

**What do you see here?**





# Traits & Functional diversity

David Hořák

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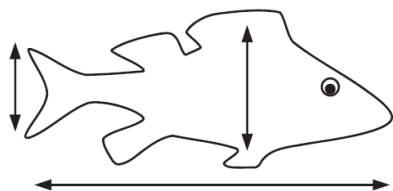
## REVIEW

## Defining and measuring ecological specialization

Vincent Devictor<sup>\*1,2,3</sup>, Joanne Clavel<sup>4</sup>, Romain Julliard<sup>4</sup>, Sébastien Lavergne<sup>5</sup>, David Mouillot<sup>6</sup>, Wilfried Thuiller<sup>5</sup>, Patrick Venail<sup>3</sup>, Sébastien Villéger<sup>6</sup> and Nicolas Mouquet<sup>3</sup>

## Eltonian

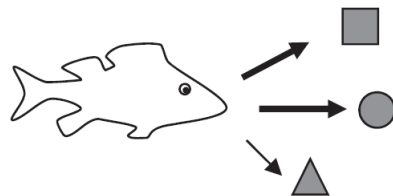
(c)



Breadth of species-specific functional roles

Species position in a functional space defined by a set of functional traits (Ferry-Graham 2002, Mouillot et al. 2006, Bellwood et al. 2006)

(d)

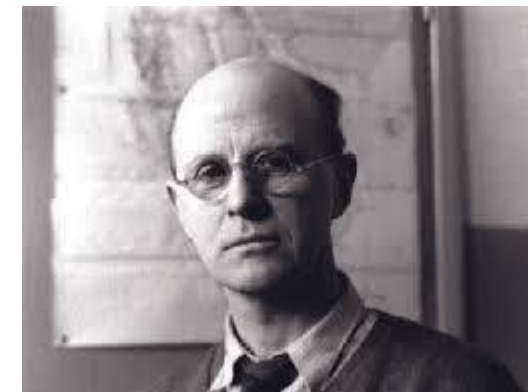
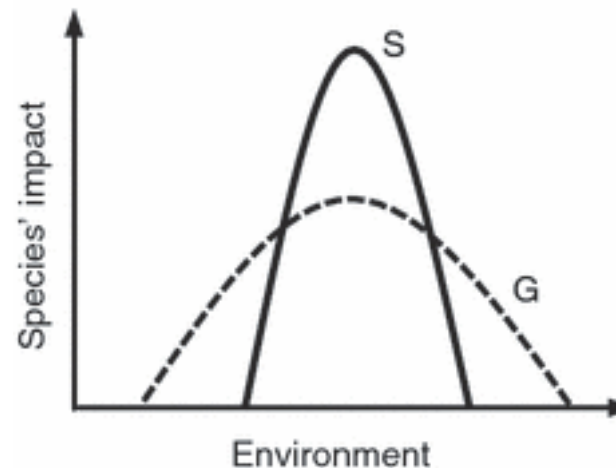


Breadth of realized species' functional roles

- Connectance index, (Blüthgen et al. 2008)
- Diversity metrics (e.g., Shannon index of prey items, Bolnick et al. 2003)
- Isotope ratios (Bearhop et al. 2004)

## Elton: reminder

(b) Eltonian specialization



**Fig. 4.** A toolbox for widely used metrics of ecological specialization. Most commonly used metrics of specialization can be positioned in this box according to the type of niche considered (Grinnellian vs. Eltonian) and whether the fundamental or the realized specialization is measured. Note that this typology is flexible (i.e. the dashed arrows underline that specialization metrics are often not belonging to a unique class but rather delineate a continuum). The figure represents a fish for which specialization is measured using different metrics: (a) the variation in species' performance in a controlled experiment (three different conditions are represented by three circles) will reflect its fundamental Grinnellian specialization; (b) the variation in performance along different resource categories (symbolized by geometrical items) using field data will reflect the realized Grinnellian specialization; (c) the fundamental Eltonian specialization would be derived from metrics based on the species-specific functional traits. (d) Finally, the realized Eltonian specialization will be quantified using the diversity and strength of impact of the species on others (symbolized by geometrical items).

Niche is the status of an animal in its community / a place in a biotic environment. It stresses the **function** of the species in the community rather than a physical place in the habitat.



“Trait is any measurable property of a thing or an average property from a collection of things.” Shipley (2010)

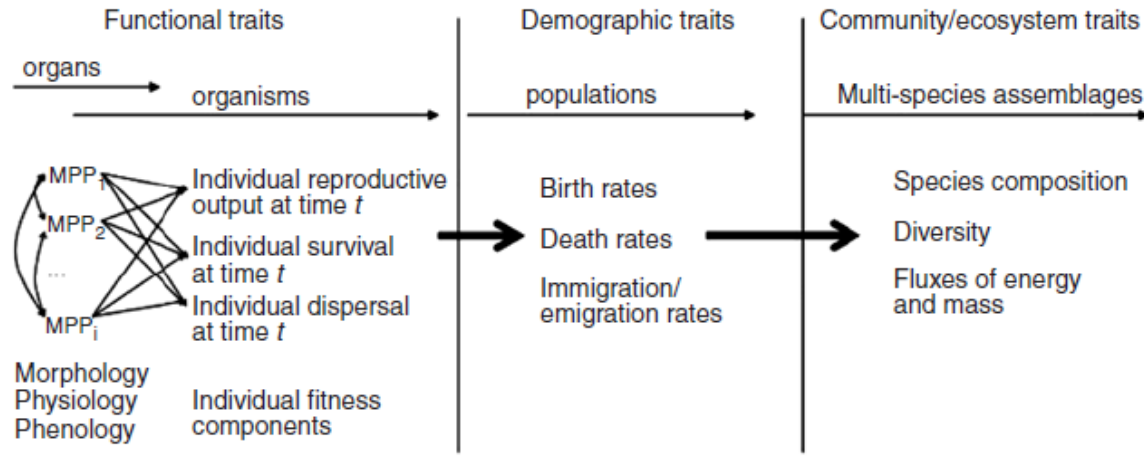


Figure 3.1. Summary of different types of traits existing at different levels of biological organization.

*“Functional traits are observable or operationally defined phenotypic characteristics that influence species performance and/or ecosystem processes.”* Evan Weiher (2011)

*“Any morphological, physiological, or phenological heritable feature measurable at the individual level, from the cell to the whole organism, without reference to the environment or any other level of organization (shaded part of the leaves).”* Garnier et al. (2016)



# Some traits are crucial

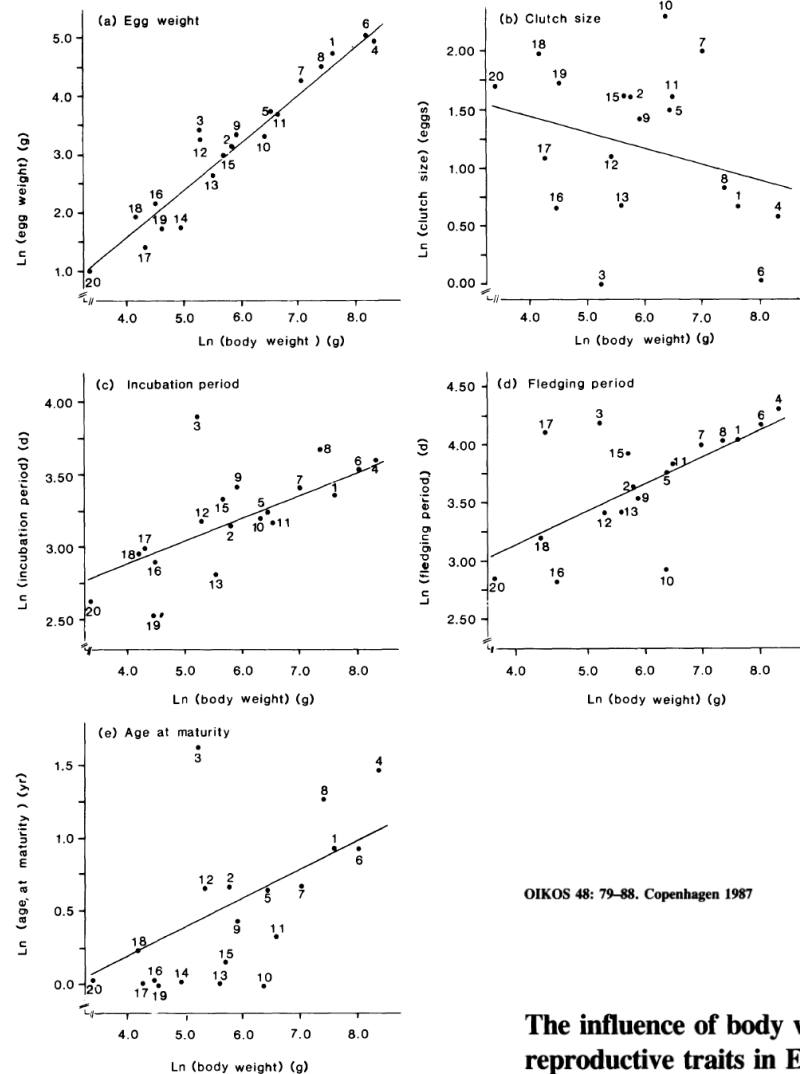
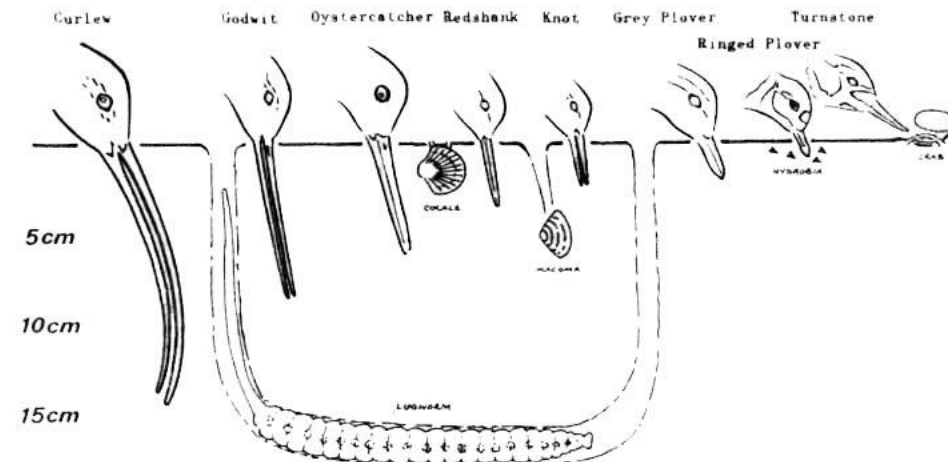
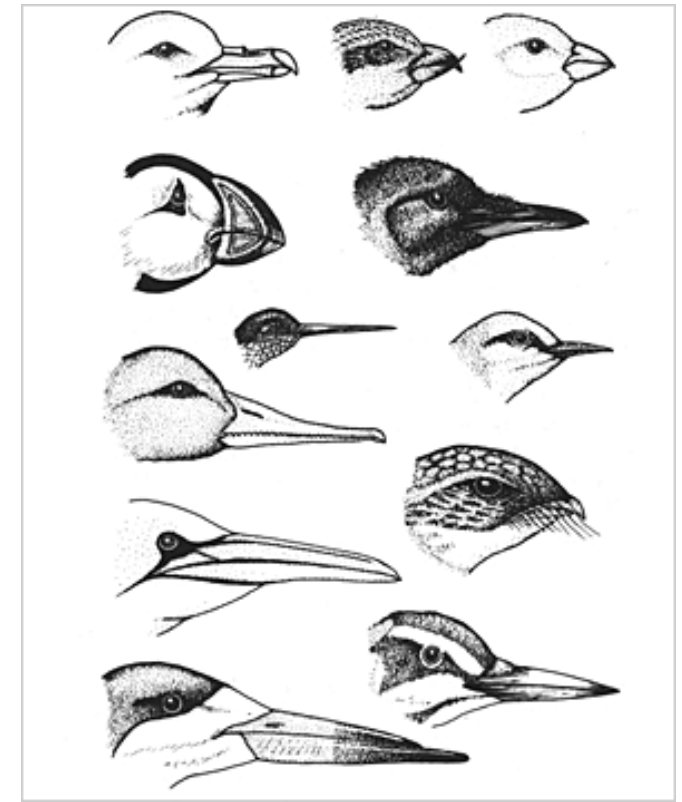


Fig. 9. Different reproductive traits (a-e) in relation to body weight for European orders. Each point represents the averages of the generic values (logarithmically transformed) for the order. The figures denote the orders: 1 - Gaviiformes, 2 - Podicepsiformes, 3 - Procellariiformes, 4 - Pelicaniformes, 5 - Ciconiiformes, 6 - Phoenicopteriformes, 7 - Anseriformes, 8 - Accipitriformes, 9 - Falconiformes, 10 - Galliformes, 11 - Gruiformes, 12 - Charadriiformes, 13 - Columbiformes, 14 - Cuculiformes, 15 - Strigiformes, 16 - Caprimulgiformes, 17 - Apodiformes, 18 - Coraciiformes, 19 - Piciformes, 20 - Passeriformes. The equations of the indicated regression lines are  $\ln y = 0.81 \ln x - 1.65$ ,  $r^2 = 0.90$ ,  $p < 0.001$ , for egg weight (a),  $\ln y = -0.14 \ln x + 2.00$ ,  $r^2 = 0.08$ ,  $p < 0.05$  for clutch size (b);  $\ln y = 0.16 \ln x + 2.23$ ,  $r^2 = 0.42$ ,  $p < 0.001$ , for fledging period (d) and  $\ln y = 0.20 \ln x - 0.62$ ,  $r^2 = 0.24$ ,  $p < 0.01$  for age at maturity (e).

OIKOS 48: 79-88. Copenhagen 1987

**The influence of body weight on the covariation between reproductive traits in European birds**

Bernt-Erik Sæther





# Functional traits

- a surrogate of a function or as this function itself
- a trait that strongly influences organismal performance (McGill et al. 2006) and/or individual fitness (Geber et al. 2003)
- it may be defined with respect to ecosystem functioning (McIntyre et al. 1999): this is the case of *functional effect traits*, defined as those traits that have an impact on ecosystem functioning (Díaz & Cabido 2001, Lavorel & Garnier 2002)

Violle et al. (2003) **propose to define a functional trait as any trait which impacts fitness indirectly via its effects on performance traits**

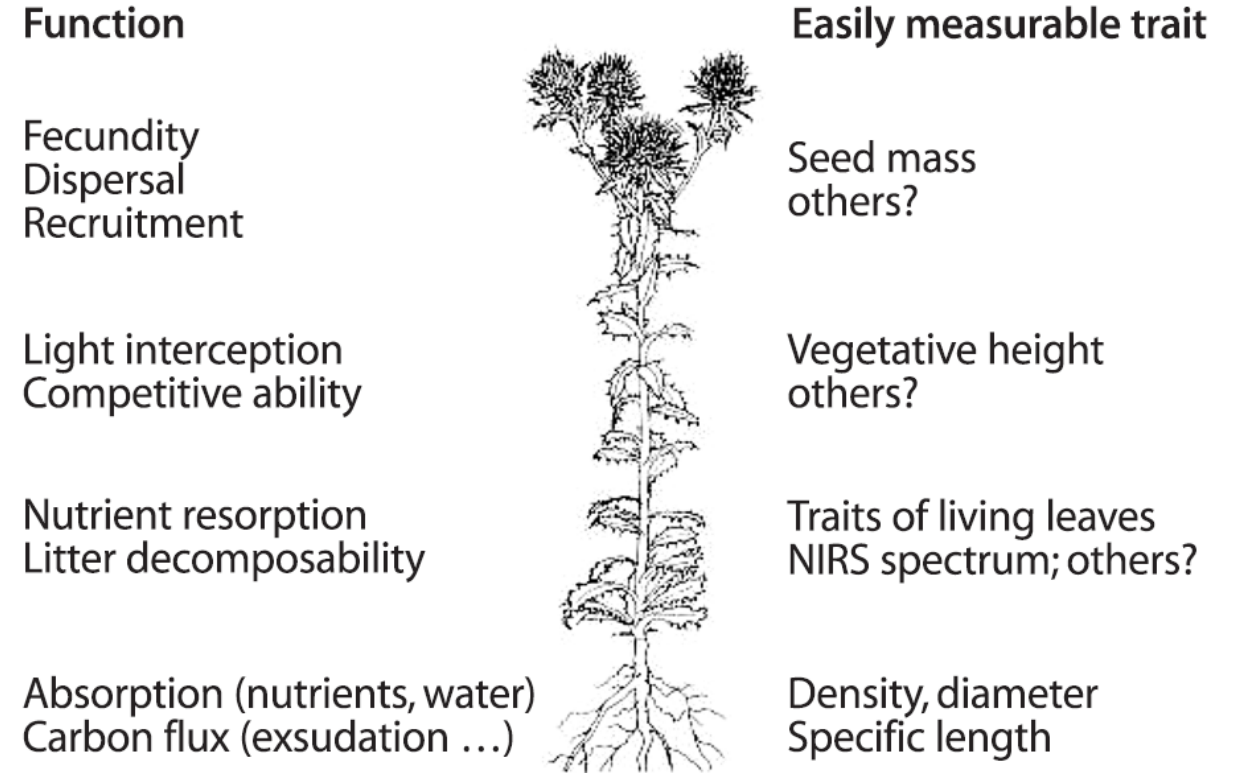


Fig. 13.1. Examples of soft traits and associated functions



# Morphology, Performance and Fitness<sup>1</sup>

STEVAN J. ARNOLD

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Chicago, Illinois 60637

**SYNOPSIS.** Selection can be measured in natural populations by the changes it causes in the means, variances and covariances of phenotypic characters. Furthermore the force of selection can be measured in conventional statistical terms that also play a key role in theoretical equations for evolutionary change. The problem of measuring selection on morphological traits is simplified by breaking the task into two parts: measurement of the effects of morphological variation on performance and measurement of the effects of performance on fitness. The first part can be pursued in the laboratory but the second part is best accomplished in the field. The approach is illustrated with a hypothetical analysis of selection acting on the complex trophic morphology of snakes.

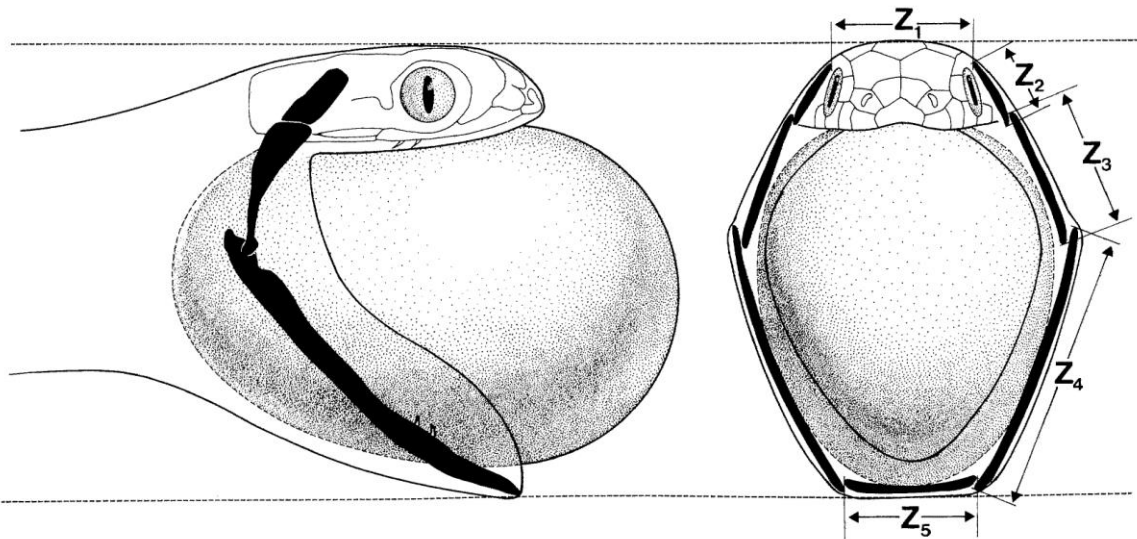


FIG. 2. A diagrammatic portrayal of an African egg-eating snake (*Dasypeltis* sp.) almost maximally distended during the ingestion of its prey (reconstructed from Rabb [1972] and Gans [1974]). Candidate structural elements contributing to swallowing ability are: width of the braincase ( $z_1$ ) and lengths of the supratemporal ( $z_2$ ), the quadrate ( $z_3$ ), the mandible ( $z_4$ ) and the mandibular symphysis ( $z_5$ ).

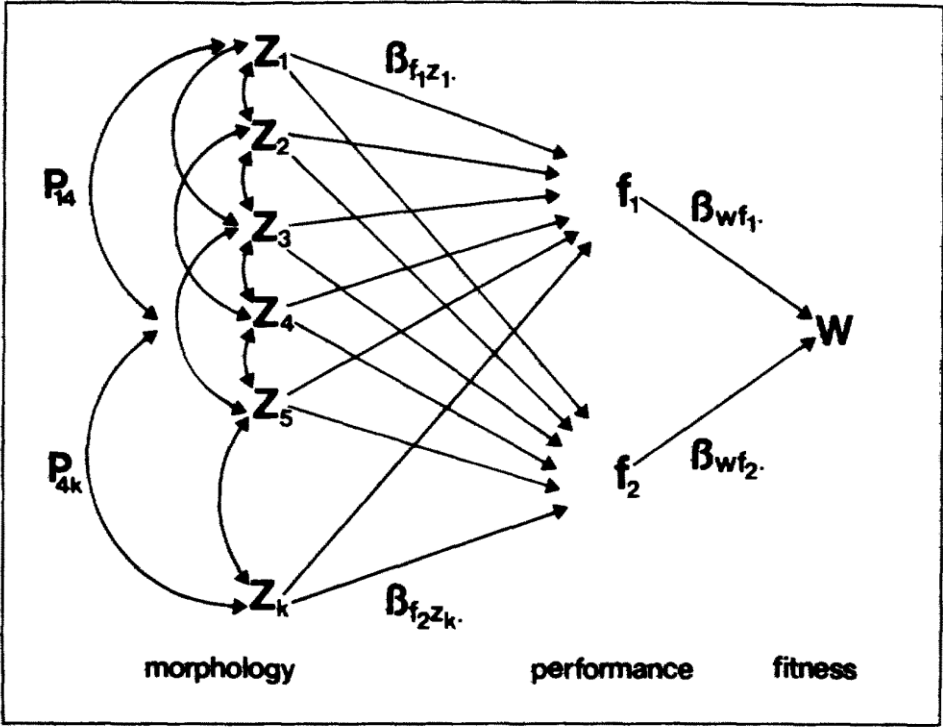


FIG. 3. The statistical relationships between morphology, performance and fitness can be represented with a path diagram. The morphological characters,  $z_1, z_2, \dots, z_5$ , are illustrated in Figure 2;  $z_k$  is some other character such as overall body size. The phenotypic covariances between these characters are represented by double headed arrows. For example  $P_{14}$  is the covariance between  $z_1$  and  $z_4$ . The two performance variables,  $f_1$  and  $f_2$ , represent ability to swallow two different kinds of prey. Relative fitness is represented by the symbol  $w$ . For simplicity here and in Figure 4, arrows indicating residual influences on performance and fitness are not shown.



# Ecological performance



Let the concept of trait be functional!

