investigate links among number of herb individuals, tree density, topographic score, functional diversity and species richness while controlling for soil and elevation. Based on the relationships in Grace, Harrison and Damschen (2011; Fig. 1a), we built an initial model (Fig. 1b) that included functional diversity as a latent variable. By modelling functional diversity in this way, we are hypothesizing that it is an underlying general property of communities very similar to 'niche space', is reflected in multiple specific indicators, is shaped by environmental gradients and measures the environmentally determined capacity of communities to support species. SEM permits us to test whether these hypotheses are consistent with the data relations. Latent variable approaches differ from other multivariate approaches, such as principal components analysis (PCA) in several ways, though both allow for the reduction in the dimensionality of data (McCune & Grace 2002). Latent variables in SEMs represent complex attributes (e.g. 'intelligence') that cannot be measured directly, but can be estimated from observed metrics (e.g. test scores). Principal component scores, on the other hand, simply summarize directly observable data.

We expected the same relationships found by Grace, Harrison and Damschen (2011) between topoclimate, number of herb individuals, number of trees and species richness. We also hypothesized that the positive relationship between topoclimate and species richness would be mediated by functional diversity, since functional diversity serves as a measure of the 'favourability' or filtering effect of the environment. All quadratic relationships that were found in the univariate screening (elevation and number of trees, elevation and number of individuals, elevation and functional dispersion) were modelled as such in the SEM. We also include a covariance between functional richness and species richness in all of our models as these two metrics are not fully independent, whereas functional dispersion is independent of species richness. All variables except topoclimate were allowed to depend on the effects of soil and elevation; however, we do not present results from these variables as they are described in Grace, Harrison and Damschen (2011). This approach is graphically equivalent to examining topography while statistically controlling for the effects of soil and elevation. For each model, we removed variables to find the model with the lowest AIC, assessed model fit with a chi-square tests, root mean square error of approximation (RMSEA) and goodness-of-fit index (GFI). Chi-square values associated with a  $P$ -value > 0.05 (suggesting that observed and expected covariance matrices are not different) and a RMSEA <0.05 and GFI >0.95

indicate a good model fit (Kline 2010). Structural equation modelling was conducted using the Lavaan package (Rosseel 2012) in R version 2.15.

## Results

### UNIVARIATE RELATIONSHIPS

Multivariate and individual functional diversity patterns for each metric of functional diversity showed varied direct relationships with topography, number of herbs and number of trees (Table 1).

### STRUCTURAL EQUATION MODELLING

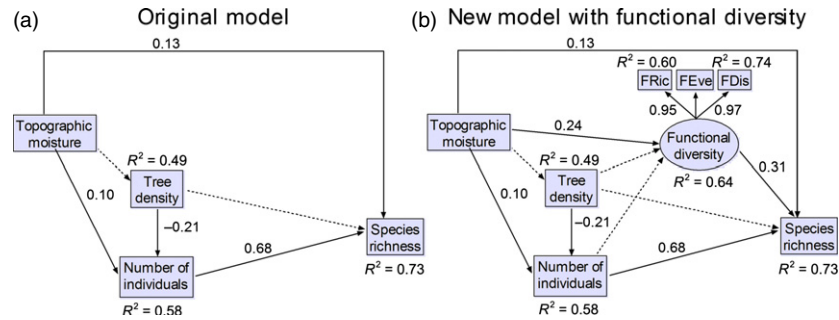
The model including functional diversity based on all traits was found to have a close fit to the data ( $\chi^2 = 0.99$ , d.f. = 9,  $P = 0.12$ ; RMSEA = 0.04; GFI = 0.98) and explained a substantial amount of the variance in species richness ( $R^2 = 0.74$ , Fig. 2b), consistent with the model without functional diversity ( $\chi^2 = 0.19$ , d.f. = 2,  $P = 0.91$ ; RMSEA = 0.00; GFI = 1.00,  $R^2 = 0.73$ , Fig. 2a). However, while topoclimate directly predicted local richness in the original model, this direct path was absent in the model that included functional diversity. This result suggests that the influence of topoclimate