Cyrille Violle, Marie-Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel,  
Irène Hummel and Eric Garnier

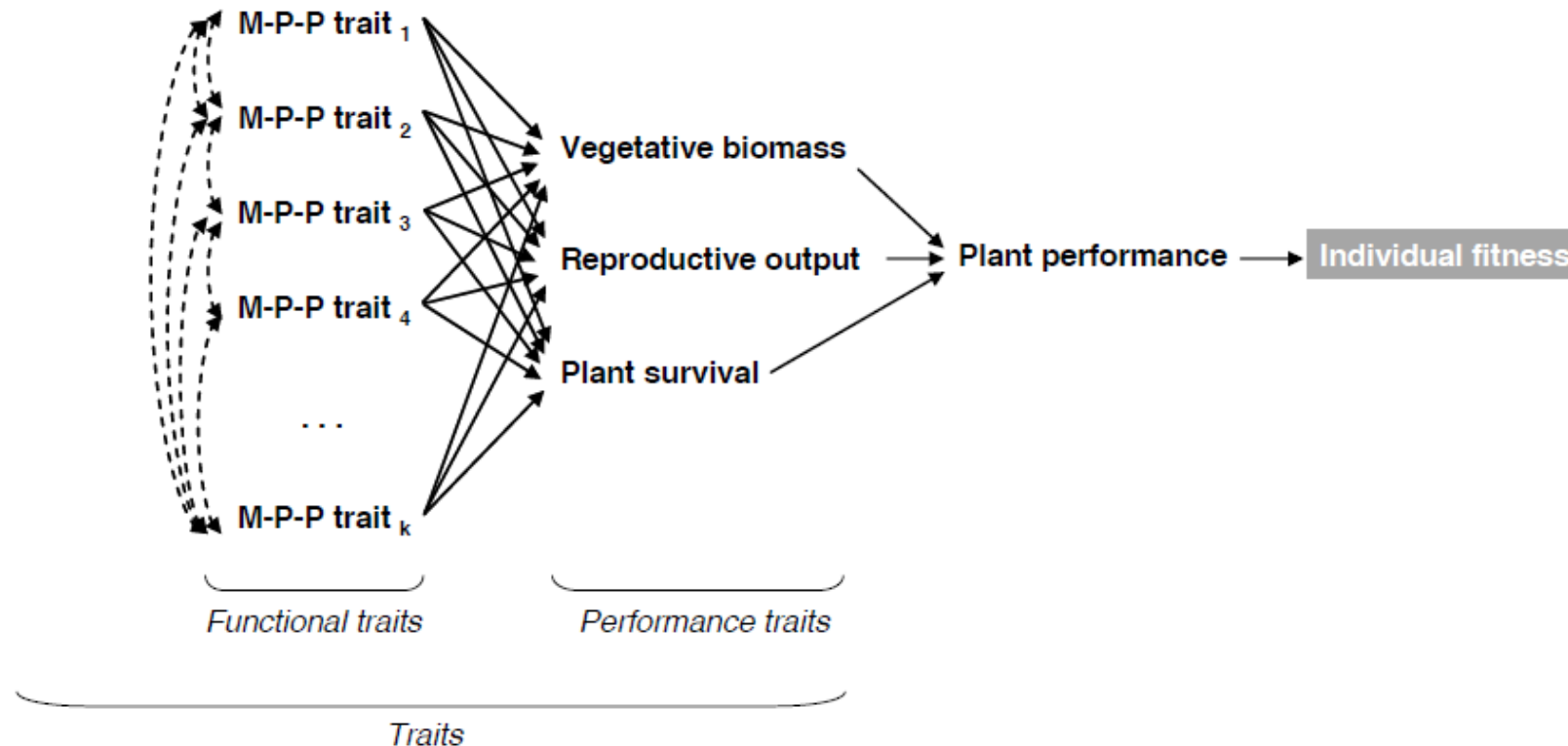


Fig. 3. Arnold's (1983) framework revisited in a plant ecology perspective. Morpho-physio-phenological (M-P-P) traits (from 1 to  $k$ ) modulate one or all three performance traits (vegetative biomass, reproductive output and plant survival) which determine plant performance and, in fine, its individual fitness. M-P-P traits may be inter-related (dashed double-arrows). For clarity, inter-relations among performance traits and feedbacks between performance and M-P-P traits are not represented.

# Trait types

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Copyright © Oikos 2007, ISSN 0030-1299  
Subject Editor: Pia Mutikainen, Accepted 8 January 2007

Let the concept of trait be functional!

Cyrille Violle, Marie-Laure Navas, Denis Vile, Elena Kazakou, Claire Fortunel, Irène Hummel and Eric Garnier

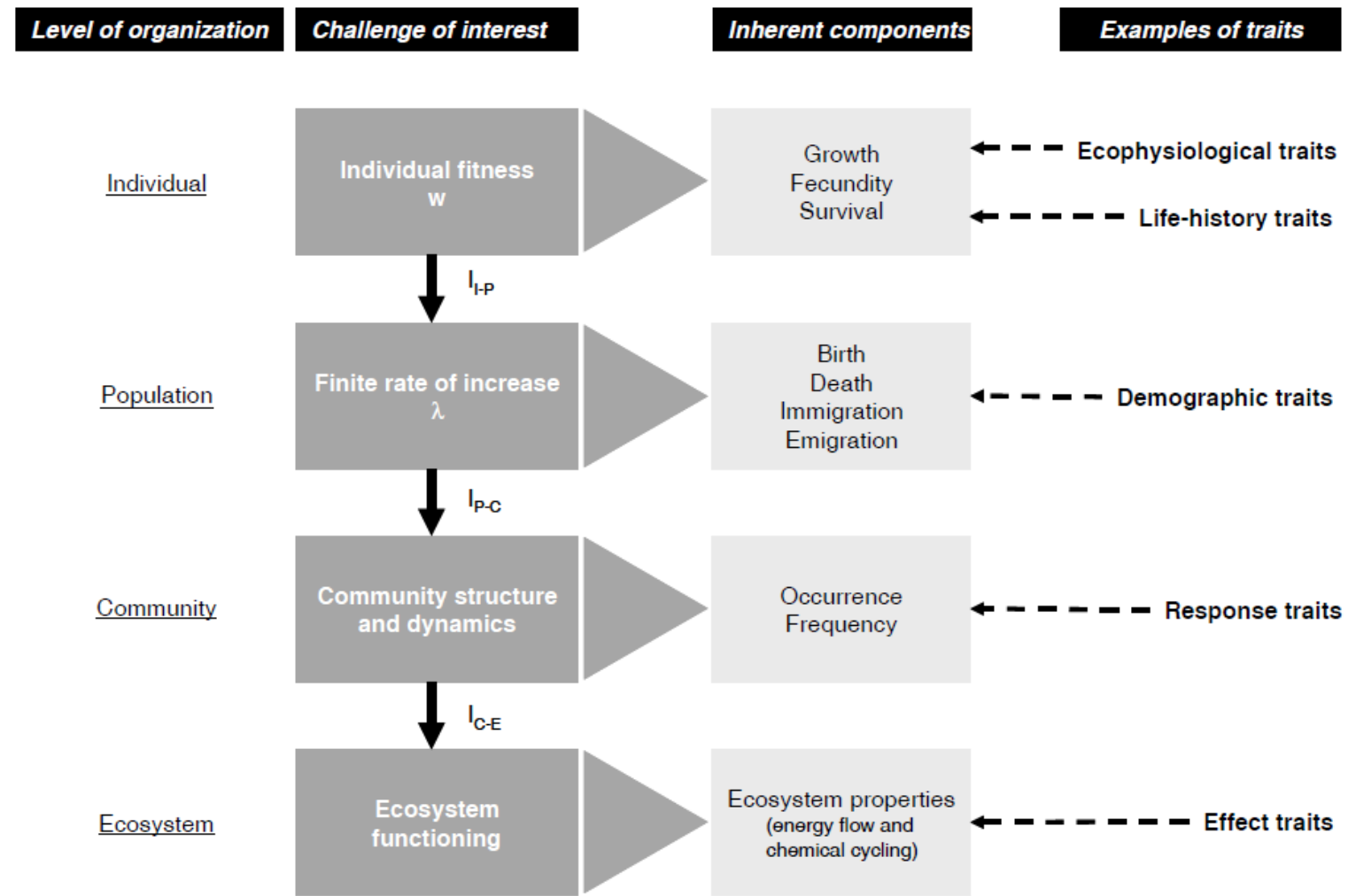


Fig. 1. Pathways linking the challenge of interest of different organizational levels, through their related inherent components, to some examples of traits found in the literature. Without trait-based information, scaling-up to higher organizational levels needs complex integration information (I). Thus fitness components of an individual determine the components of the finite rate of increase ( $\lambda$ ) of the population ( $I_{I-P}$ ). Occurrence and frequency of species at the community level encompass components of  $\lambda$  through complex integration (e.g. biotic interactions) ( $I_{P-C}$ ). Finally, scaling-up to ecosystem properties can be done by combining functional property of each species of the community ( $I_{C-E}$ ). Using traits as proxies of a process at a particular organizational level can sometimes be done without such integration function. For example, at the ecosystem level, ecosystem productivity (one component of ecosystem functioning) shows a strong positive relationship with plant height (an effect trait) (Saugier et al. 2001).





traits are inter-related  
and the relationships may hold across scales

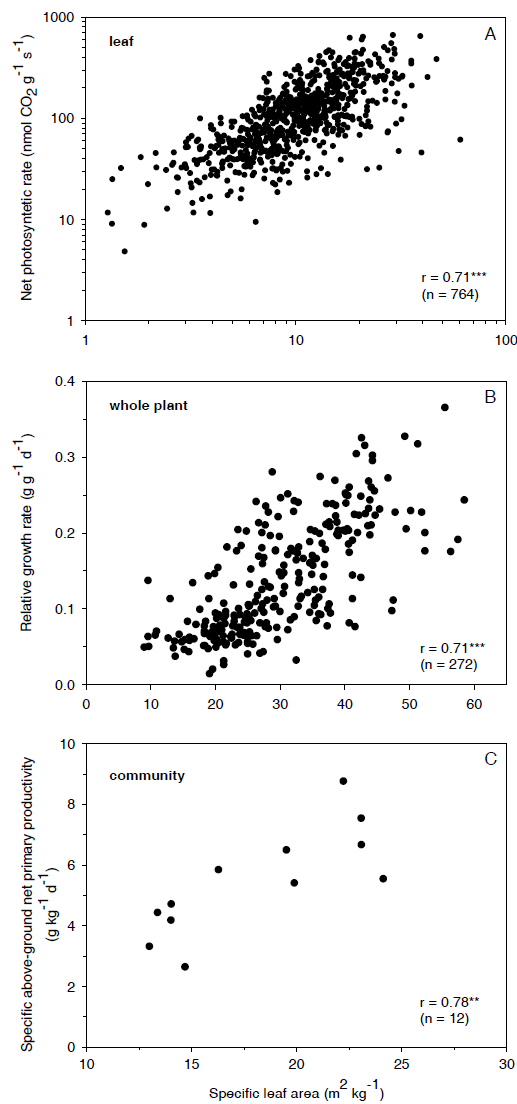


Fig. 4. Relationships between specific leaf area and processes measured at three different organization levels. (A): leaf level (drawn from data taken in Wright et al. 2004); (B): whole plant level (drawn from data taken in Wright and Westoby 2001); (C): community level (drawn from data taken in Garnier et al. 2004); in this latter case, specific leaf area is weighed by the abundance of species in the communities (community functional parameter). Pearson correlation coefficients ( $r$ ) and number of data points (between brackets) are given for each relationship. Significance levels: \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ . Note that the quantities on both axes are equivalent and expressed in comparable units across the three organizational levels.

# Trait attributes –

There is no single species specific value of the trait

- (1) the particular value or modality taken by the trait at any place and time is called an “attribute” (Lavorel et al. 1997);
- (2) within a species, the trait, either continuous or categorical, may show different attributes along environmental gradients (Fig. 2) or through time;
- (3) the attribute for a trait is usually assessed for one population (average of attributes of a set of individuals)

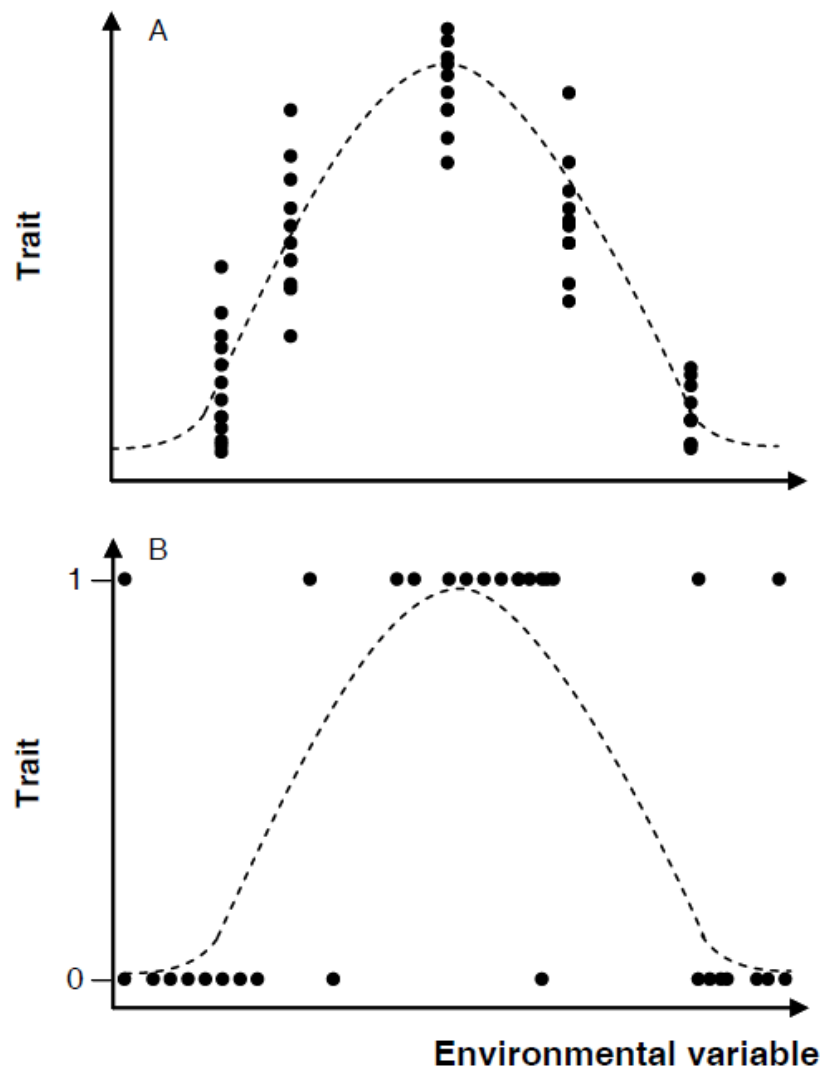
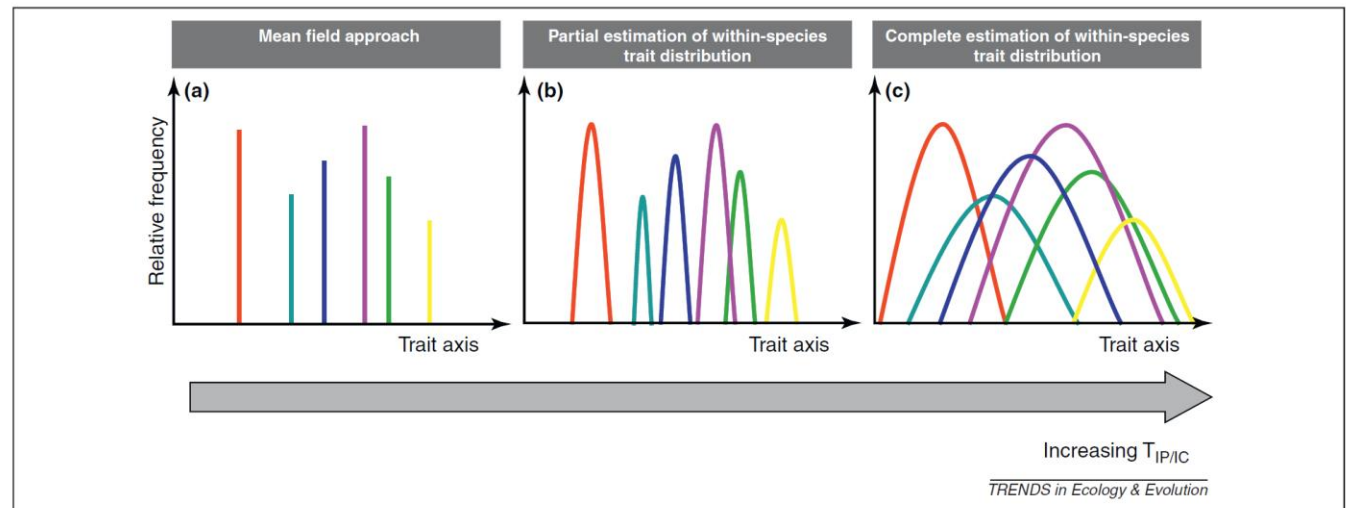


Fig. 2. Theoretical examples of intraspecific variability of a trait (continuous: A, categorical: B) in response to environmental changes. Each point corresponds to the trait value taken by one individual at a point of an environmental gradient. The dashed line represents an example of fitted functions; in the case of categorical trait (B), logistic regressions can be performed (here a quadratic function has been used).



**Figure 1.** The mean field approach to community structure overemphasizes significant differences between species. In the mean field approach, the traits of species are described by single mean values (a). Each stick is the trait value for a given species. The trait frequency can be different between species if the abundance of species is taken into account (in this case, the trait value of a species is weighed by its relative abundance in the community; [89]). When accounting for intraspecific trait variation, the trait distributions of species in the community can overlap (b,c). The level of differentiation between species can be assessed by the  $T_{IP/IC}$ -statistic (Box 2). Note that a partial sampling of intraspecific variation (e.g. in the case of measurements of plant functional traits, standardized protocols minimizing intraspecific variation are used; [67]) can underestimate the degree of overlap between species (b).

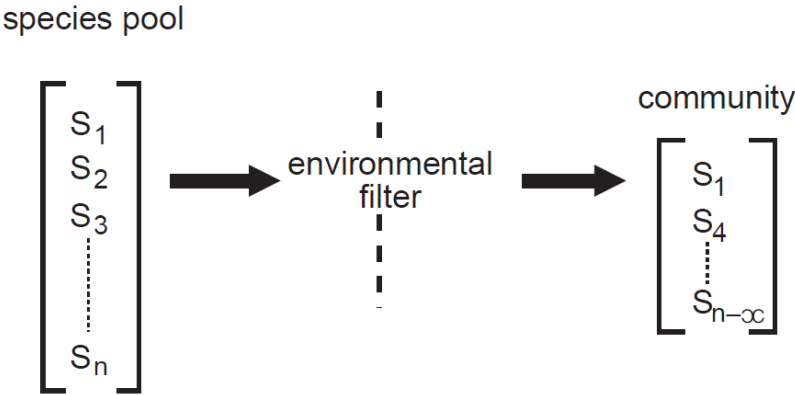


# Assembly and response rules: two goals for predictive community ecology

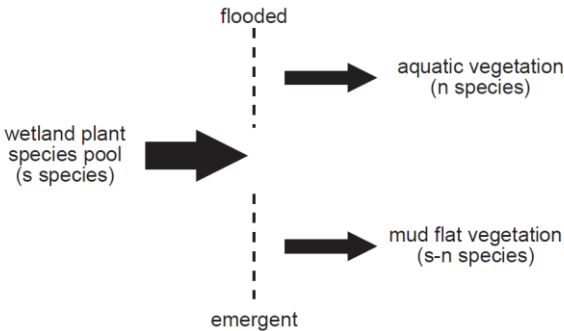
Keddy, Paul A.

**Abstract.** Assembly rules provide one possible unifying framework for community ecology. Given a species pool, and measured traits for each species, the objective is to specify which traits (and therefore which subset of species) will occur in a particular environment. Because the problem primarily involves traits and environments, answers should be generalizable to systems with very different taxonomic composition. In this context, the environment functions like a filter (or sieve) removing all species lacking specified combinations of traits. In this way, assembly rules are a community level analogue of natural selection. Response rules follow a similar process except that they transform a vector of species abundances to a new vector using the same information. Examples already exist from a range of habitats, scales, and kinds of organisms.

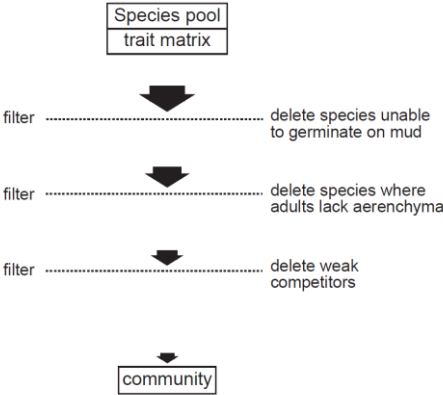
# Environmental filter



**Fig. 1.** Assembly rules specify which subset of species in the total pool (left) would tolerate specified conditions and form a community (right).



**Fig. 3.** An example of assembly rules from vegetation cycles in prairie marshes (van der Valk 1981). The species pool (left) can yield either aquatic vegetation or mud flat vegetation depending upon water levels for germination. Ability to germinate under water is the sole trait which must be measured to make this prediction.

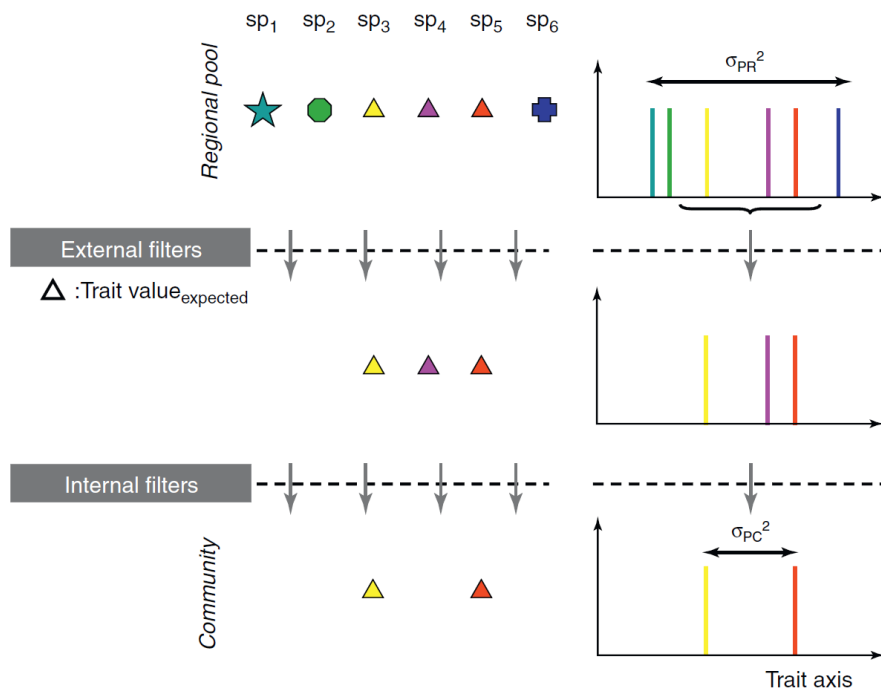


**Fig. 4.** Several sequential deletion rules can be likened to filters which progressively reduce the subset of species which will form a community.