**Table 1.** The relationships between the three metrics of functional diversity and the predictor variables in our model for models with all traits combined and each trait separately analysed. Direction of relationship indicated by + (positive relationship) or – (negative relationship)

Trait	Functional diversity metric	Predictor	Direction of relationship	$r^2$	$F$ -statistic
All traits	FRic	Number of individuals	NS	NS	NS
		Tree density	–	0.03	8.81**
		TMG	+	0.02	5.55*
	FEve	Number of individuals	NS	NS	NS
		Tree density	NS	NS	NS
		TMG	NS	NS	NS
	FDis	Number of individuals	+	0.10	28.92***
		Tree density	–	0.03	9.08**
		TMG	+	0.07	19.38***
Height	FRic	Number of individuals	NS	NS	NS
		Tree density	–	0.01	4.70*
		TMG	NS	NS	NS
	FEve	Number of individuals	NS	NS	NS
		Tree density	NS	NS	NS
		TMG	+	0.02	7.30**
	FDis	Number of individuals	+	0.05	12.41***
		Tree density	–	0.02	6.03*
		TMG	NS	NS	NS
SLA	FRic	Number of individuals	–	0.08	21.81***
		Tree density	NS	NS	NS
		TMG	+	0.06	17.66***
	FEve	Number of individuals	NS	NS	NS
		Tree density	+	0.02	5.35*
		TMG	NS	NS	NS
	FDis	Number of individuals	NS	NS	NS
		Tree density	NS	NS	NS
		TMG	+	0.01	3.84*
LWC	FRic	Number of individuals	+	0.03	7.31**
		Tree density	NS	NS	NS
		TMG	+	0.12	33.85***
	FEve	Number of individuals	NS	NS	NS
		Tree density	NS	NS	NS
		TMG	NS	NS	NS
	FDis	Number of individuals	+	0.14	39.97***
		Tree density	–	0.02	6.53*
		TMG	+	0.06	17.13***
C:N	FRic	Number of individuals	NS	NS	NS
		Tree density	NS	NS	NS
		TMG	+	0.03	8.61**
	FEve	Number of individuals	+	0.12	35.62***
		Tree density	–	0.03	7.65**
		TMG	NS	NS	NS
	FDis	Number of individuals	NS	NS	NS
		Tree density	NS	NS	NS
		TMG	+	0.06	18.05***

FRic, functional richness; FEve, functional evenness; FDis, functional dispersion; TMG, topographic moisture gradient; NS, non-significant relationships. \* $P < 0.05$ , \*\* $P < 0.001$ , \*\*\* $P < 0.001$ .





**Fig. 2.** (a) Structural equation model results for the original Grace, Harrison and Damschen (2011) model controlling for soil and elevation effects and (b) the updated model with functional diversity represented by all functional traits combined. Path coefficients are standardized prediction coefficients (Grace & Bollen 2005). Pathways not found to be influential (non-significant  $P > 0.05$ ) are represented by dotted lines.

on richness was mediated by functional diversity. In the final model, topoclimate also influenced species richness indirectly via the number of individuals, though this pathway was weak (Table 2). As with the original model (and all subsequent models), increasing densities of trees were associated with declines in species richness via an indirect influence of trees on number of herb individuals (Table 2). In all models, functional richness and functional dispersion were associated relatively equally with functional diversity, while functional evenness had no internal validity as an indicator and/or no independent contribution to the models (Figs 2b and 3a–d).

Functional diversity based on leaf water content ( $\chi^2 = 5.36$ , d.f. = 6,  $P = 0.50$ ; RMSEA = 0.00; GFI = 0.99) and foliar C:N ( $\chi^2 = 0.14$ , d.f. = 2,  $P = 0.95$ ; RMSEA = 0.00; GFI = 1.00) both behaved similarly to multivariate functional diversity; they linked topoclimate to species richness in the expected positive direction and eliminated the direct path from topography to species richness in the model (Fig. 3a–b; and Table 2). Functional diversity of specific leaf area ( $\chi^2 = 1.65$ , d.f. = 2,  $P = 0.39$ ; RMSEA = 0.00; GFI = 0.99) also linked topoclimate to species richness in the expected direction, but for this trait, the direct effects of topoclimate were retained in the model (Fig. 3c; Table 2). Functional diversity of plant height ( $\chi^2 = 1.88$ , d.f. = 5,  $P = 0.90$ ; RMSEA = 0.00; GFI = 0.99) was not related to topoclimate, and in this model, direct effects of topoclimate on species richness persisted, indicating that the diversity of plant height did not explain the effect of topoclimate on richness (Fig. 3d and Table 2).

## Discussion

Our results support the hypothesis that benign climates support higher species richness by permitting a wider variety of plant functional strategies to coexist (Currie *et al.* 2004) and provide a novel approach to understand patterns of multivariate functional diversity using latent variables. We found that climatically benign locations (mesic north-facing slopes), where water is more available and temperatures are less extreme, supported plant species with a broader range and dispersion of traits (specific leaf area, foliar water content, foliar C:N) than hotter and drier locations (xeric south-facing slopes). In turn, this greater breadth of functional diversity is

able to explain the effects of topoclimate on species richness in our structural equation model. These results support and quantify Whittaker's (1960) idea that high species richness on mesic slopes is associated with greater environmental 'favourability', as well as agreeing with the conclusion of Grace, Harrison and Damschen (2011) that environmental 'filtering' progressively removes intolerant species from communities as conditions become more xeric. While the indirect effect of topoclimate on species richness via functional diversity is relatively small (an effect size between 0.04 and 0.07 depending on the traits), the loss of a significant direct effect of topoclimate for several traits indicates that this may be an important pathway mediating the topoclimate–richness relationships.

Individual traits that differ in their contribution to specific assembly processes may help shed light on the mechanisms by which functional diversity may lead to increased species richness. Moist environments often have greater productivity, which can lead to partitioning of the light environment by species (Aan, Hallik & Kull 2006). However, the lack of a significant relationship between topoclimate and functional diversity based on plant height suggests this is not occurring in our data. Instead, model results suggest the topographic moisture gradient influenced species richness via its effects on the diversity of foliar traits: water content, C:N and to a lesser extent specific leaf area. Leaf water content is directly related to water availability and drought tolerance (Farooq *et al.* 2009). Specific leaf area and C:N are more directly related to N availability (Hobbie 1992; Aerts & Chapin 2000), but this is often highly dependent on water availability (Chapin, Matson & Mooney 2002; Vitousek *et al.* 2002). Mesic environments in our data set support herb species with a wider range and dispersion of functional strategies related to water use than xeric environments. The contrast in results using foliar traits vs. plant height demonstrates the potential for individual trait patterns to provide additional information about community assembly mechanisms (Violle *et al.* 2007; Spasojevic & Suding 2012); in this case, water use appeared to be a more important driver than light availability.

While the physiological tolerance hypothesis suggests that in more benign environments, there should be greater functional diversity leading to greater richness, this hypothesis does not account for other local-scale mechanisms that may influence patterns of functional diversity such as competition