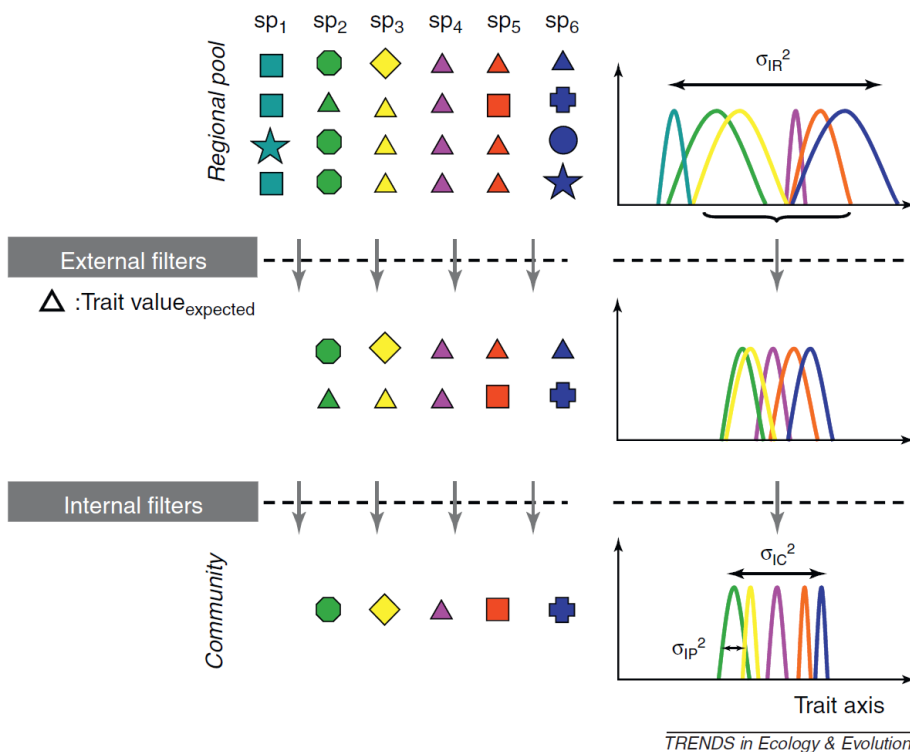
# The return of the variance: intraspecific variability in community ecology

Cyrille Violle<sup>1,2</sup>, Brian J. Enquist<sup>1,3</sup>, Brian J. McGill<sup>4</sup>, Lin Jiang<sup>5</sup>, Cécile H. Albert<sup>6,7</sup>, Catherine Hulshof<sup>1</sup>, Vincent Jung<sup>8,9</sup> and Julie Messier<sup>1</sup>

(a) Mean field approach to the regional pool



(b) Including intraspecific variability in the regional pool

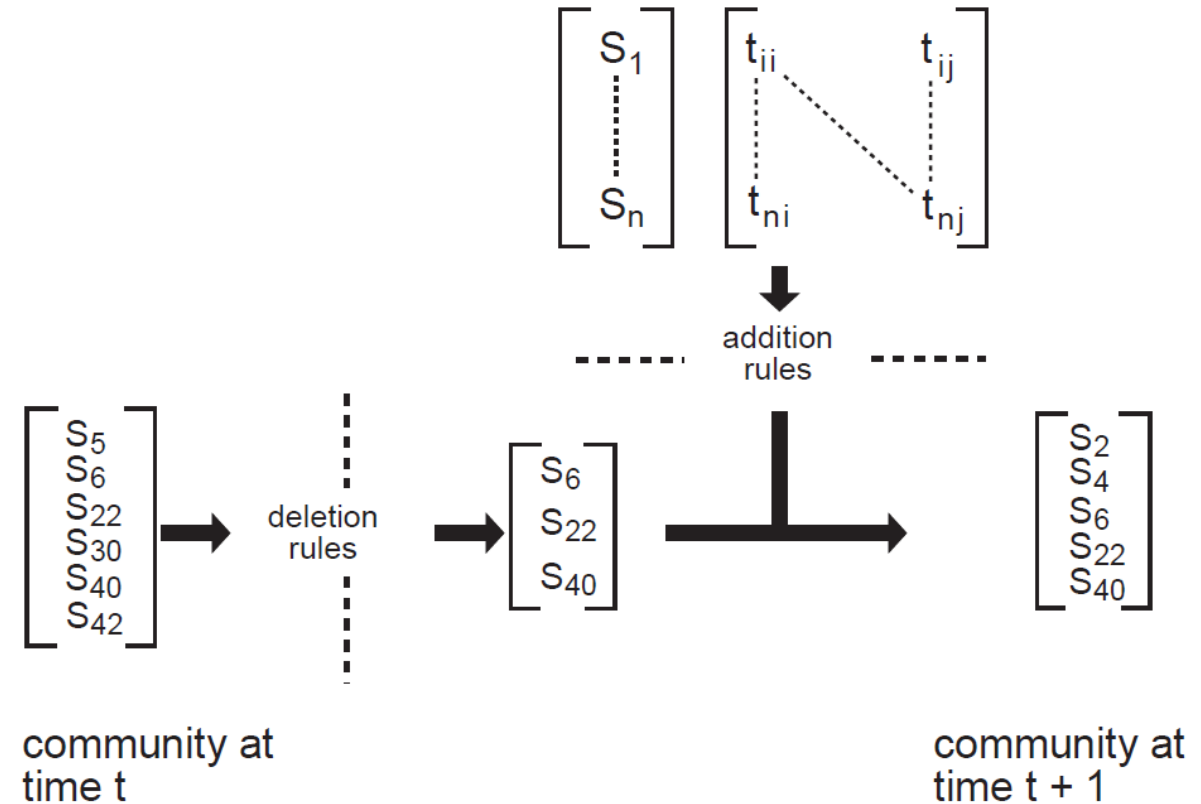


**Figure 2.** Community assembly theory and intraspecific variability. **(a)** Community assembly theory has been traditionally rooted in mean field theory. Only mean trait values of species present in the regional pool are considered. Dashed lines represent external and internal filters (Box 1). Each color represents a species and each symbol is a given trait value. Species enter in the community if their mean trait values match external conditions  $E_j$ . In established communities, species that possess trait values that are too similar cannot coexist (limiting similarity hypothesis) [8]. **(b)** We propose a revised community assembly theory rooted on the amount of regional intraspecific variation. Species enter in the community if their regional intraspecific variation matches, at least partially, external conditions  $E_j$ . In established communities, diversity is expected to be higher than in the mean field theory because species that display intraspecific variability can escape competitive exclusion, predation pressures or occupy more microsites. This theory is tested by partitioning variances among hierarchical levels (Box 2; Figure 3).



# Response rules

Response rules grow out of assembly rules. They specify how an initial vector of species composition will respond when an environmental factor is changed; [Lewontin (1974) has called this ‘transformation rules’]. Examples would include: how will prairie vegetation respond to fire or grazing? How will bird communities respond to forest clearance? How will stream invertebrates respond to siltation? There are two ways in which response rules would differ in form from assembly rules. First, one begins with a subset of species already present, and must predict how these will respond to the perturbation (deletion rules). Second, one must re-examine the species pool and trait matrix for species likely to replace those presently occurring (Fig. 5) (addition



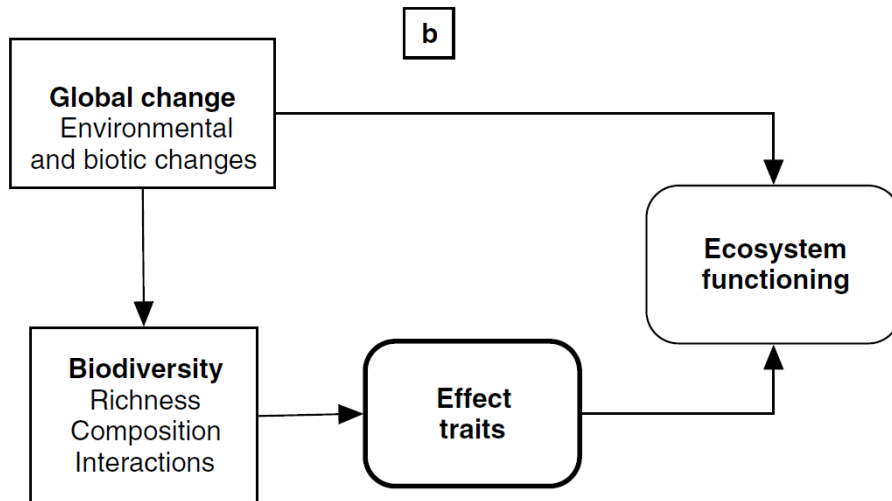
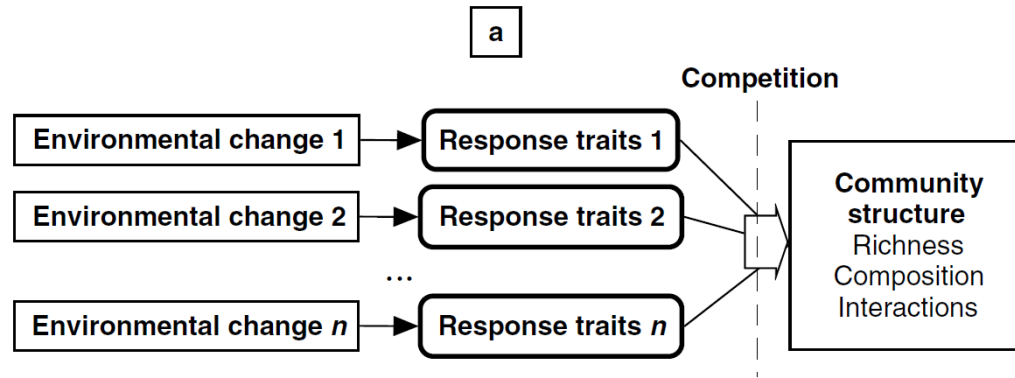
**Fig. 5.** General procedure for response rules. First the perturbation deletes species from the community, and then based upon the trait matrix, new species are added from the pool. In this case, the vegetation initially consists of six species. Three ( $S_5, S_{30}, S_{42}$ ) disappear from the perturbation. They are replaced by two ( $S_2, S_4$ ) from the trait matrix, producing a final predicted community of five species.

ESSAY REVIEW

# Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail

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## Response x effect traits

traits associated with species' response to the environment

traits that determine the effect of species on ecosystem functions



Revisiting the Holy Grail: using plant functional traits to understand ecological processes

Jennifer L. Funk<sup>1,\*</sup>, Julie E. Larson<sup>1</sup>, Gregory M. Ames<sup>2</sup>, Bradley J. Butterfield<sup>3</sup>, Jeannine Cavender-Bares<sup>4</sup>, Jennifer Finn<sup>5</sup>, Daniel C. Laughlin<sup>6</sup>, Ariana E. Sutton-Grier<sup>7,8</sup>, Laura Williams<sup>4</sup> and Justin Wright<sup>2</sup>



Example traits	Organismal processes	Community processes	Ecosystem processes
Leaf chemistry and longevity	Carbon balance Disease resistance Growth rate	Competition Herbivory Succession	Decomposition Nutrient cycling Productivity
Leaf and stem hydraulic traits	Drought tolerance	Competition and facilitation	Hydrology Precipitation patterns
Fine root traits	Soil resource uptake Growth rate	Competition and facilitation Community invasibility	Decomposition Soil development

**Fig. 1.** Functional traits can be used to understand a wide range of ecological processes occurring at organismal, community, and ecosystem scales. Examples are given here of how leaf, stem, and fine root traits influence a variety of ecological processes.

Diversity of response and effect traits provides complementary information about avian community dynamics linked to ecological function






Lisbeth A. Hordley<sup>1</sup>  | Simon Gillings<sup>2</sup>  | Owen L. Petchey<sup>3</sup>  | Joseph A. Tobias<sup>4</sup>  | Thomas H. Oliver<sup>1</sup> 

TABLE 1 Functional traits chosen for the analysis, description of each trait, the category chosen (effect, response or both), the rationale for including the trait as either effect, response or both and source of trait data

Trait	Description	Category	Rationale	Source
Beak length	Length from the anterior edge of the nostril to the tip of the beak	Effect	Bill shape and size predict the size and type of food (i.e. seeds and insects) to be handled and consumed (Luck et al., 2012; Wheelwright, 1985)	Pigot et al. (2020)
Beak width	Width of the beak measured from the anterior edge of the nostril			
Beak depth	Vertical height measured from the anterior edge of the nostril			
Gape width	The external distance between commissural points			

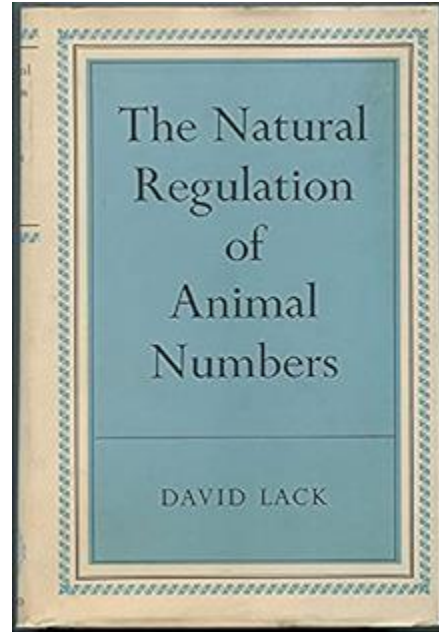
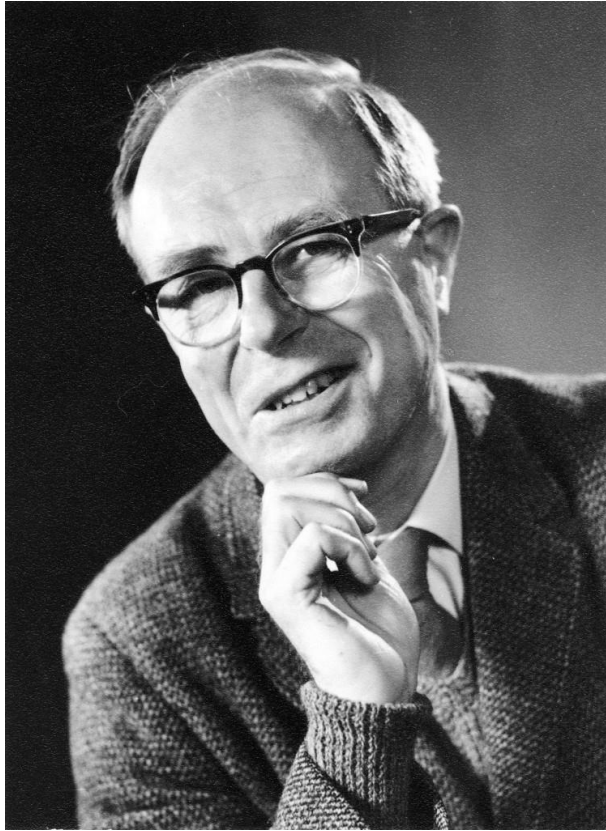
effect / response trait classification is not always easy...

Species specialization index	Coefficient of variation ( <i>SD</i> /mean) of the species density in six habitat categories—high values indicate more specialized species and low values indicate more generalized species	Response	More specialized species have traits associated with slow reproduction (Mckinney & Lockwood, 1999) and are less able to respond to environmental variation and novel environments (Sol et al., 2002)	Johnston et al. (2014)	Body mass	Geometric mean of average values provided for both sexes	Both	Body size is strongly related to resource use and foraging behaviour, hence indicates species' capacity to consume seeds and invertebrates (Luck et al., 2012)	Pigot et al. (2020) and Sheard et al. (2020)
Species temperature index	Long-term average temperature experienced by individuals over its breeding range		Species temperature index indicates a species climate envelope, with warm species better able to adapt to increasing temperatures (Devictor et al., 2012)	Devictor et al. (2012)				Body mass is also strongly related to reproductive output, longevity and dispersal abilities (Luck et al., 2012), and hence species' response to environmental conditions	
Thermal maximum	Mean temperature of the 5% hottest cells of the breeding range		Species with a lower thermal maximum are less tolerant to changing climatic conditions and show negative population trends (Jiguet et al., 2007)	Jiguet et al. (2007)	Hand-wing index	Aspect ratio of the wing		Wing and leg morphological traits align with movement or dispersal ability, which in turn influences resource use and frugivore (Luck et al., 2012; Miles et al., 1987; Sheard et al., 2020)	
Mean latitude	The mean latitude of an individual species calculated from its geographic range		Changes in temperature are strongest at northern latitudes; hence, these species are likely to respond more strongly to these changes (Parmesan, 2007)	<a href="http://datazone.birdlife.org/">http://datazone.birdlife.org/</a>	Kipp's distance	The distance between the tip of the longest primary and the first secondary feather measured on the folded wing		These traits also indicate locomotory behaviour (Miles et al., 1987) and provide species with the ability to withstand environmental changes, for example, disrupted landscape connectivity (Luck et al., 2012)	
Lifespan	Maximum recorded longevity for a species		Long lifespan can be correlated with small clutch size and infrequent breeding (Zammuto, 1986); therefore, species are less able to recover from environmental perturbations (Luck et al., 2012)	Myhrvold et al. (2015)	Wing length	The distance between the bend of the wing and the tip of the longest primary feather			
					Tarsus length	Length from the middle of the rear ankle joint to the end of the last scale of acrotarsium			
Clutch size	Number of eggs per clutch		These traits measure the reproductive potential of species, and species with high clutch size/ multiple broods will recover more quickly after an environmental disturbance (Newbold et al., 2013)	Myhrvold et al. (2015)					
Number of broods	Number of clutches produced per year			Myhrvold et al. (2015) and Johnston et al. (2014)					



# How traits help: Population regulation

David Lack, Food limitation hypothesis

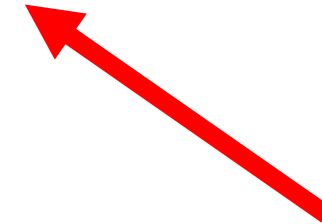


Mortality

Population density

Food

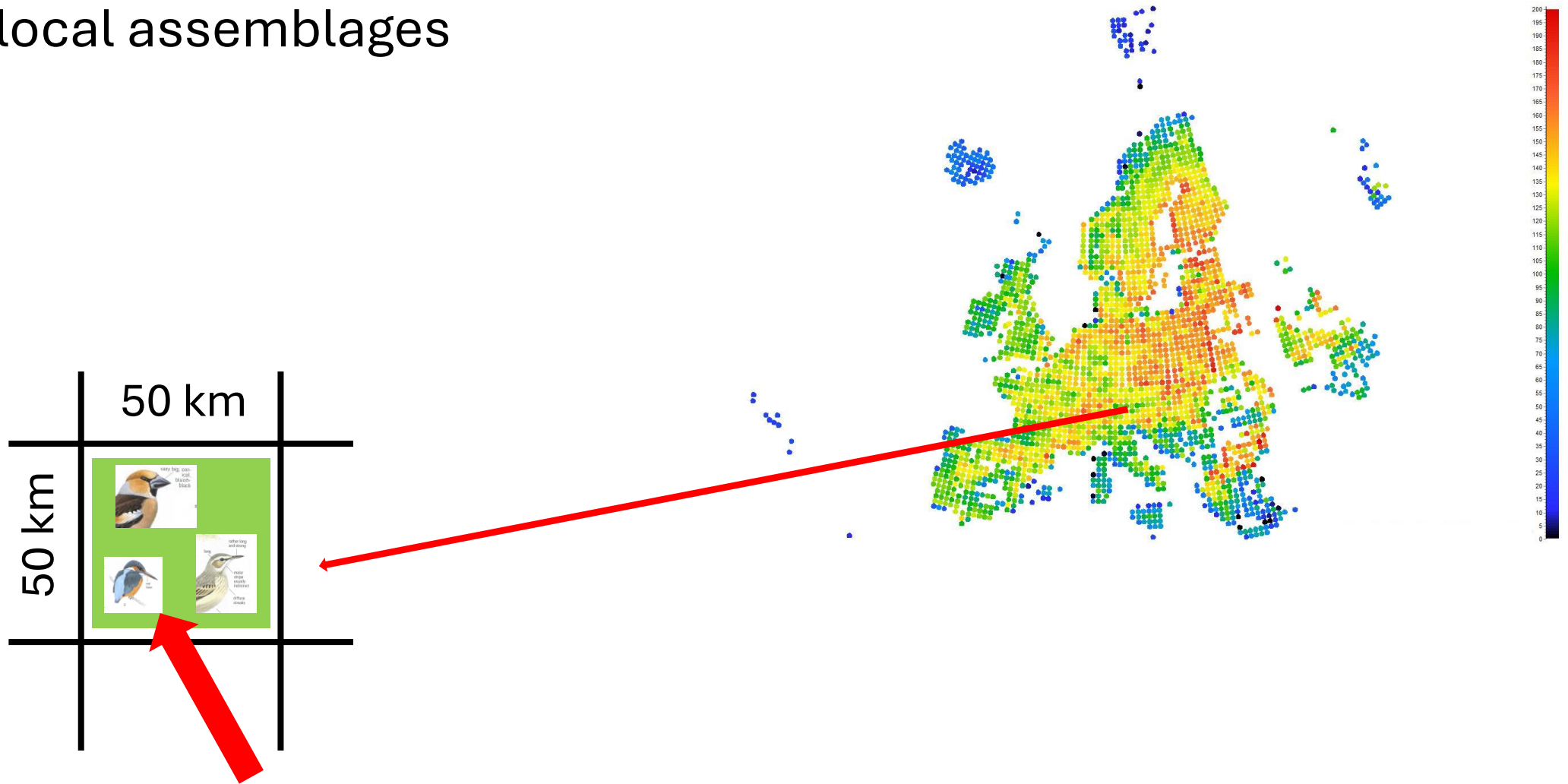
Population growth rate





# A brief intro to large scale “trait maps”

...using local assemblages



Local assemblage / mean trait value

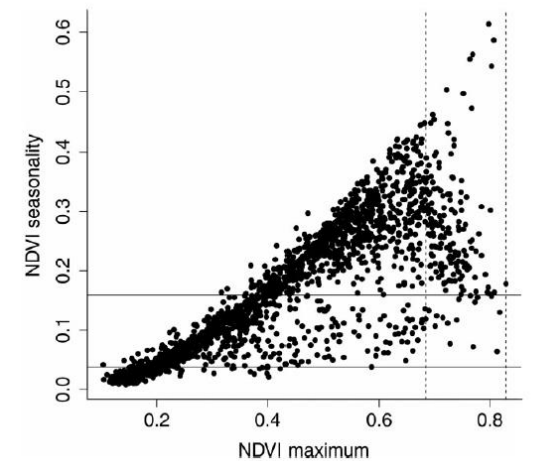
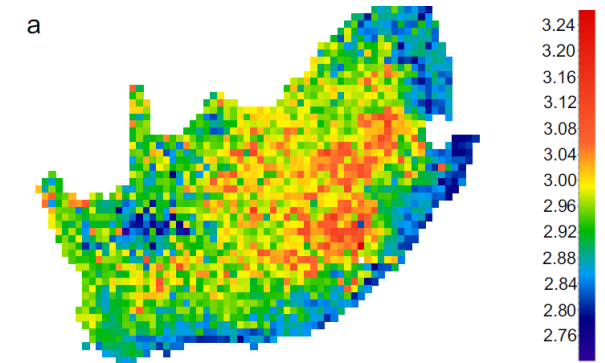
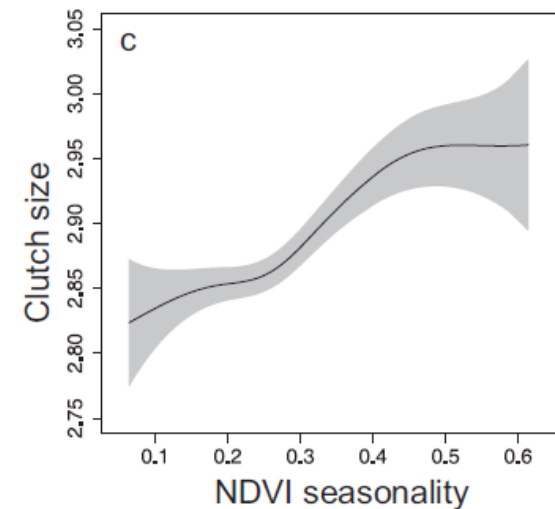
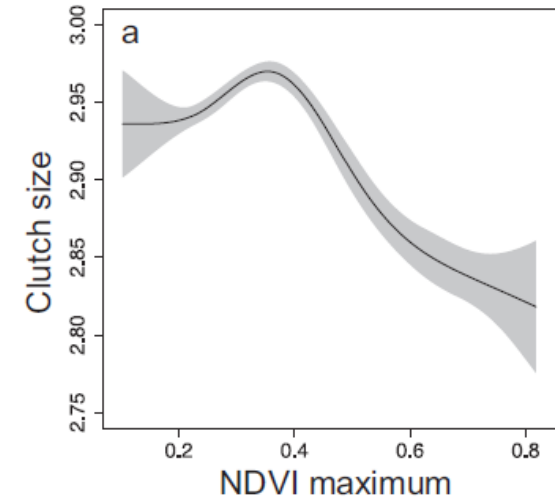
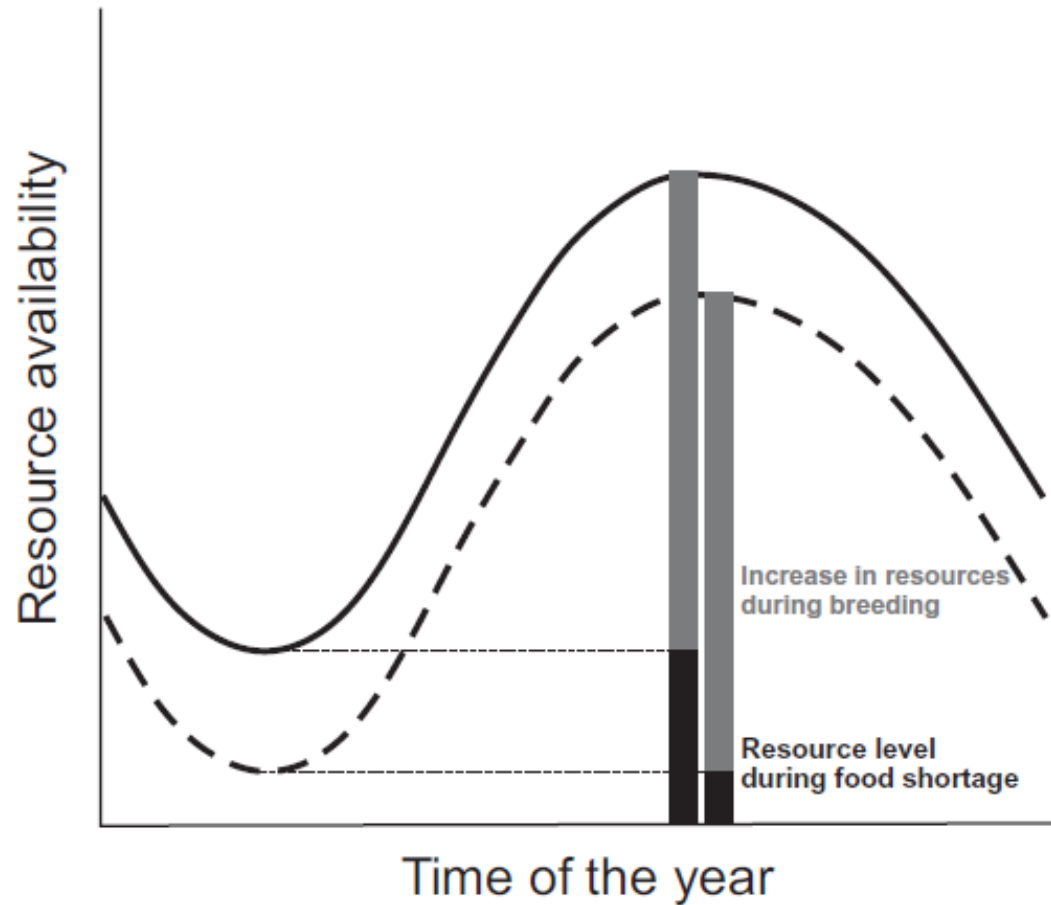


RESEARCH  
PAPER

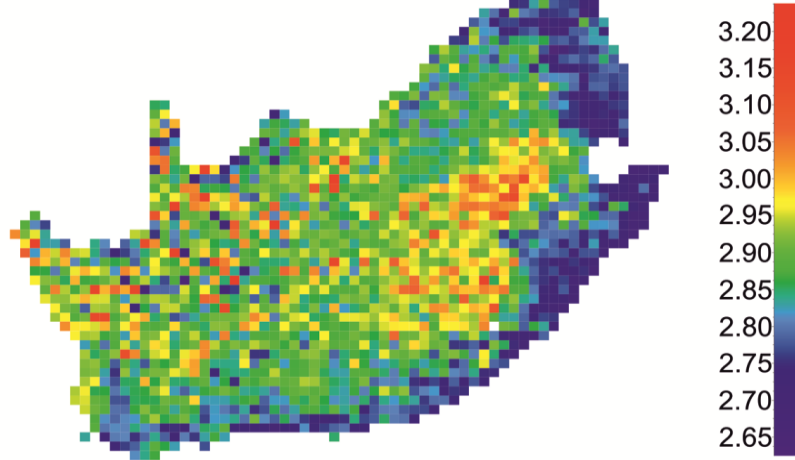
# Relative food limitation drives geographical clutch size variation in South African passerines: a large-scale test of Ashmole's seasonality hypothesis

David Hořák<sup>1,\*</sup>, Anna Tószögyová<sup>1,2</sup> and David Storch<sup>1,2</sup>

## (avian) clutch size as a *proxy* for investment into reproduction

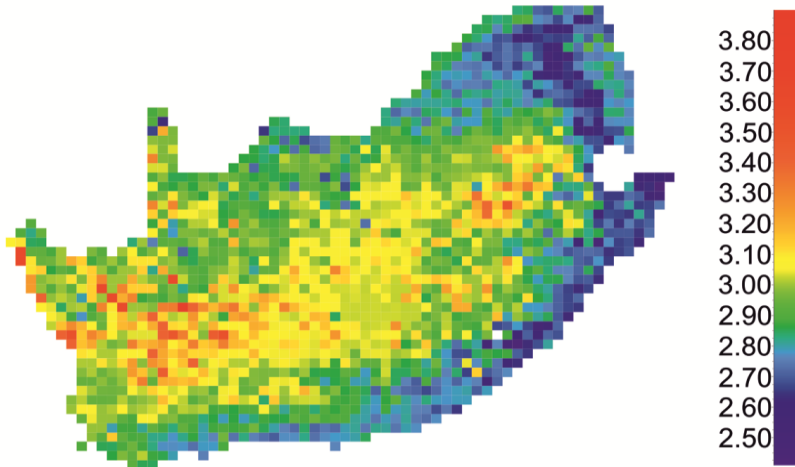


a



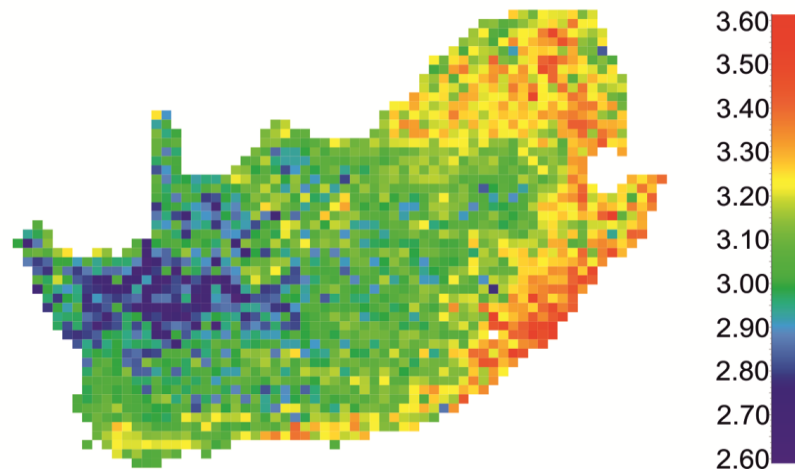
**insectivorous**

b



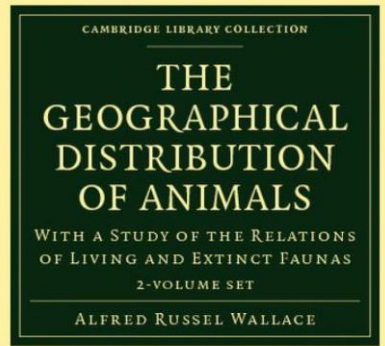
**frugivorous**

c



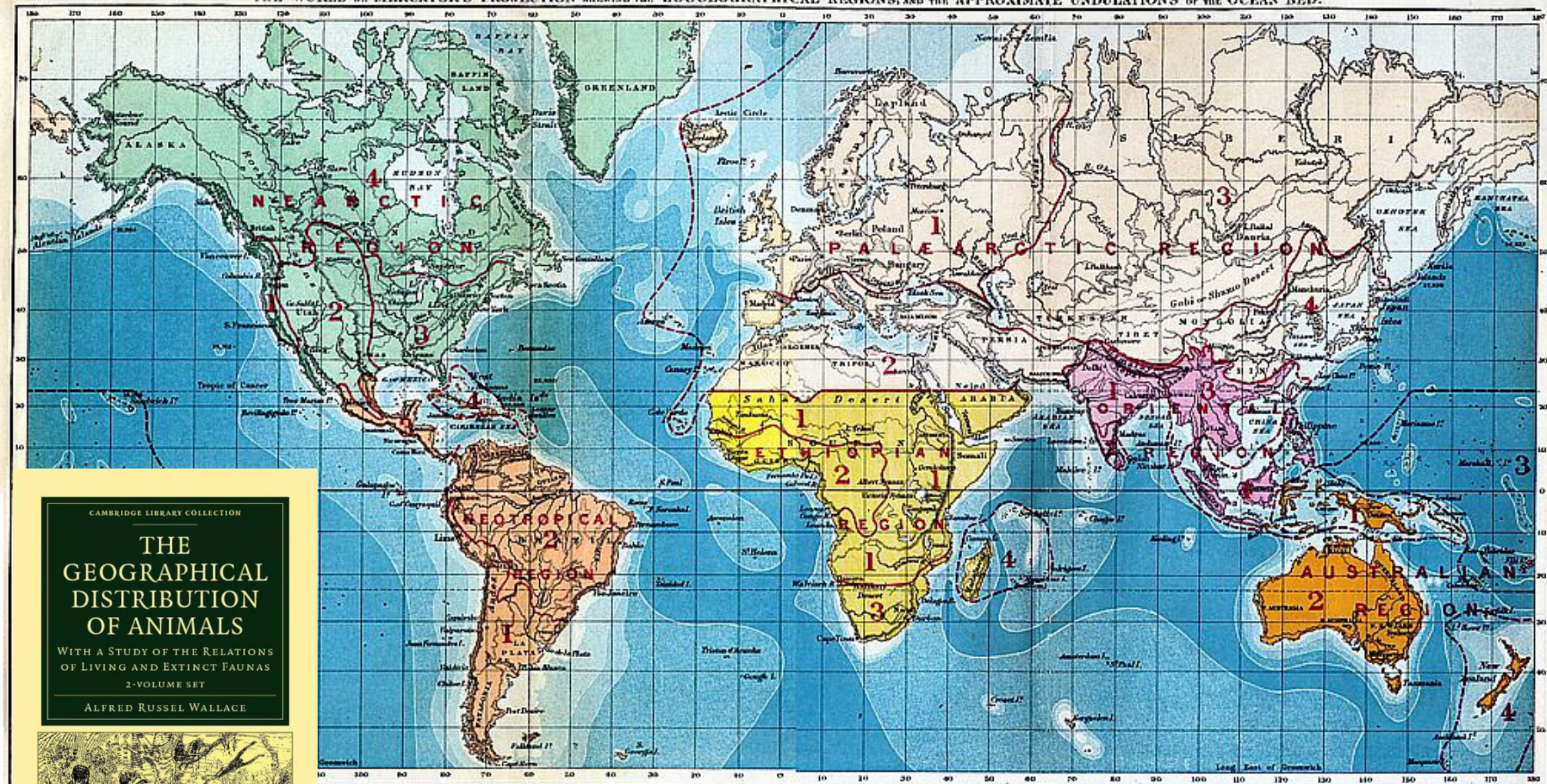
**granivorous**





CAMBRIDGE

THE WORLD ON MERCATOR'S PROJECTION SHOWING THE ZOOGEOGRAPHICAL REGIONS, AND THE APPROXIMATE UNDULATIONS OF THE OCEAN BED.



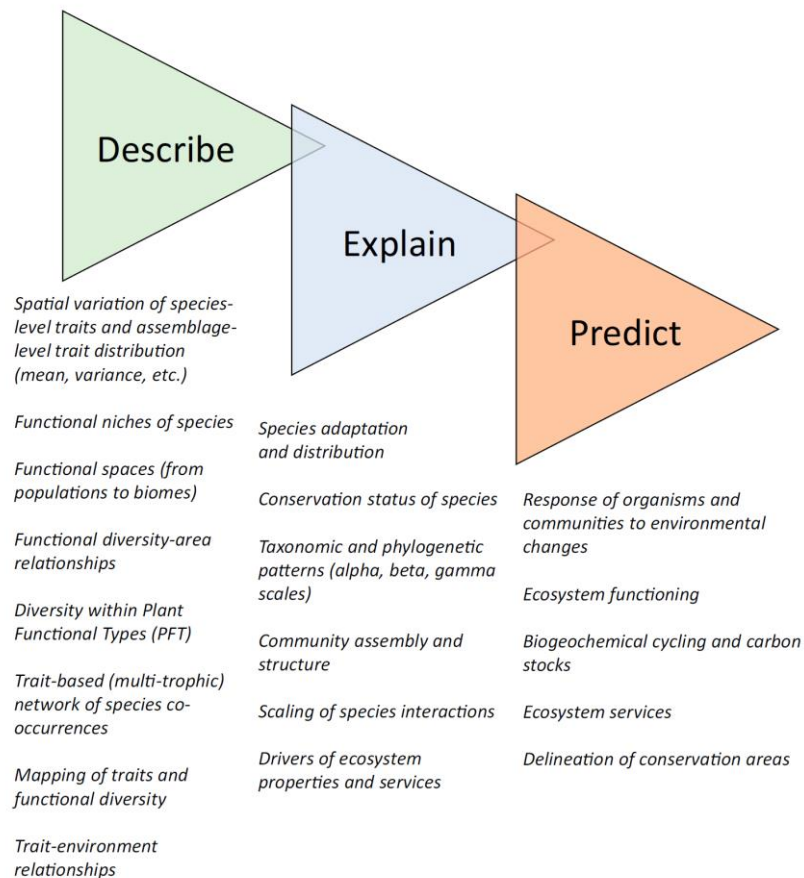
New York: Harper & Brothers.

Mapping species' distributions is an old story...

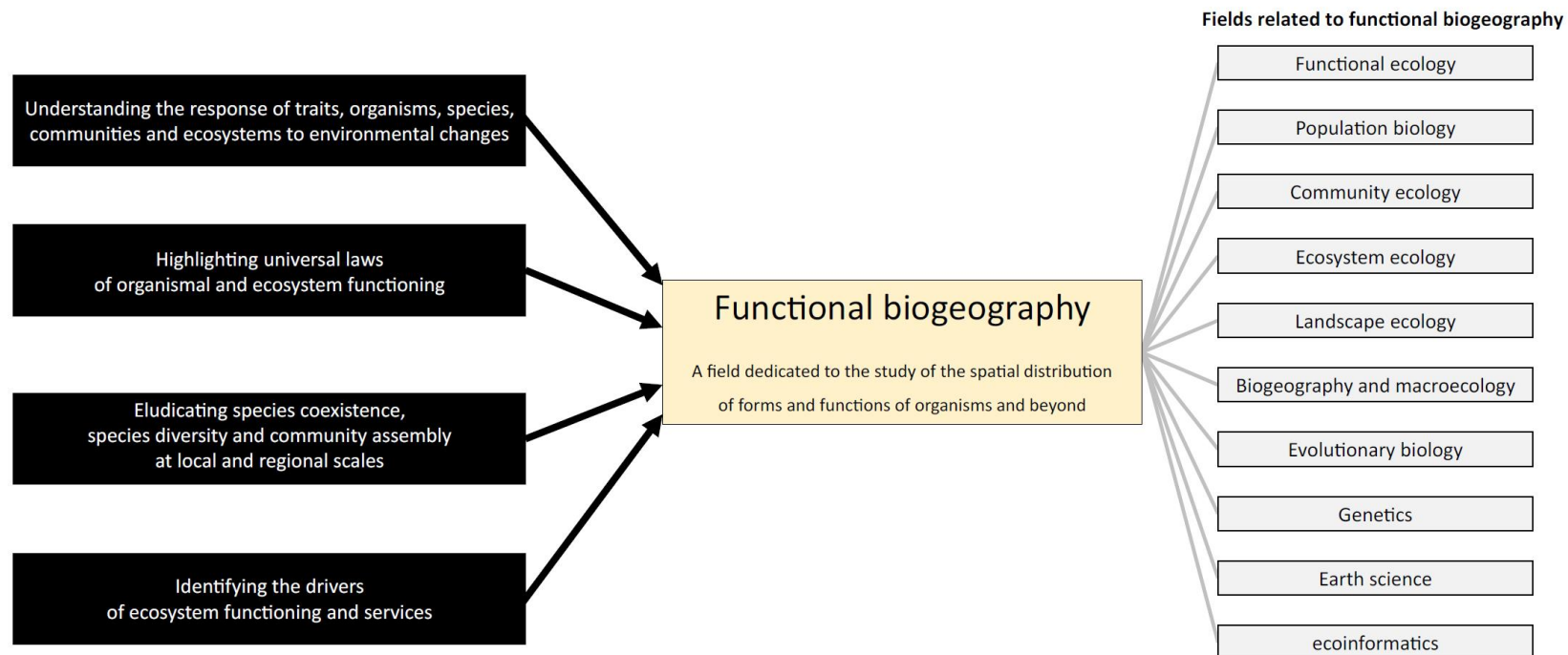


# The emergence and promise of functional biogeography

Cyrille Violle<sup>a,b,1</sup>, Peter B. Reich<sup>c,d</sup>, Stephen W. Pacala<sup>e</sup>, Brian J. Enquist<sup>f,g,h</sup>, and Jens Kattge<sup>i,j</sup>



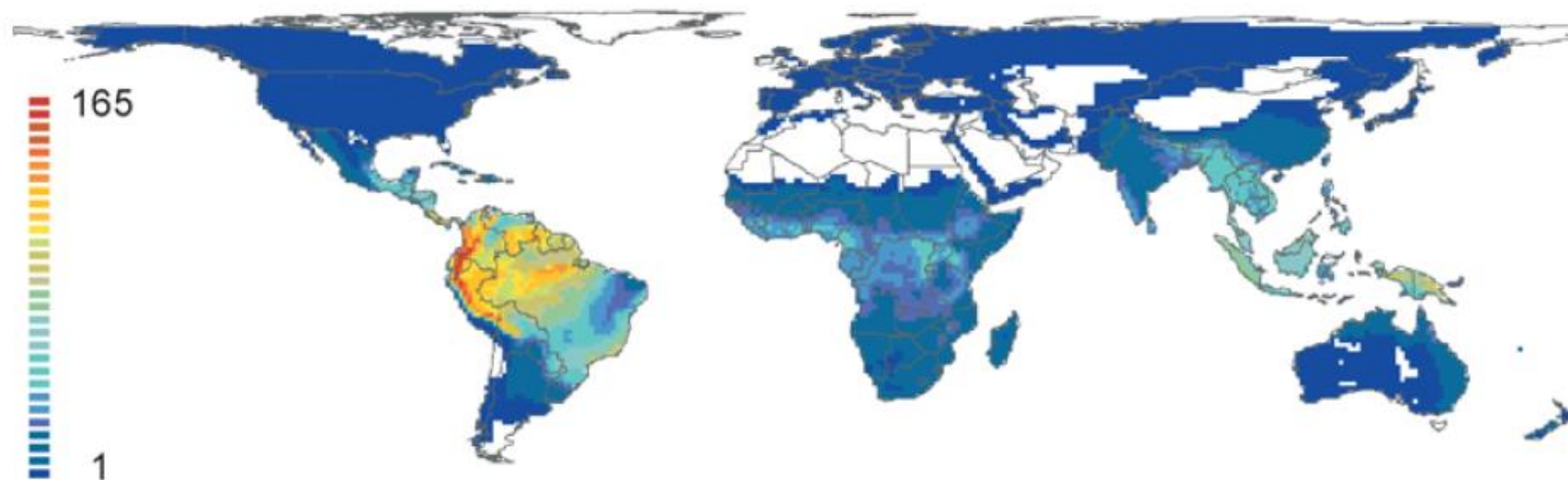
**Fig. 2.** The three tenets of functional biogeography: describe, explain, predict. The first tenet of functional biogeography is to describe the distribution of forms and functions along environmental gradients and across spatial scales. The second is to use this information to explain the geographic distribution of organisms, biodiversity (notably species and phylogenetic diversity) patterns, and ecosystem processes and services. The third is to predict their responses to environmental changes using trait-based predictive functions and models.



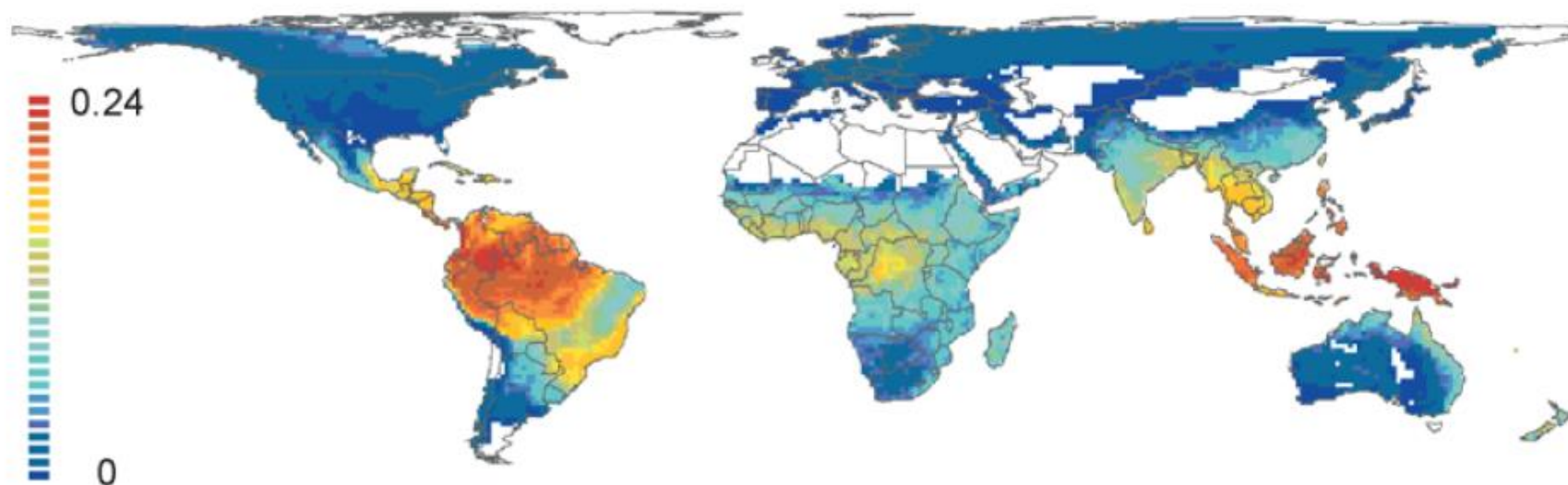
**Fig. 1.** Functional biogeography: an emergent field at the crossroads of several science fields. Functional biogeography calls for knowledge from multiple fields to answer questions related to the distribution of forms and functions of organisms, populations, communities, ecosystems, and biomes across spatial scales.