**Table 2.** Direct, indirect and total standardized effects on species richness based on structural equation models

Functional diversity	Predictor	Pathway to species richness	Effect	
All traits	Functional diversity	Direct	0.31	
		Number of individuals	Direct	0.78
	Tree Density	Indirect through functional diversity	Indirect through functional diversity	NS
			Total effect	0.78
			Direct	NS
			Indirect through functional diversity	NS
		Indirect through individuals	Indirect through individuals	-0.19
			Total effect	-0.19
			Direct	NS
	Topography	Indirect through individuals	Indirect through individuals	0.07
			Indirect through trees	NS
			Indirect through functional diversity	0.07
			Indirect through individuals and functional diversity	NS
		Indirect through trees and functional diversity	Indirect through trees and functional diversity	NS
			Total effect	0.14
Direct			0.20	
Height	Functional diversity	Direct	0.79	
		Number of individuals	Indirect through functional diversity	NS
	Tree Density	Total effect	Total effect	0.79
			Direct	NS
			Indirect through functional diversity	NS
			Indirect through individuals	-0.19
		Total effect	Total effect	-0.19
			Direct	0.13
			Indirect through individuals	0.07
	Topography	Indirect through trees	Indirect through trees	NS
			Indirect through functional diversity	NS
			Indirect through individuals and functional diversity	NS
			Indirect through trees and functional diversity	NS
		Total effect	Total effect	0.20
			Direct	0.17
Number of individuals			Direct	0.71
SLA	Indirect through functional diversity	Indirect through functional diversity	0.08	
		Total effect	0.79	
		Direct	NS	
		Indirect through functional diversity	NS	
	Tree Density	Indirect through individuals	Indirect through individuals	-0.18
			Total effect	-0.18
			Direct	0.07
			Indirect through individuals	0.07
		Indirect through trees	Indirect through trees	NS
			Indirect through functional diversity	0.04
			Indirect through individuals and functional diversity	0.01
	Topography	Indirect through trees and functional diversity	Indirect through trees and functional diversity	NS
			Total effect	0.19
			Direct	0.14
			Number of individuals	Direct
LWC		Indirect through functional diversity	Indirect through functional diversity	NS
			Total effect	0.77
			Direct	NS
	Indirect through functional diversity		-0.03	
	Indirect through individuals	Indirect through individuals	-0.19	
		Total effect	-0.22	
		Direct	NS	
Topography	Indirect through individuals	Indirect through individuals	0.07	
		Indirect through trees	NS	
		Indirect through functional diversity	0.04	
		Indirect through individuals and functional diversity	NS	
	Indirect through trees and functional diversity	Indirect through trees and functional diversity	NS	
		Total effect	0.11	
		Direct	0.11	

Table 2. (continued)

Functional diversity	Predictor	Pathway to species richness	Effect	
C:N	Functional diversity	Direct	0.21	
		Direct	0.71	
		Indirect through functional diversity	0.08	
	Tree Density	Total effect	0.79	
		Direct	NS	
		Indirect through functional diversity	0.05	
	Topography	Number of individuals	Indirect through individuals	-0.19
			Total effect	-0.14
			Direct	NS
		Topography	Indirect through individuals	0.07
			Indirect through trees	NS
			Indirect through functional diversity	0.05
			Indirect through individuals and functional diversity	0.01
			Indirect through trees and functional diversity	NS
			Total effect	0.13

NS, non-significant relationships.