(a) Frugivore richness



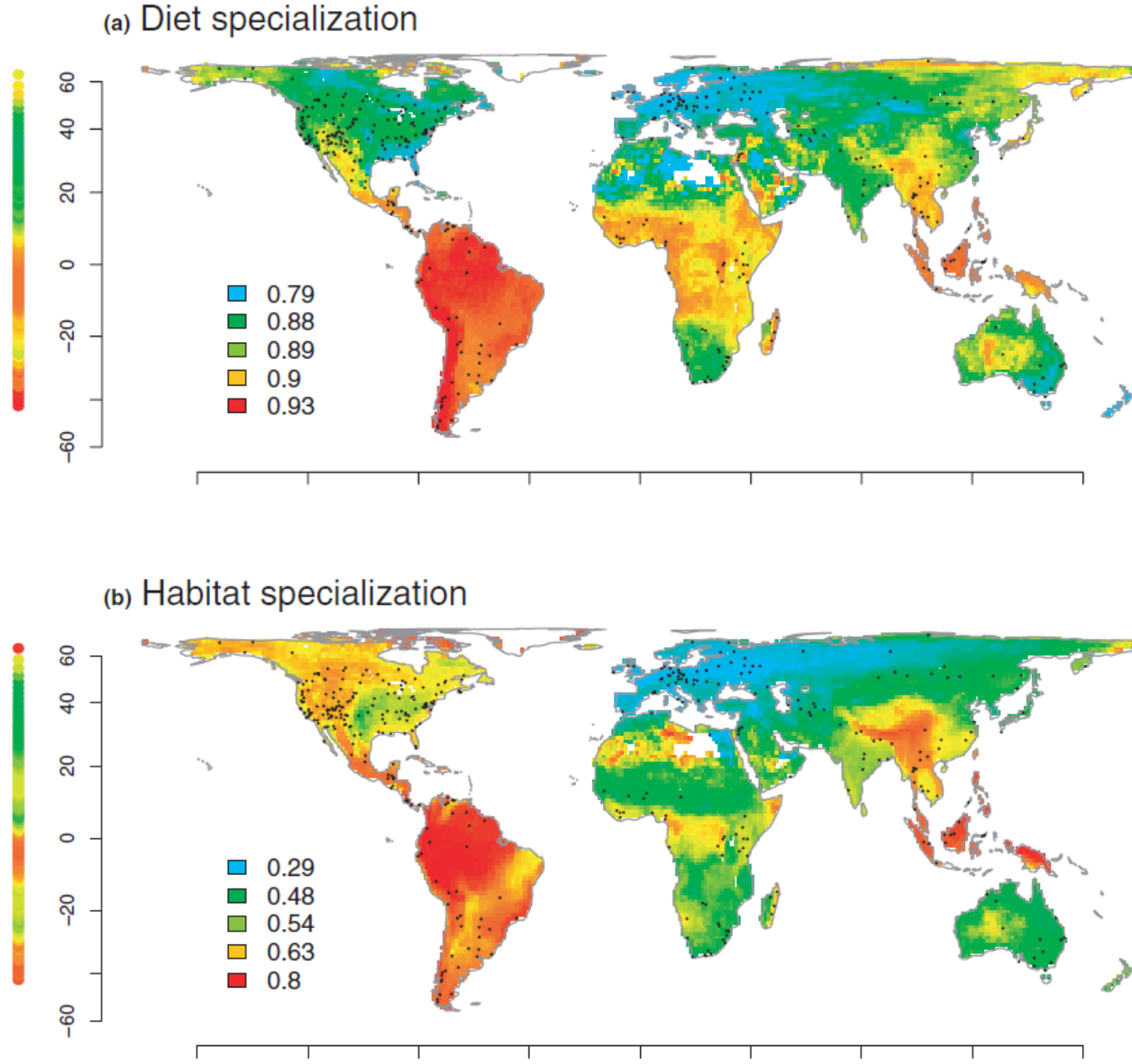
(b) Proportion of frugivores





# Global patterns of specialization and coexistence in bird assemblages

Jonathan Belmaker<sup>1,\*†</sup>, Cagan H. Sekercioglu<sup>2‡</sup> and Walter Jetz<sup>1†</sup>



# Beyond species richness...functional diversity

80

- traits provide more insight into the structure of ecological space
- you can quantify the overall amount of ecological space
- improve understanding of community assembly
- influences ecosystem dynamics, stability, productivity, nutrient balance, and other aspects of ecosystem functioning

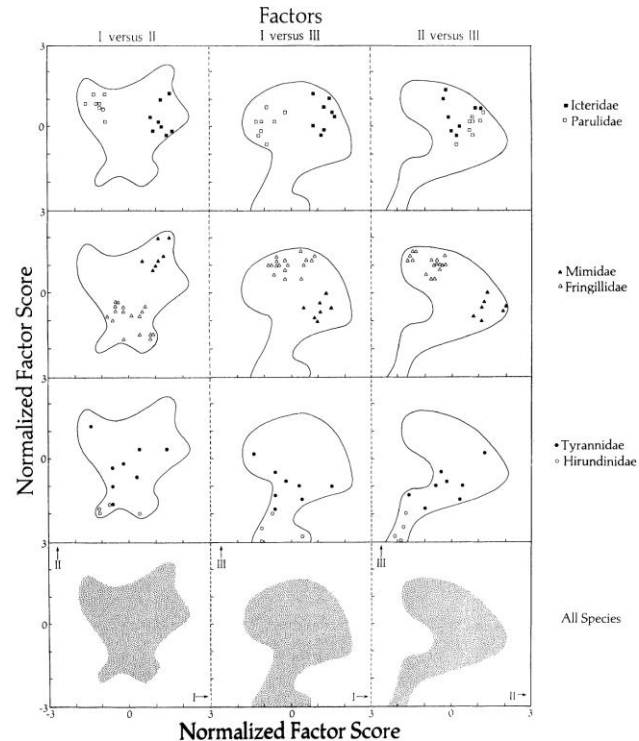
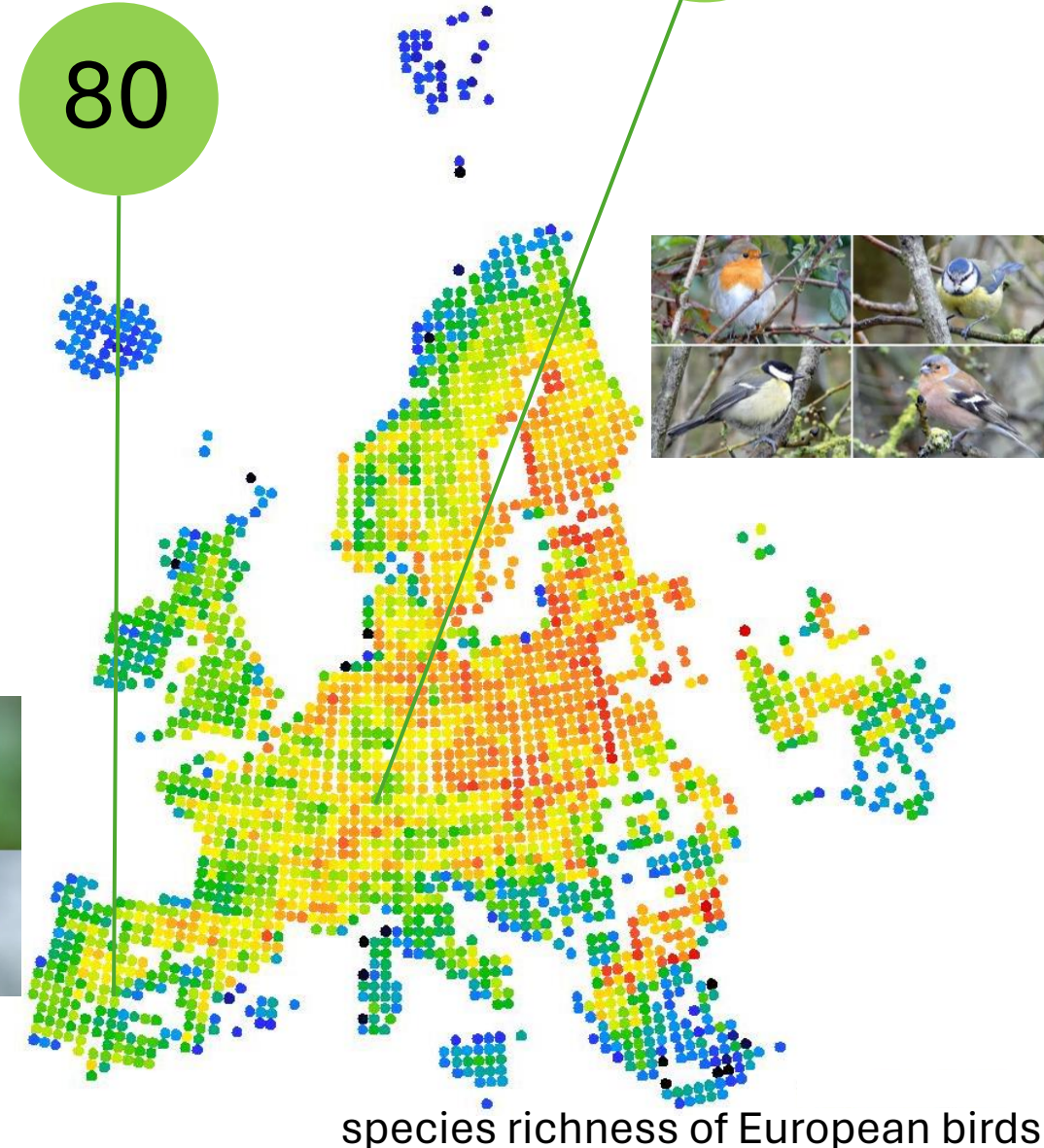


Fig. 1. Positions of species in a variety of families represented in scrub communities with respect to the first three principal components in the morphological space defined by all 83 species and forms. Projections on factors are presented in pairwise fashion. Factor scores were normalized by the mean and standard deviation of the species' projections. The shaded areas in the bottom set of boxes represent the area occupied by all 83 species and forms in morphological space. These areas are outlined in the boxes above.



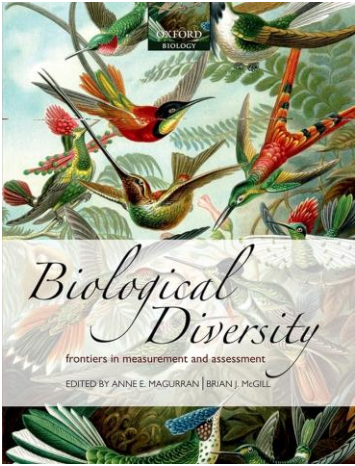
Jiménez-Franco et al. 2019



species richness of European birds

Table 13.1 A general classification of trait diversity indices.

	Species presences only	Abundances incorporated
Trait richness		
Zero trait dimensions		Genus:species ratio Phylogenetic methods (Chapter 14)
One trait dimension		Range Variance (Platy)kurtosis
N trait dimensions		Minimum spanning tree (MST) distance Mean distance, MD Sum of distances, FAD, MFAD Dendrogram-based FD Convex hull volume, FRic Slope of the cumulative MST, $\alpha_{MST}$
Trait diversity		
One trait dimension		Variance-based $FD_{var}$
N trait dimensions		Quadratic entropy, $FD_Q$ Functional divergence, $FD_{Dis}$ Functional dispersion, $FD_{Dis}$
Trait evenness		
One trait dimension		Functional regularity index, $FRO$
N trait dimensions	Evenness in NND	Functional evenness, $FEve$
Trait dispersion/density of species packing		
N trait dimensions	Mean NND	Abundance-weighted Mean NND



zero or one dimension

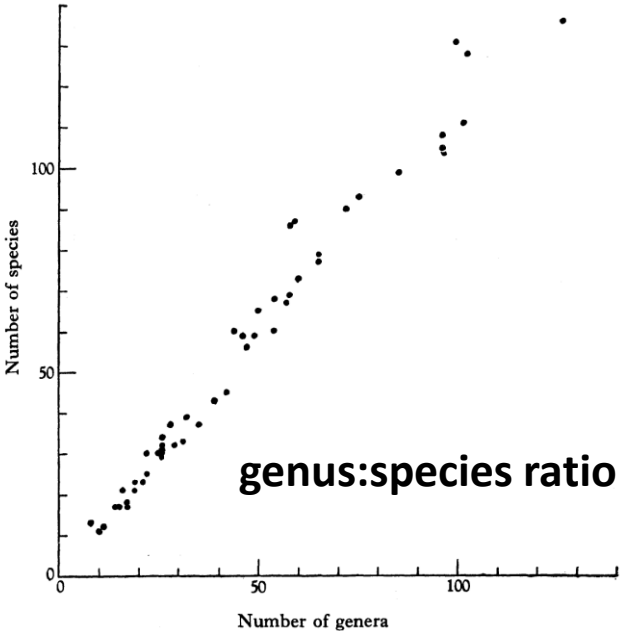
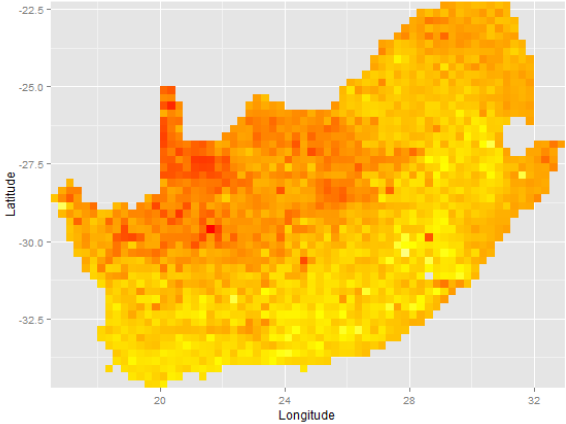
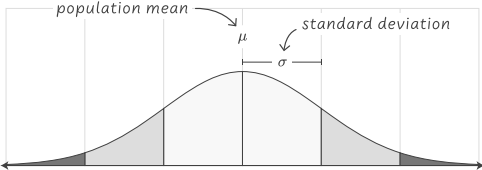


Fig. 1. Relation between the number of species and the number of genera present in forty-nine animal communities (from Table 1).

CV of avian bill size, South Africa



Coefficient of Variation



Note that any measure that can incorporate  $N$  trait dimensions can always deal with individual traits. Indices are ordered historically, starting with the oldest. See text for explanation of terms.

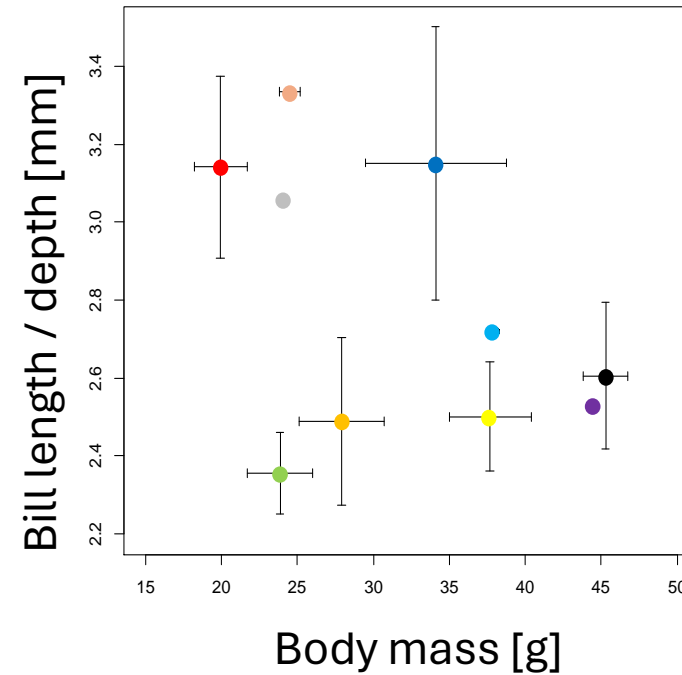
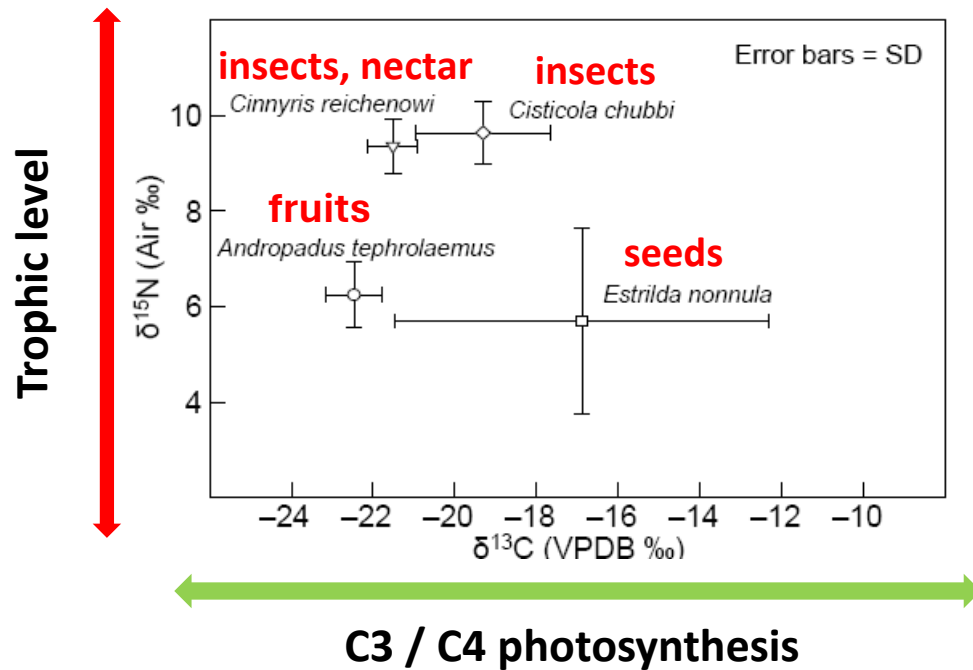


# Occupation of ecological space

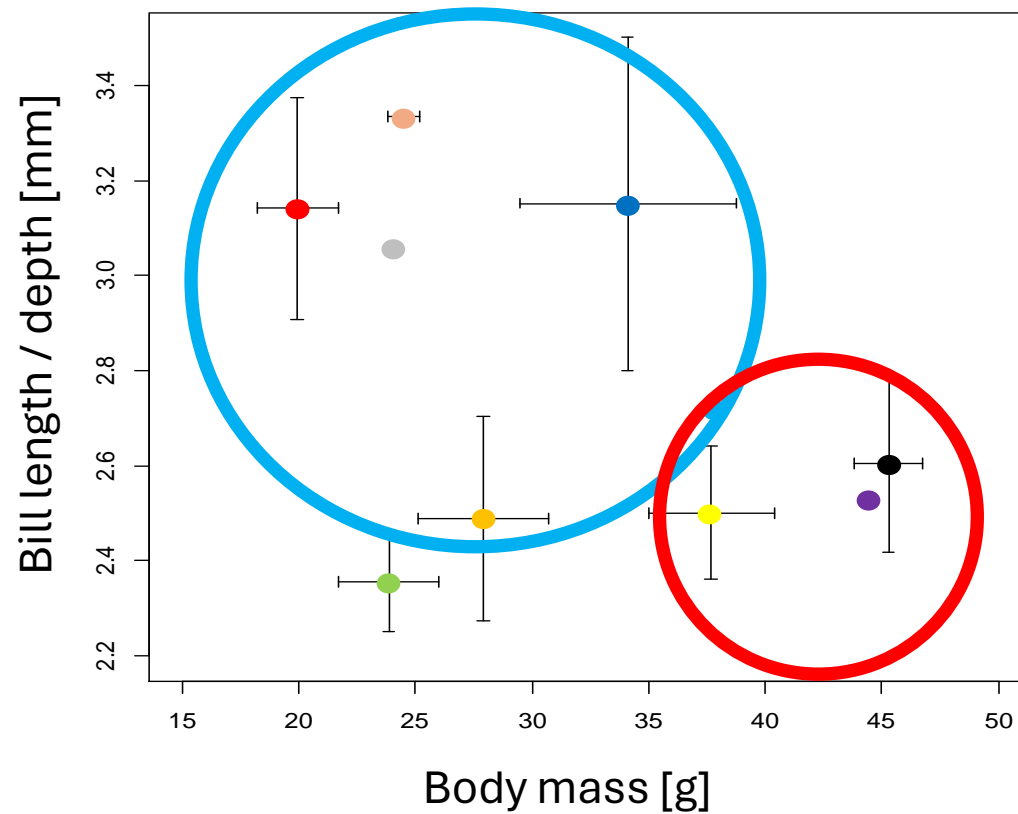
*A species' niche*  
is a part of n-dimensional  
ecological / niche space

Using stable isotopes to trace resource acquisition and trophic position in  
four Afrotropical birds with different diets

Petr Procházka<sup>1\*</sup>, Jiří Reif<sup>2</sup>, David Hořák<sup>3</sup>, Petr Klvaňa<sup>4</sup>, Raymond W Lee<sup>5</sup> and Elizabeth Yohannes<sup>6</sup>



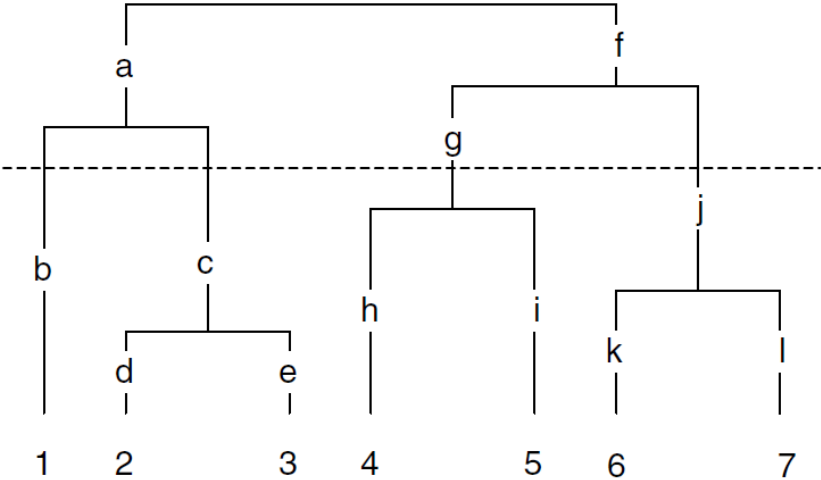
# Assemblages can differ...



REPORT

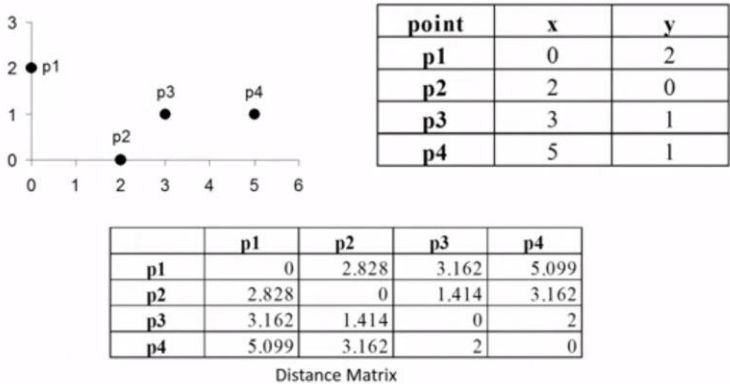
Functional diversity (FD), species richness and community composition

two-dimensions  
dendrograms



**Figure 1** An example functional dendrogram of the relations between species 1–7. The dendrogram has been “cut” by the dashed line at an arbitrary level to assign species to four functional groups: {1}, {2, 3}, {4, 5}, {6, 7}. The total branch length (FD) for species 1–7 is the total length of branches *a*–*l*. The branch length remaining after species 6 and 7 are lost is the length of branches *a*–*i* (branches *j*, *k*, and *l* lost). Horizontal lines on this dendrogram do not contribute to FD.

Euclidean Distance



distance matrix

$$D = \begin{pmatrix} 0 & d_{1,2} & d_{1,3} & \dots & d_{1,s} \\ d_{2,1} & 0 & d_{2,3} & \dots & d_{2,s} \\ d_{3,1} & d_{3,2} & 0 & \dots & d_{3,s} \\ \dots & \dots & \dots & 0 & \dots \\ d_{s,1} & d_{s,2} & d_{s,3} & \dots & 0 \end{pmatrix}$$



**Rao’s quadratic entropy as a measure of functional diversity  
based on multiple traits**

**Botta-Dukát, Zoltán**

**the probability that two individuals randomly  
selected from a community are different**

(similar to Simpson's diversity index, probability that  
two individuals drawn from a community are from  
different species)

I propose an index of functional diversity based on the quadratic entropy of Rao (1982) that incorporates both the relative abundances of species and a measure of the pairwise functional differences between species. Consider an  $S$ -species community characterized by the relative abundance vector  $\mathbf{p} = (p_1, p_2, \dots, p_s)$  such that

$$\sum_{i=1}^S p_i = 1. \tag{1a}$$

Rao (1982) defined quadratic entropy as

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij} p_i p_j$$

(1b)

where  $d_{ij}$  is the difference between the  $i$ -th and  $j$ -th species ( $d_{ij} = d_{ji}$  and  $d_{ii} = 0$ ) and  $FD_Q$  expresses the average difference between two randomly selected individuals with replacements.

# Multidimensional Functional diversity

*Ecology*, 89(8), 2008, pp. 2290–2301  
© 2008 by the Ecological Society of America

## NEW MULTIDIMENSIONAL FUNCTIONAL DIVERSITY INDICES FOR A MULTIFACETED FRAMEWORK IN FUNCTIONAL ECOLOGY

SÉBASTIEN VILLÉGER,<sup>1</sup> NORMAN W. H. MASON,<sup>2</sup> AND DAVID MOUILLOT<sup>1,3</sup>

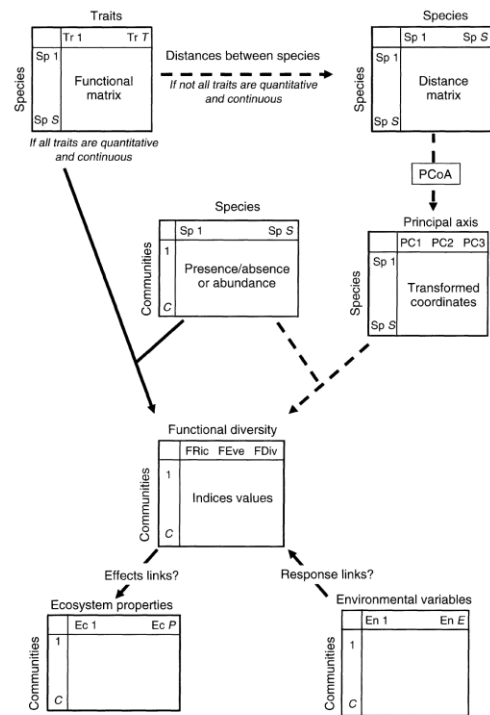


FIG. 5. General framework to study the effect of environmental conditions on functional diversity or the effect of functional diversity on ecosystem properties.

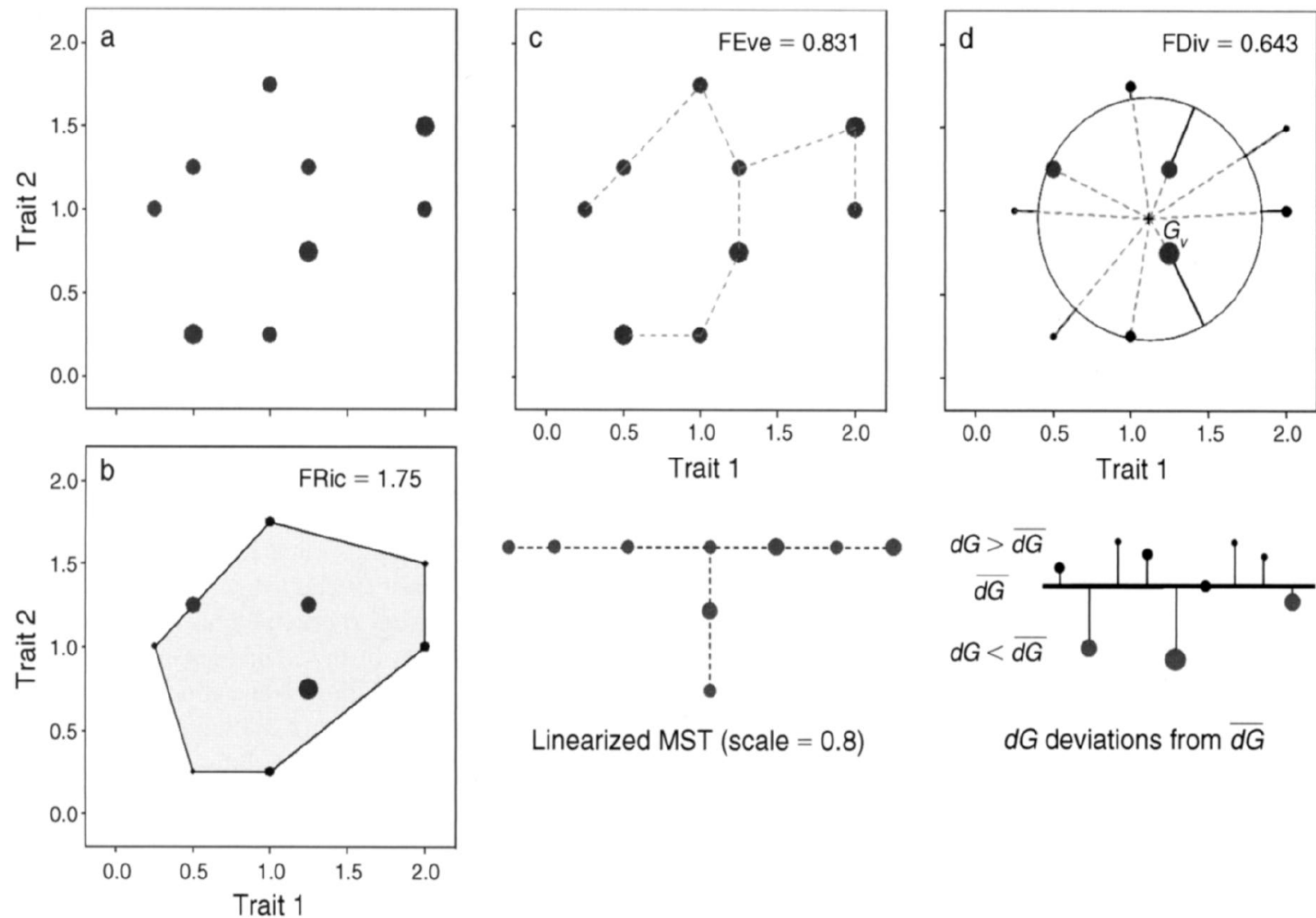
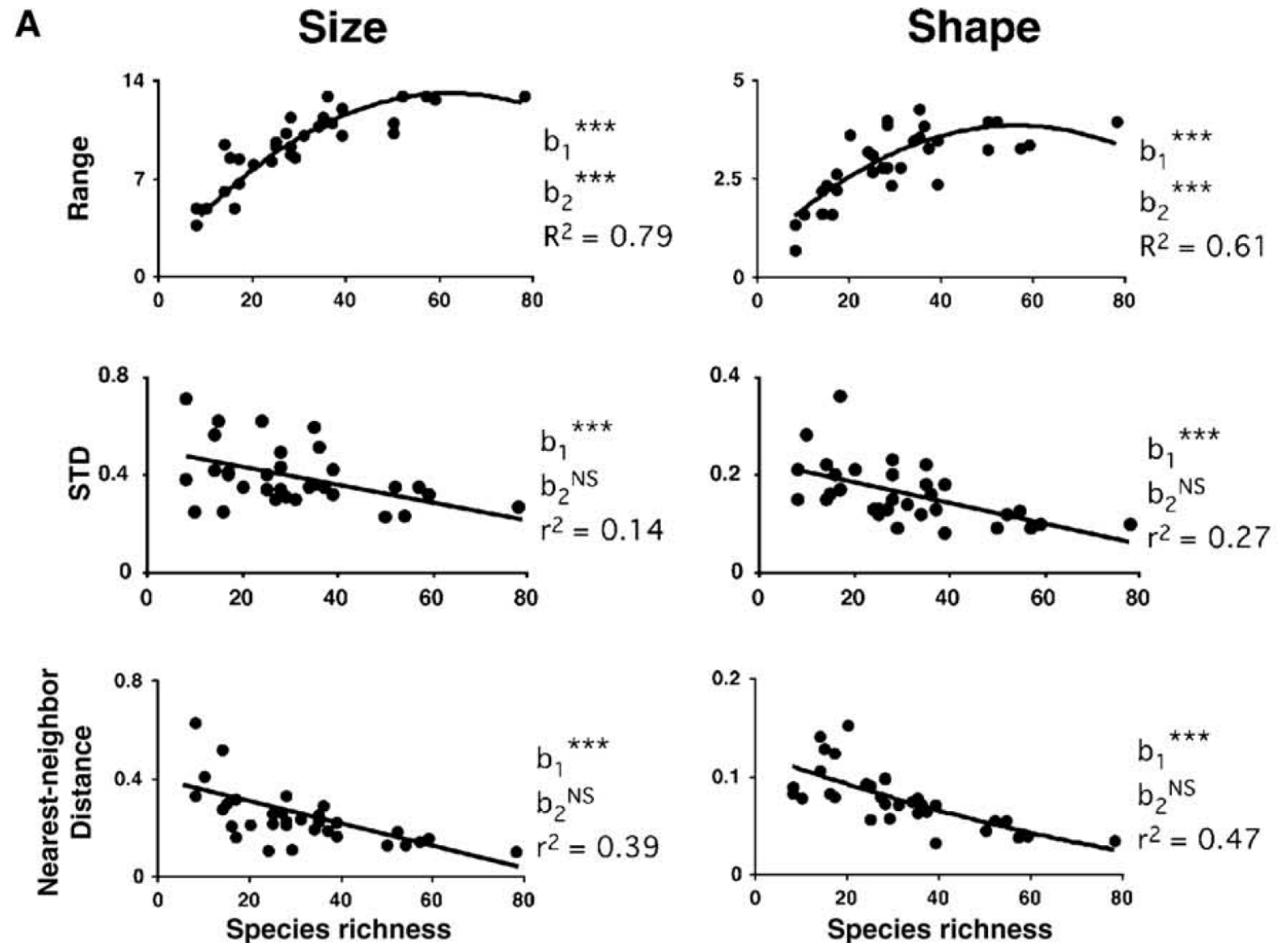


FIG. 1. Estimation of the three functional diversity indices in multidimensional functional space. For simplification, only two traits and nine species are considered. (a) The points are plotted in the space according to the trait values of the corresponding species. Circle diameters are proportional to species abundances. In (b), the convex hull is drawn with a solid black line; the points corresponding to the vertices are black, and the convex hull volume is shaded in gray. The functional richness (FRic) corresponds to this volume. (c) The minimum spanning tree (MST, dashed line) links the points. Functional evenness (FEve) measures the regularity of points along this tree and the regularity in their abundances. For convenience, the tree is plotted stretched under the panel. (d) The position of the center of gravity of the vertices (“G<sub>v</sub>,” black cross), the distances between it and the points representing the species (gray dashed lines), and the mean distance to the center of gravity (large circle with the black line border). The deviation of the distances from the mean corresponds to the length of the black line linking each point and the large circle with the black line border. This distribution is also represented under the panel. The more the high abundances are greater than the mean, the higher the functional divergence (FDiv).

# Functional diversity relates to species richness

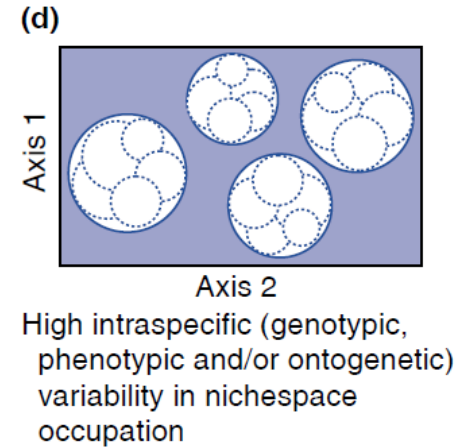
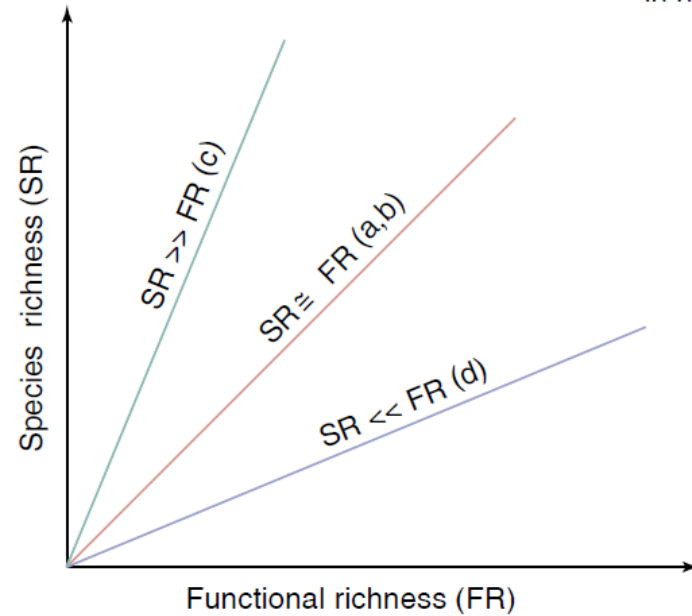
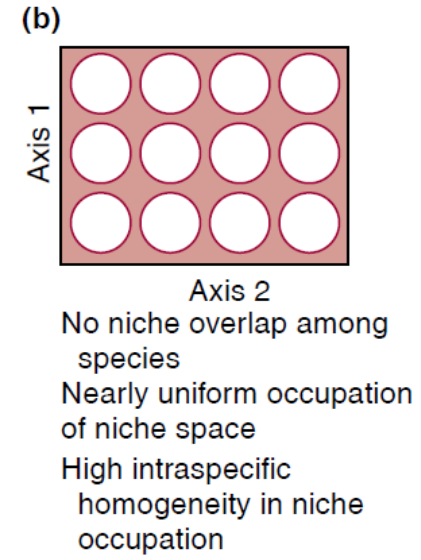
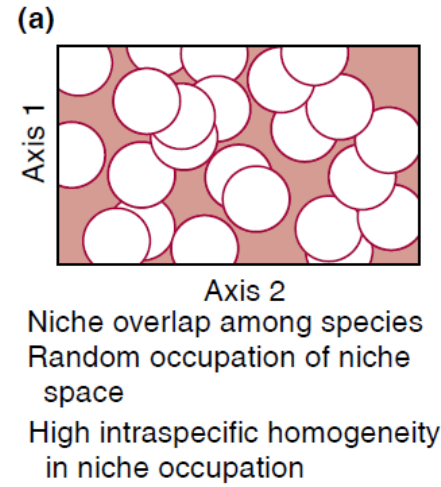
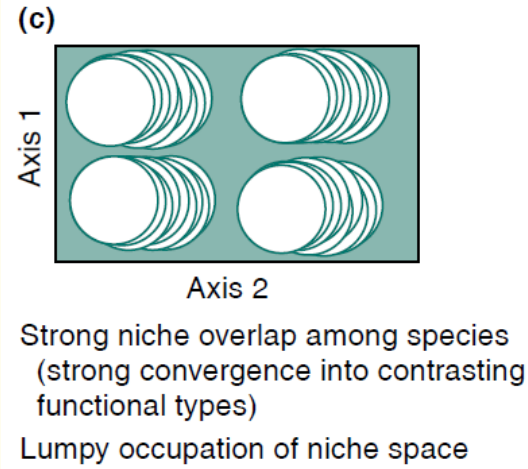
Fig. 3. Relationships of phenetic diversity with species richness (A) and latitude (B) on size (left column) and shape (right column) axes. Range refers to the range of phenetic values among species. STD refers to the standard deviation of minimum spanning-tree segment lengths.  $b_1$  refers to the linear slope,  $b_2$  refers to the quadratic slope,  $r^2$  refers to the coefficient of determination associated with the linear model,  $R^2$  refers to the coefficient of determination associated with the quadratic model. NS refers to a nonsignificant regression whereas asterisks refer to significance. Solid lines indicate situations in which variation in the independent variable accounted for a significant amount of the variation in a measure of phenetic diversity (determined by orthogonal polynomial regression analysis). Experiment-wise error rate was held constant at five percent for measures of size separately from measures of shape by imposing two different Bonferroni sequential adjustments (Rice 1989).



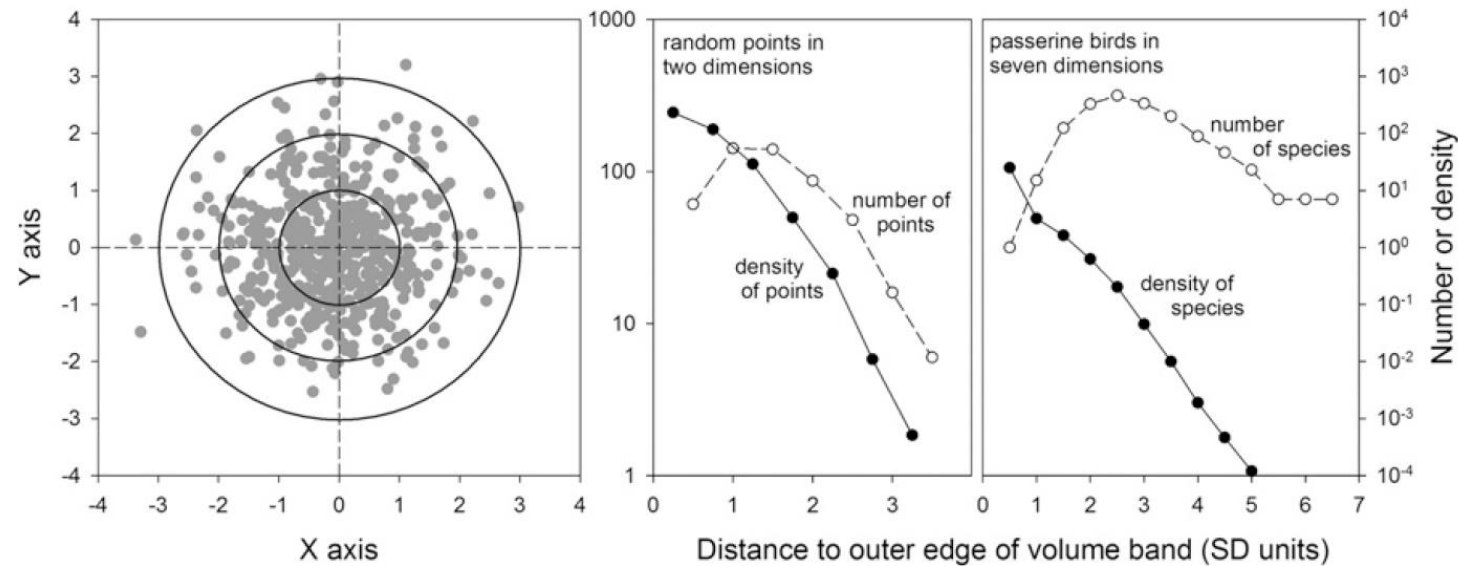


# Vive la différence: plant functional diversity matters to ecosystem processes

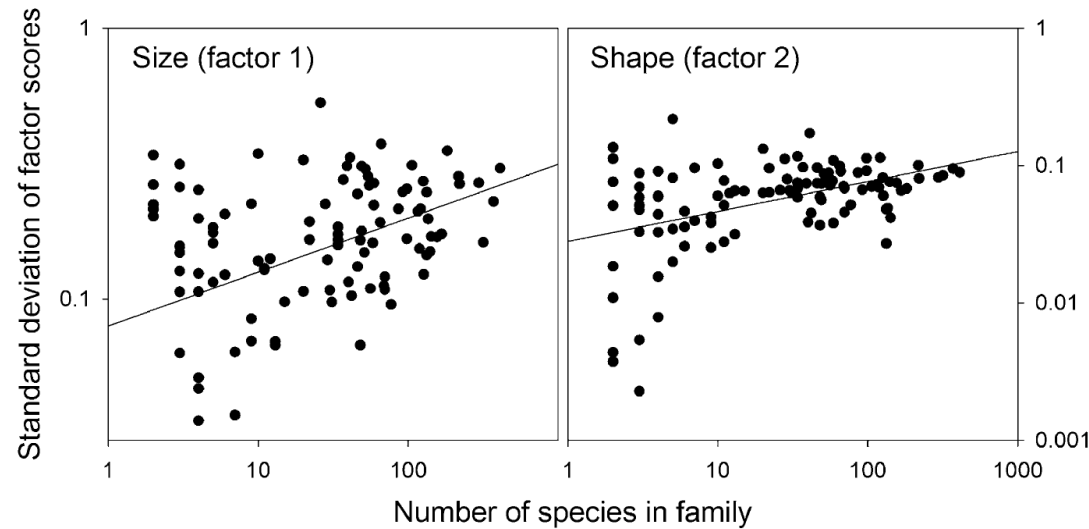
Sandra Díaz and Marcelo Cabido



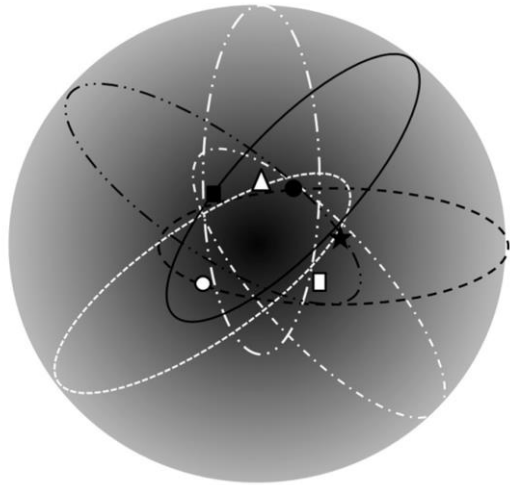
# Occupation of a new part of trait space is weakly related to species richness in passerines



**Fig. 1.** Distribution of species in morphological space exhibits a strong central tendency. *Left:* Symbols represent 500 points whose x and y coordinates were drawn at random from bivariate normal distributions, each axis having a mean of 0 and SD of 1. The circles outline concentric shells with diameters 1, 2, or 3 SD units. Points and densities are shown for 0.5-SD-thick bands. *Center:* The number and density of random points at *Left* within 0.5-unit-thick concentric shells around the centroid. *Right:* Number and density of species of passerine birds within 0.5-SD-unit-thick concentric shells around the centroid of the seven-dimensional morphological space. The volume of progressively more distant concentric shells increases as the power of the number of dimensions. Although the number of species in these shells initially increases with distance from the centroid, the density of species decreases monotonically.