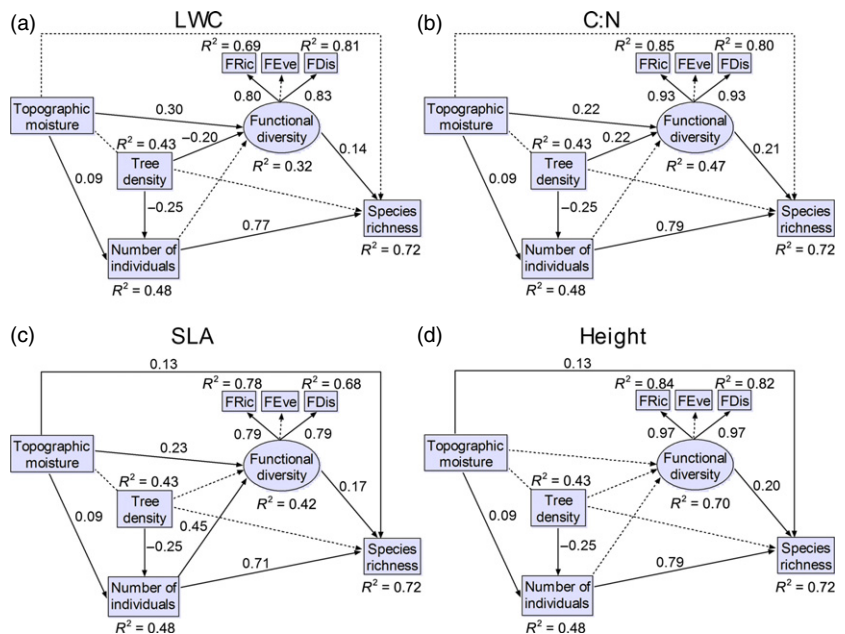


Fig. 3. Structural equation model results for individual traits: (a) height, (b) SLA, (c) LWC and (d) C:N path coefficients are standardized prediction coefficients (Grace & Bollen 2005). Pathways not found to be influential (non-significant  $P > 0.05$ ) are represented by dotted lines.

or facilitation. Indeed, competitive interactions via limiting similarity have been found to promote increased functional diversity of coexisting species while simultaneously reducing species richness (e.g. Spasojevic & Suding 2012). This pattern reinforces the importance of considering multiple mechanisms of community assembly (Cornwell & Ackerly 2009; Mouchet *et al.* 2010; Mason *et al.* 2011). Moreover, the use of resource-acquisition traits can only be used to test one set of hypotheses relating species richness to functional diversity. A similar analytic approach, focusing on other functional traits, such as traits related to anti-herbivore defence, below-ground mutualisms or recovery from disturbances, may be a useful way to test additional hypotheses for species richness along environmental gradients.

Our inclusion of a latent functional diversity variable provides a novel approach to understanding patterns in multivariate

functional diversity, as opposed to running separate models for each metric or focusing on a single metric. Since there is no clear consensus on when to use specific functional diversity measures (e.g. Mouchet *et al.* 2010; Schleuter *et al.* 2010), our approach allows for the simultaneous inclusion of multiple functional diversity metrics and an assessment of their relative associations with the response variable of interest. For example, we found that functional evenness did not reflect functional diversity, while functional richness and functional dispersion did. Our result suggests that while there is greater functional richness and dispersion in more benign environments, functional evenness is unaffected, perhaps reflecting the significance of niche partitioning in community assembly.

An important caveat to our results is that functional diversity and species richness may be related in alternative ways (Velend & Geber 2005). Environments may affect species richness



and functional diversity; similarly, species richness may directly influence functional diversity, and/or functional diversity may influence species richness as we propose here. Purely observational analyses cannot entirely disentangle these possibilities. However, our study does demonstrate the consistency between observational data and a specific a priori hypothesis that is also supported by other evidence (e.g. Kleidon & Mooney 2000; Currie *et al.* 2004). While experiments may have greater power to distinguish among mechanisms, they have less utility for explaining large-scale natural gradients in the assembly of long-lived communities, making trait-based observational evidence an important if imperfect surrogate.

One question yet to be explored in this field is why higher functional diversity should lead to higher species richness. Why, for example, have more species not evolved to acquire stress-tolerant traits, enabling them to occupy xeric environments? One possible avenue of explanation lies in the 'niche conservatism' or 'tropical conservatism' hypothesis (Wiens & Donoghue 2004), which proposes that the earth's long Eocene history of a warm and wet climate, combined with limits to adaptive evolution (i.e. phylogenetic inertia), underlie the strong affinities of many modern lineages for mesic environments. Analyses combining phylogenetic, trait and community data are a promising avenue for exploring the evolutionary basis of climate–richness relationships (Wiens *et al.* 2010).

## Conclusions

Our results provide novel trait-based support for the physiological tolerance hypothesis which suggests that benign climates may support more species because they allow a wider range of functional traits. Additionally, we illustrate a latent variable approach that permits the multiple facets of functional diversity to be evaluated when testing hypotheses about community assembly.

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