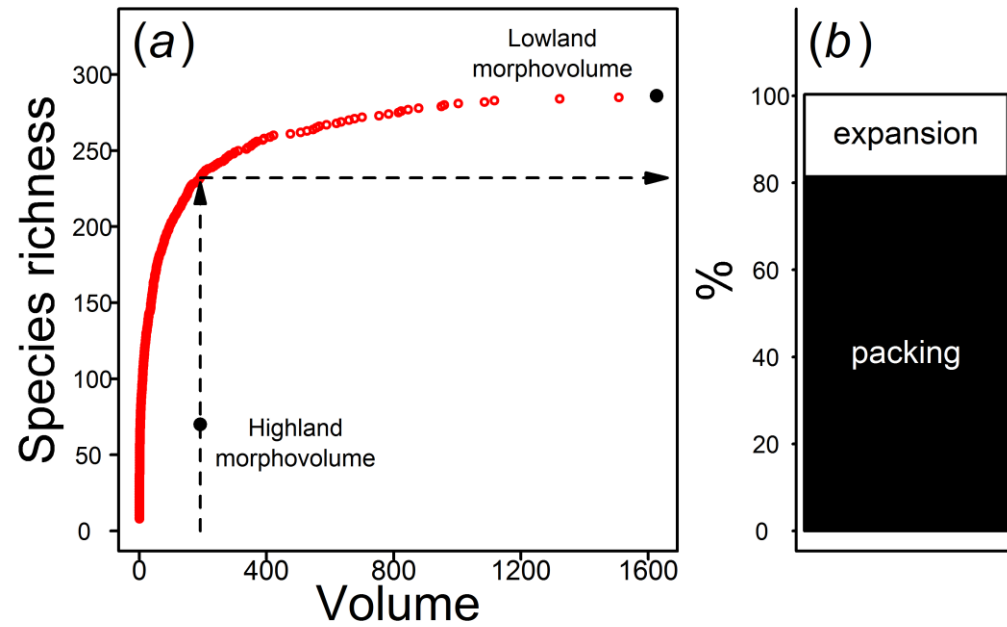
**Fig. 2.** Morphological space is weakly related to the number of species in a taxonomic family. Relationship between the SDs of PC1 and PC2 factor scores ( $s_i$ ) and species richness ( $S_F$ ) within 107 families with two or more species in the sample. The slopes of the regressions of  $\log(s_i)$  on  $\log(S_F)$  were factor 1 = 0.199 ( $\pm 0.042$  SE), factor 2 = 0.218 ( $\pm 0.043$  SE), and between 0.090 and 0.253 for components 3 through 7; all  $P < 0.0001$ , except for PC7,  $P = 0.014$ .



**Fig. 4.** Exploitation of niche space by a variety of species (ellipses) whose niches overlap broadly on a central core of abundant resources, for which a generalized morphology is selected (central tendency), but which are specialized to exploit exclusive peripheral resources (indicated by lighter color of the background toward the margin of the figure, representing the entire resource space in two dimensions).

**Although independently diversified regional faunas exhibit convergent morphology, species are clustered rather than evenly distributed, the volume of the morphological space is weakly related to number of species per taxonomic family, and morphological volume is unrelated to number of species within both regional avifaunas and local assemblages. These results seemingly contradict patterns expected when species interactions constrain regional or local diversity, and they suggest a larger role for diversification, extinction, and dispersal limitation in shaping species richness.**

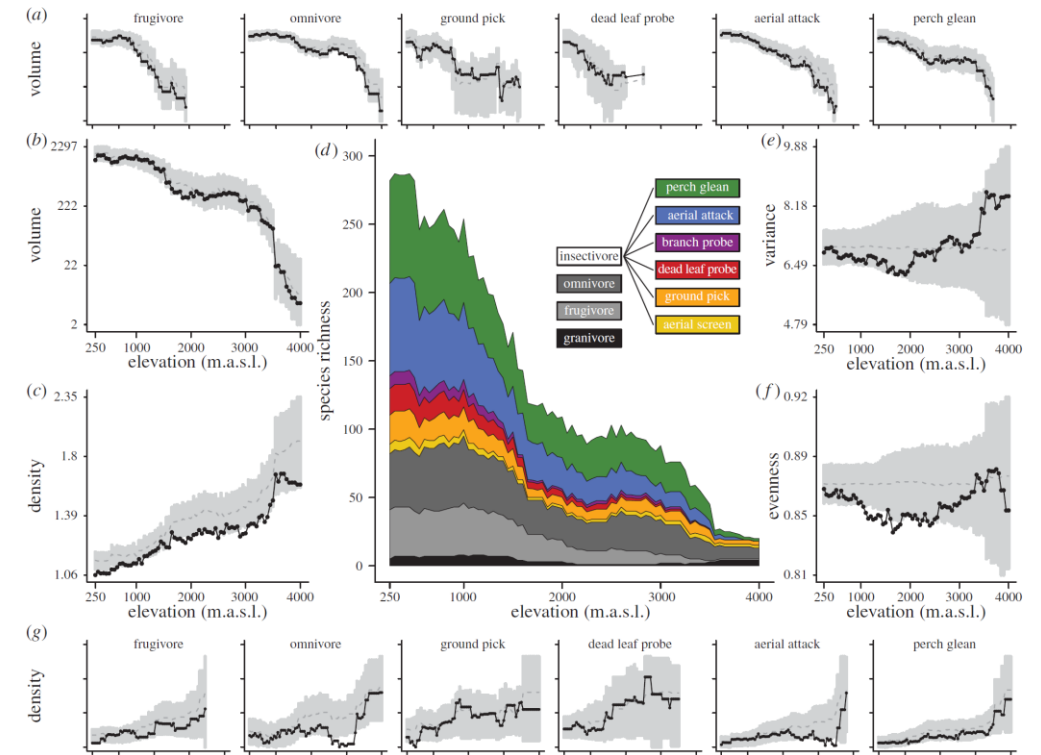




Partitioning assemblage richness into trait packing and expansion components. For illustration purposes we quantify packing and expansion in the most species rich lowland assemblage ( $A_1$ , 300 m,  $N = 286$  species) compared to a selected highland assemblage ( $A_2$ , 3250 m,  $N = 70$  species), representing a four-fold increase in richness (a) black solid points show the observed assemblages in morphovolume/richness space. Red points indicate the decrease in the volume of  $A_1$  after sequentially removing the species contributing the most to morphovolume (from right to left). Arrows indicate the richness at which the morphovolume of  $A_1$  equals that of  $A_2$  (b) the % of the additional species in  $A_1$  attributable to trait packing (i.e. occurring within the volume of  $A_2$ ) or trait expansion (i.e. occurring outside the volume of  $A_2$ ).

## Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds

Alex L. Pigot<sup>1,2</sup>, Christopher H. Trisos<sup>2,3</sup> and Joseph A. Tobias<sup>2,4</sup>



**Figure 2.** The Andes–Amazon elevational gradient in assemblage richness and the structure of functional trait space across passerines and ecological guilds. (a) The volume of morphospace (MCPV) occupied by individual guilds (results are shown for the six most speciose guilds); (b) the volume and (c) density of morphospace (MNND) across passerines; (d) the gradient in species richness and contribution of each ecological guild; (e) the variance in trait values (VAR) and (f) evenness (FEve) of trait spacing across passerines and (g) the density of morphospace within individual guilds. Grey bars (a–c,e–g) show the expected (95% CI) value for each morphospace metric under the null model.

**However,  
some indices  
relate to species  
richness  
by definition!**

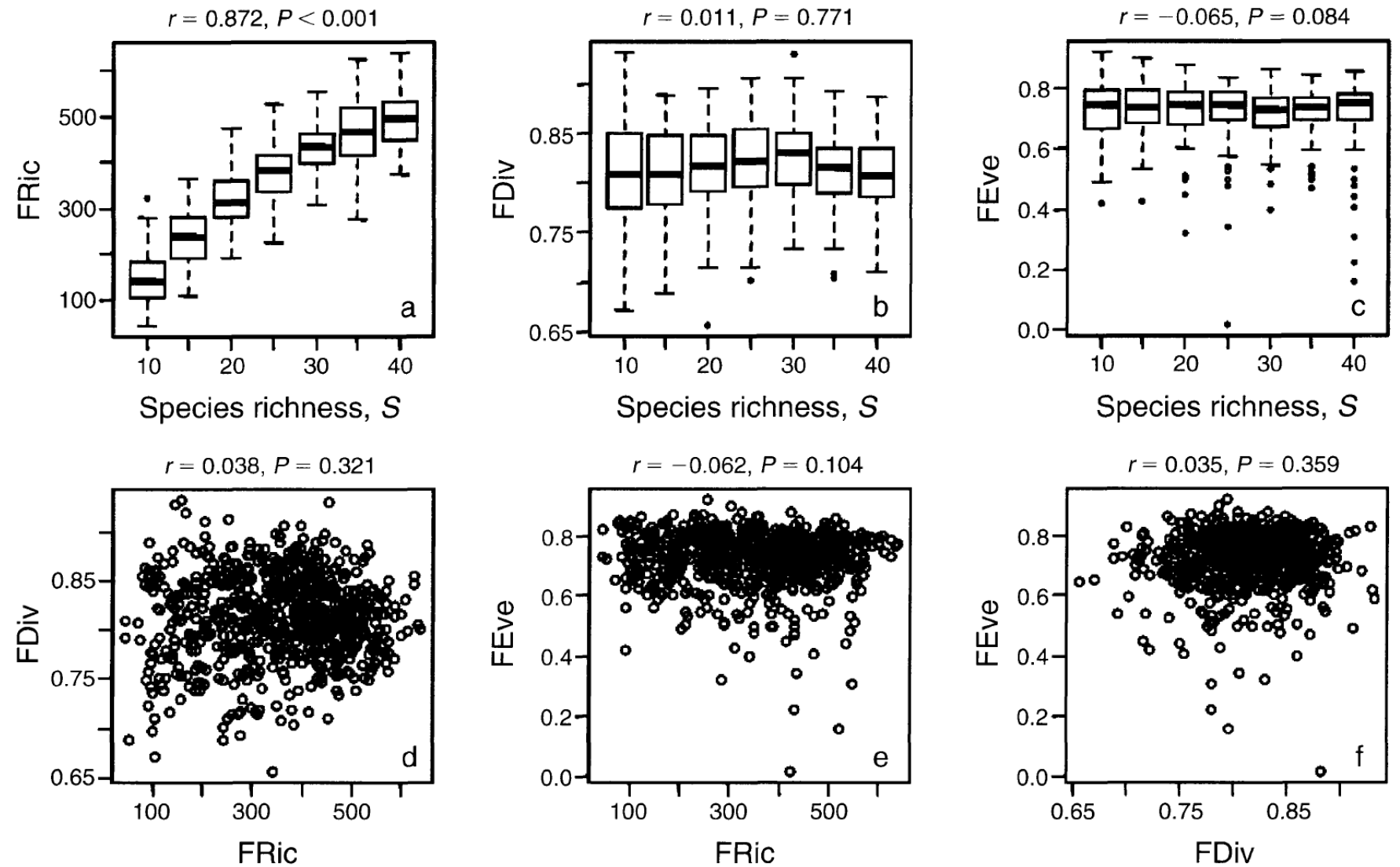
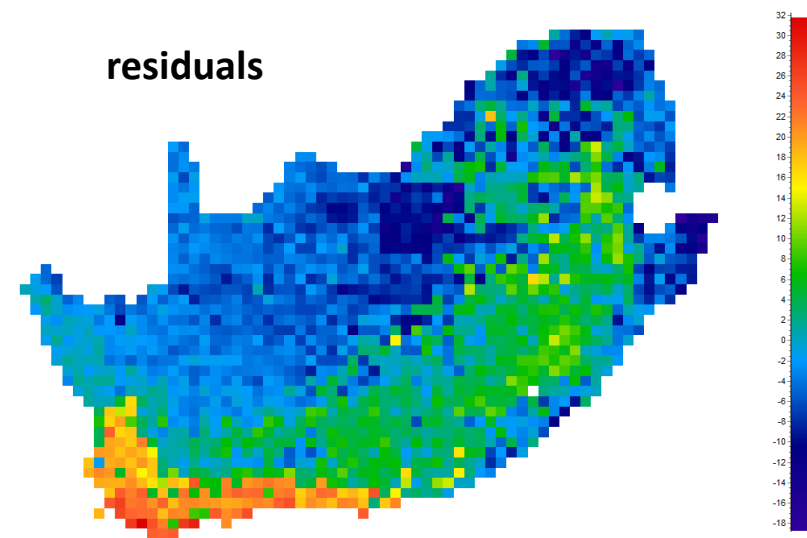
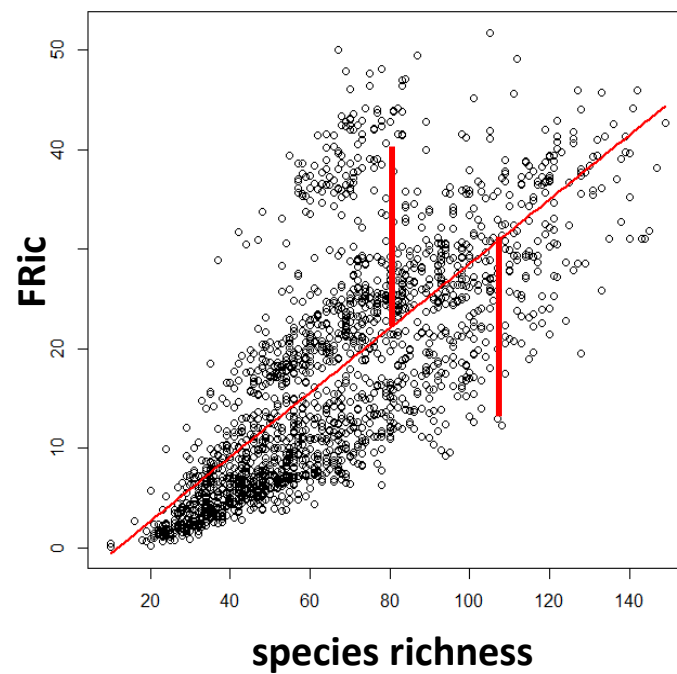
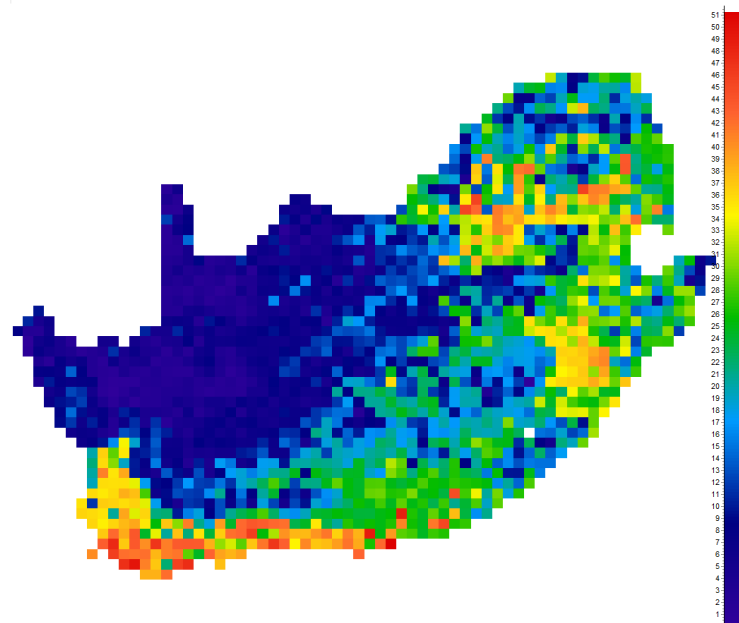
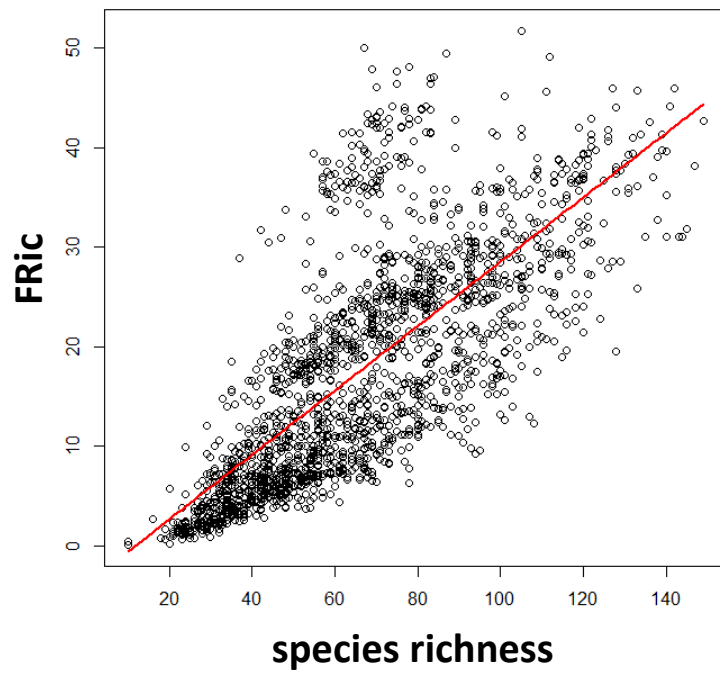


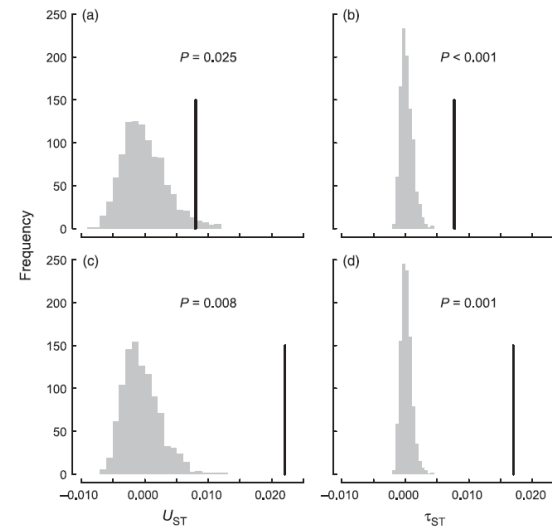
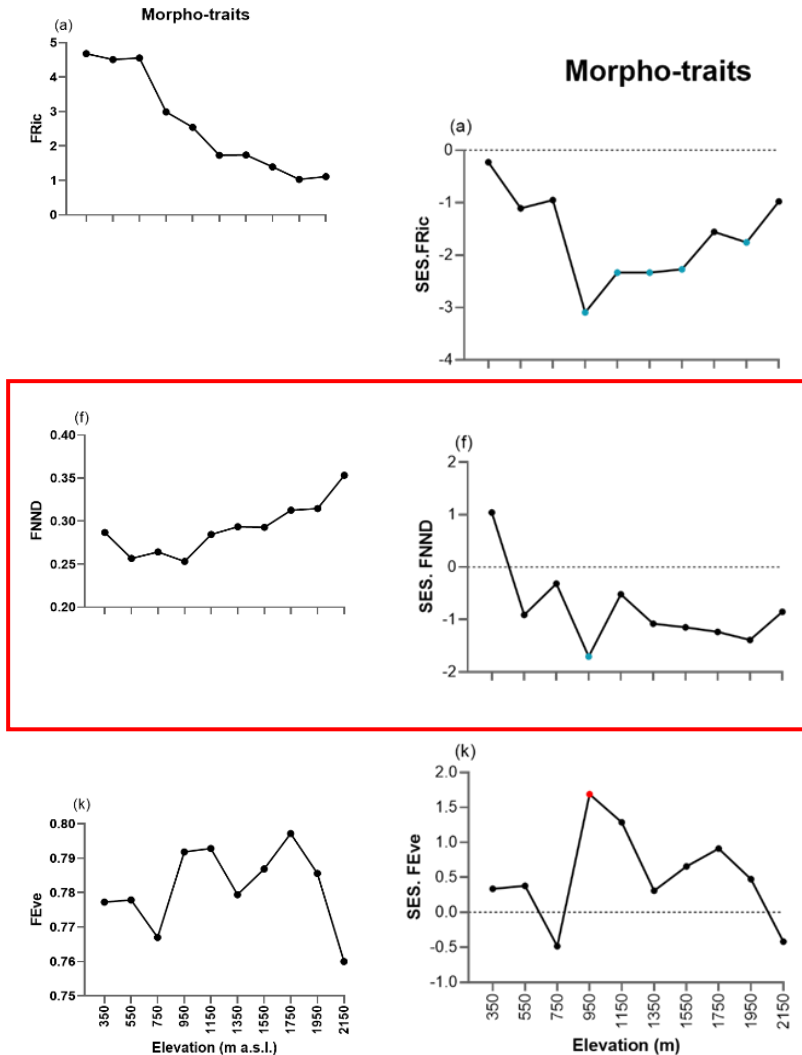
FIG. 4. Properties of the three functional diversity indices for artificial communities. Three traits were considered, and both the coordinates and the abundances of the species were generated under a uniform law (with respective range of 10 and 100). Seven species richness levels ( $S$ ) were considered. Each species richness level was replicated 100 times. For each community, functional richness (FRic), functional divergence (FDiv), and functional evenness (FEve) were estimated. The first three panels (a, b, c) show the relations between each index and species richness. The three last panels (d, e, f) present the correlations between the three indices. Pearson's coefficients of correlation and levels of significance are given above the panels. FRic is the only index correlated to species richness. The three indices are independent of each other.





# Null models: Standard Effect Size

$$SES = (Obs - Exp) / SD_{exp}$$



Selects randomly from the “basket” of available species until it reaches the local species richness, and calculates FD, “1000” times...

Fig. 1. Community-wide trait structure as measured based on all 17 functional traits (panels a and b) or on the two PCA loadings (panels c and d), and both abundance-based metrics ( $U_{ST}$ , panels a and c) and abundance-independent metrics ( $\tau_{ST}$ , panels b and d). In all four cases, 1000 randomizations were performed to construct the null distribution (grey histogram), compared with the observed value (black vertical bar). Co-occurring individuals and species had more similar traits than expected by chance. The observed values were as follows: (a) 0.008, (b) 0.0077, (c) 0.0221, (d) 0.0171.

*Journal of Ecology* 2012, **100**, 690–701

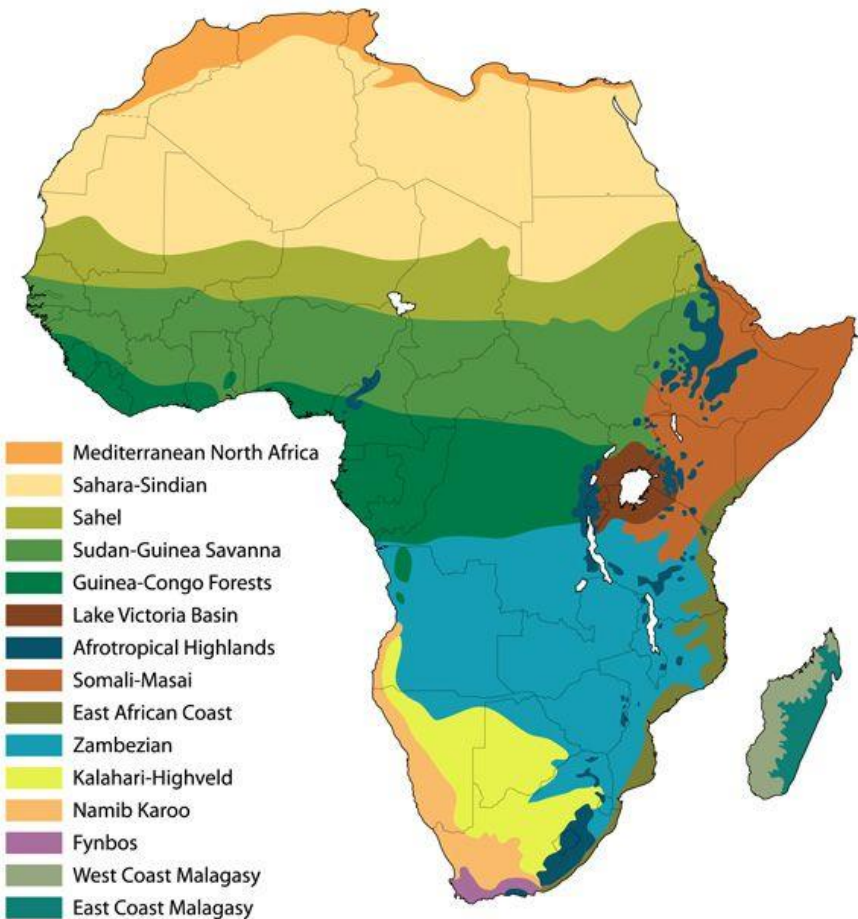
doi: 10.1111/j.1365-2745.2012.01966.x

**Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities**

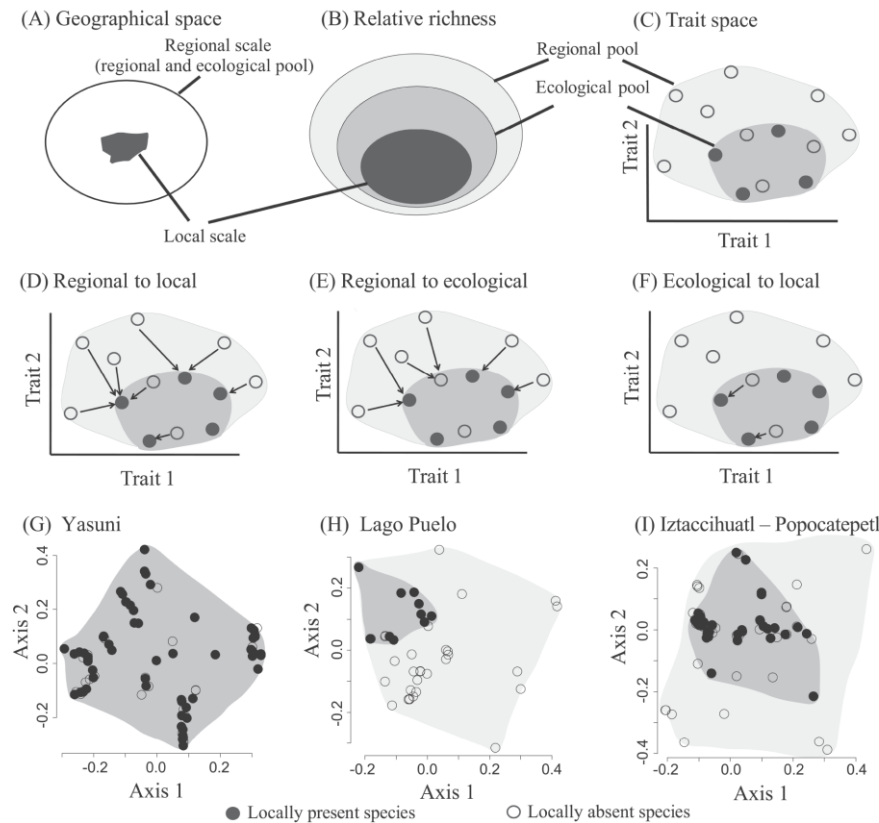
Christopher Baraloto<sup>1,2</sup>, Olivier J. Hardy<sup>3</sup>, C. E. Timothy Paine<sup>4,5</sup>, Kyle G. Dexter<sup>6</sup>, Corinne Cruaud<sup>7</sup>, Luke T. Dunning<sup>8,9</sup>, Mailyn-Adriana Gonzalez<sup>6,10</sup>, Jean-François Molino<sup>11</sup>, Daniel Sabatier<sup>11</sup>, Vincent Savolainen<sup>8,12</sup> and Jerome Chave<sup>6\*</sup>

# Spatial Scaling of Functional Structure in Bird and Mammal Assemblages

Jonathan Belmaker<sup>1,2,\*</sup> and Walter Jetz<sup>1</sup>



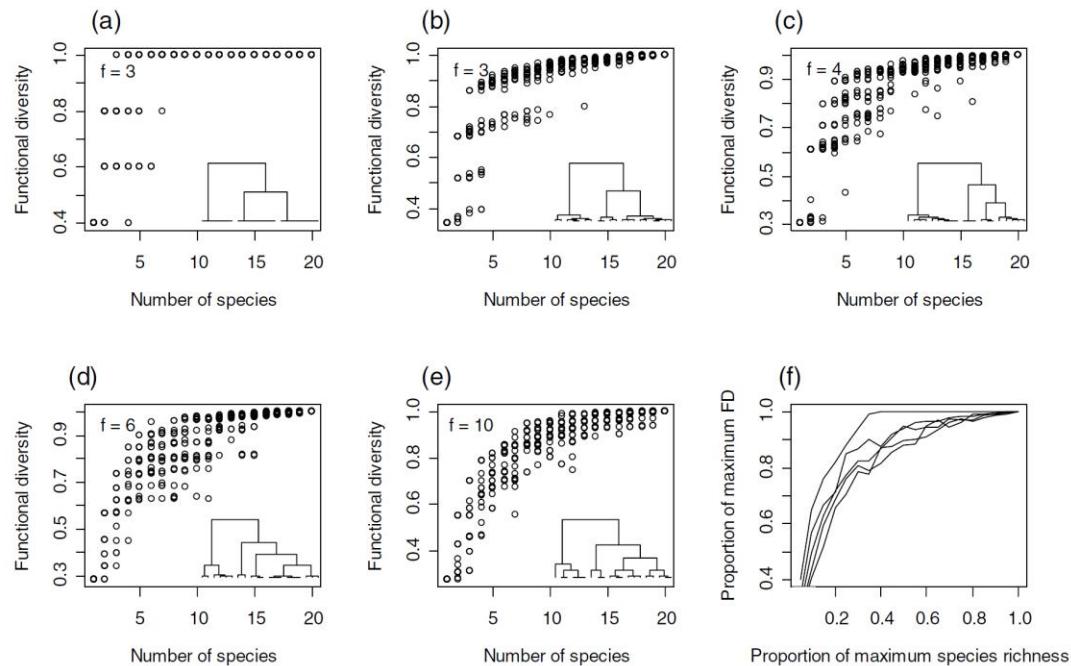
# Pool definition is important!



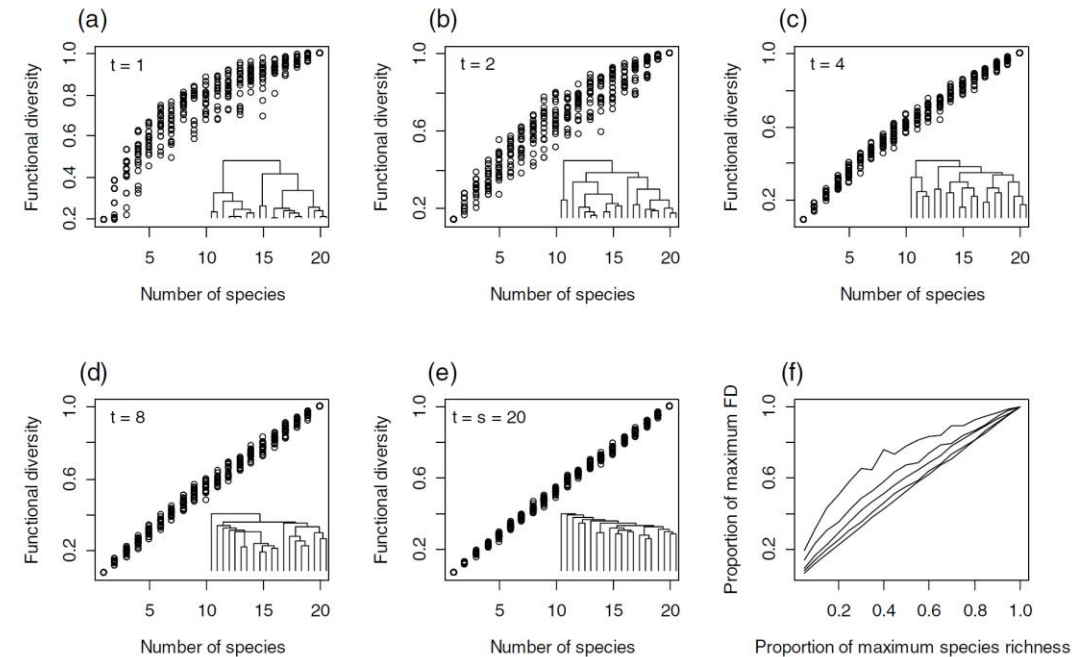
**Figure 2:** The different types of assemblages and species pools used to calculate functional difference. Each circle represents a single species, and therefore adjacent dots represent species that have similar trait values (for simplicity, only two are shown). Only a subset of the regional species (light gray) may have trait combinations that enable them to potentially inhabit a particular local environment. These species delimit the ecological species pool (intermediate gray). However, only part of the ecological pool is actually observed at the local scale (dark gray). Consequently, local assemblages are nested within ecological pools, which are in turn nested within the entire regional pool (A–C). Functional difference can thus be calculated in three ways: between the regional pool and the local assemblage (D), between the regional pool and the ecological pool (E), and between the ecological pool and the local assemblage (F). In D–F, arrows represent the minimum trait distance between the assemblages compared. While the functional difference depicted in D is the most straightforward to calculate (as it does not require estimating the ecological pool), the results are hard to interpret as they represent the effect of two opposing patterns. G–I depict functional differences for three empirical mammalian assemblages (between scales of 200-km diameter and biological inventory): G, Yasuni National Park (00°56'S, 75°24'W); F, Lago Puelo National Park (42°04'S, 71°37'W); I, Iztaccihuatl–Popocatepetl National Park (19°10'N, 98°38'W).

# Functional diversity (FD), species richness and community composition

# Trait types and dimensionality of trait space affects the FD x SD relationship



**Figure 4** Effects of functional clumping  $f$  in trait values (in matrix  $B_f$ ) on the relationships between FD and species richness. The number of clumps along a resource use axis is an analogue of the number of functional groups in a community. (a–e)  $f = 3, 3, 4, 6$ , and  $10$ , respectively, for 20 random draws of species at each species richness level. In (a) all species within a clump are identical; in (b) species differ slightly within clumps. (f) Means of the 20 random draws for each of (a–e) plotted on standardized axes. The four horizontal strata in (b) result from the four combinations of functional clumps that result in very different FD: lowest = {A}, {B}, {C}; low = {B,C}; high = {A,B}, {A,C}; highest = {A,B,C}. FD was standardized to vary between 1 and 0.



**Figure 2** Effects of the number of traits  $t$  that vary among species (the number of traits in matrix  $A_t$ ) on the relationships between FD and species richness. (a–e)  $t = 1, 2, 4, 8, 20$ , respectively, for 20 random draws of species at each richness level from the same functional dendrogram. FD was standardized to vary between 1 and 0. (f) Means of the 20 random draws for each of (a–e) plotted on standardized axes (highest to lowest lines are for  $t = 1, 2, 4, 8, 20$ , respectively). There was one functional dendrogram for each of (a–e), though numerous simulations of different functional dendrograms for the same number of traits show qualitatively identical results.



# ...and of course, different traits tell us different stories...

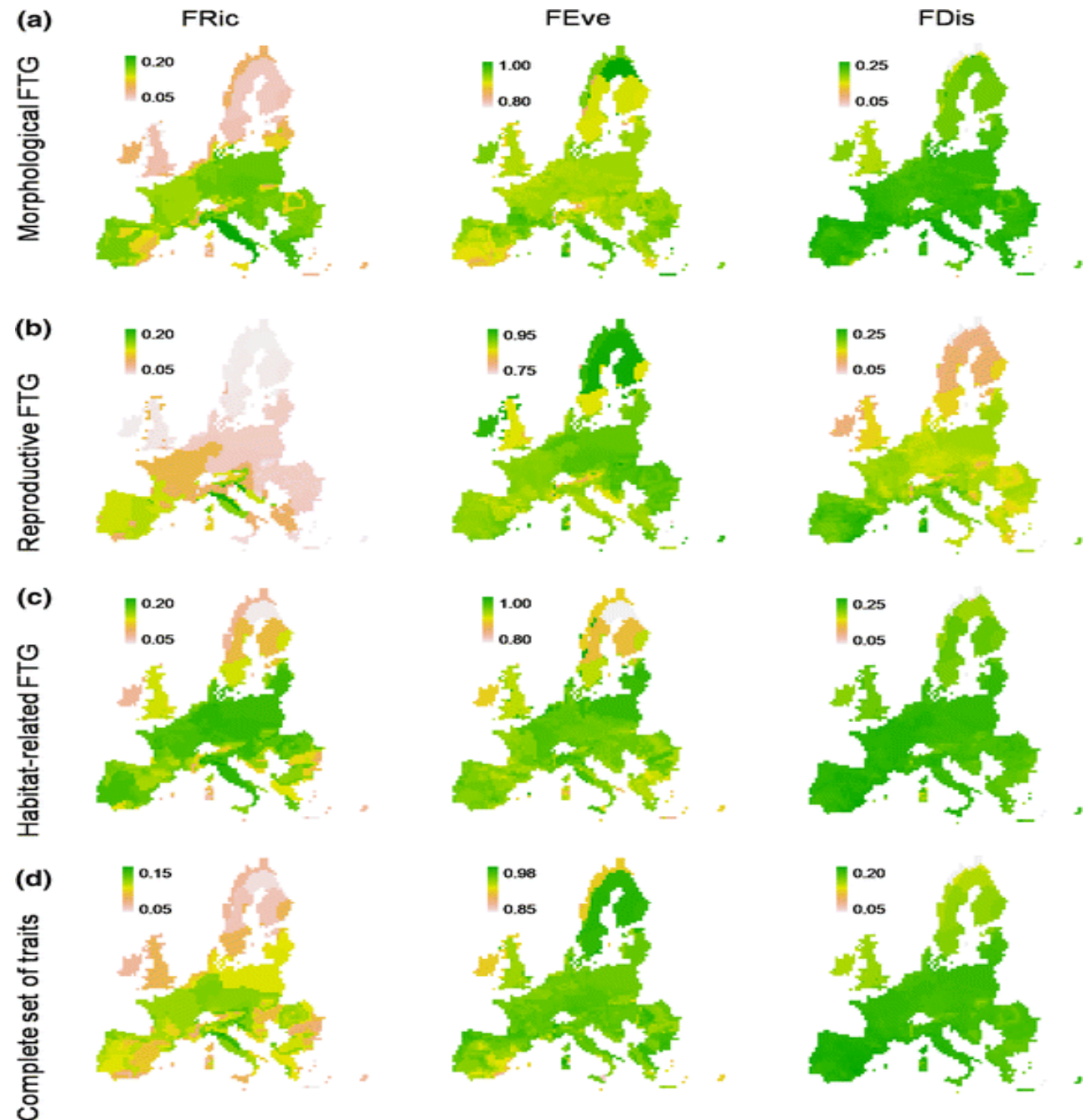
Biodivers Conserv (2016) 25:117–132  
DOI 10.1007/s10531-015-1038-x



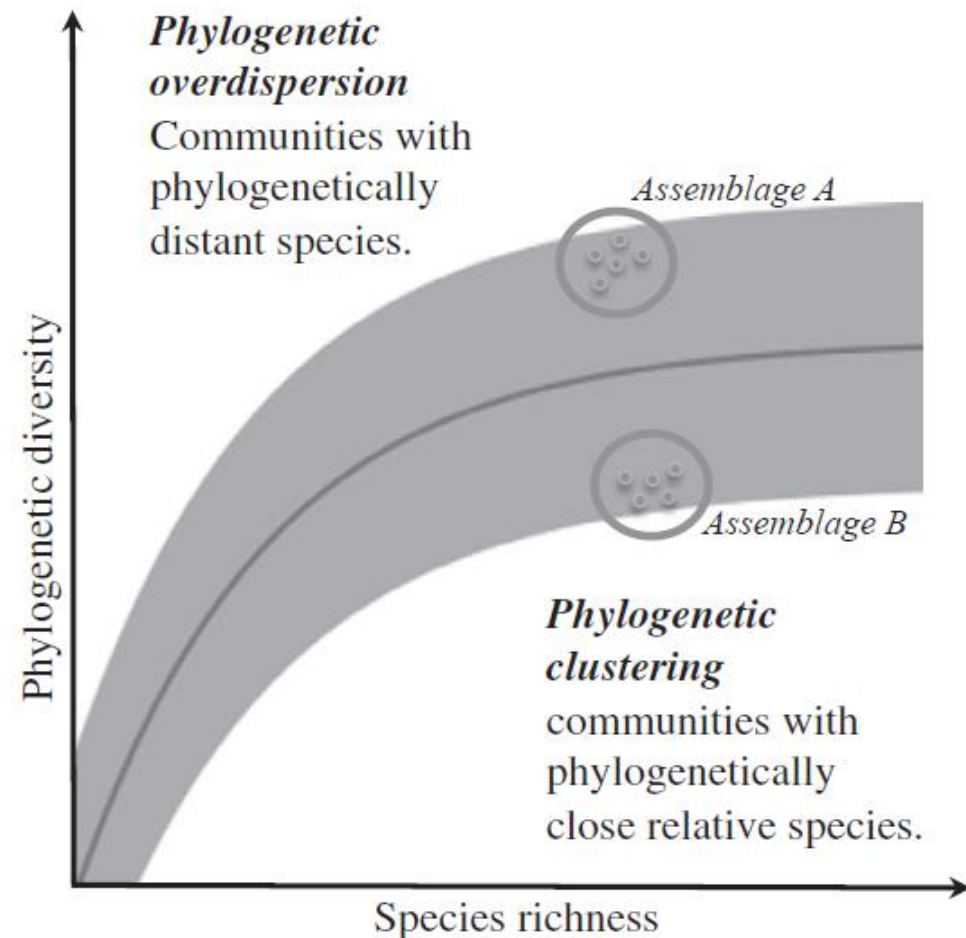
ORIGINAL PAPER

## Different species traits produce diverse spatial functional diversity patterns of amphibians

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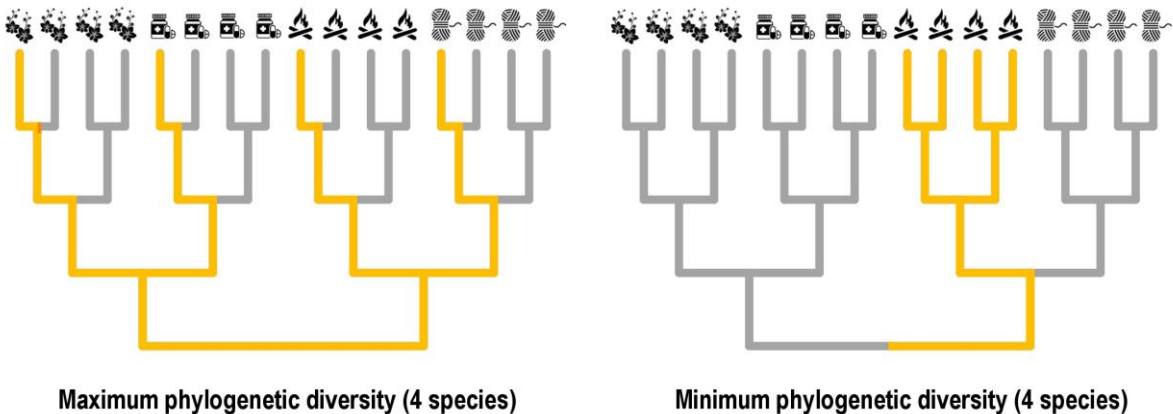


# Phylogenetic diversity



**Table 14.2** Type II metrics of phylogenetic diversity.

Metric	Presence-absence (PA) version	Abundance-weighted (AW) version	Equation	References
Phylogenetic diversity (PD)	Sum of all branch lengths in the portion of a phylogenetic tree connecting the focal set of species (PD, PDn)	For the subset tree, the number of branches multiplied by the weighted mean branch length, with weights equal to the average abundance of species sharing that branch* (PDaw, PDnaw)	$B \times \frac{\sum_i^B L_i A_i}{\sum_i^B A_i}$	PA: Faith (1992) AW: Barker (2002)
Mean phylogenetic distance (MPD) <sup>†</sup>	Mean phylogenetic distance between each pair of species in the focal set (MPD, MPDn)	Mean phylogenetic distance between pairs of individuals (or other units of abundance), excluding same-species pairs (MPDaw, MPDnaw)	$\frac{\sum_m \sum_{n < m} d_{mn} a_m a_n}{\sum_m \sum_{n < m} a_m a_n}$	PA: Webb (2000) AW: Warwick & Clarke (1995)
		Modification: Mean phylogenetic distance between pairs of individuals (or other units of abundance), including same-species pairs	$\frac{\sum_m \sum_n d_{mn} a_m a_n}{\sum_m \sum_n a_m a_n}$	Rao (1982); Warwick & Clarke (1995)
Sum of phylogenetic distances (SPD) <sup>‡</sup>	Sum of phylogenetic distances between each pair of species Equivalent to MPD multiplied by the number of species pairs	Abundance-weighted MPD multiplied by the number of species pairs	$\left( \frac{S(S-1)}{2} \right) \times \frac{\sum_m \sum_{n < m} d_{mn} a_m a_n}{\sum_m \sum_{n < m} a_m a_n}$	PA: Crozier (1997); Helmus et al. (2007) AW: none
Mean nearest neighbour distance (MNND)	Mean phylogenetic distance from each species to its closest relative in the focal species set (MNND, MNNDn)	Weighted mean phylogenetic distance from each species to its closest relative, with weights equal to species' abundance (MNNDaw, MNNDnaw)	$\sum_m \min(d_{mn}) a_m$	PA: Webb (2000) AW: none



# Phylogenetic structure in tropical hummingbird communities

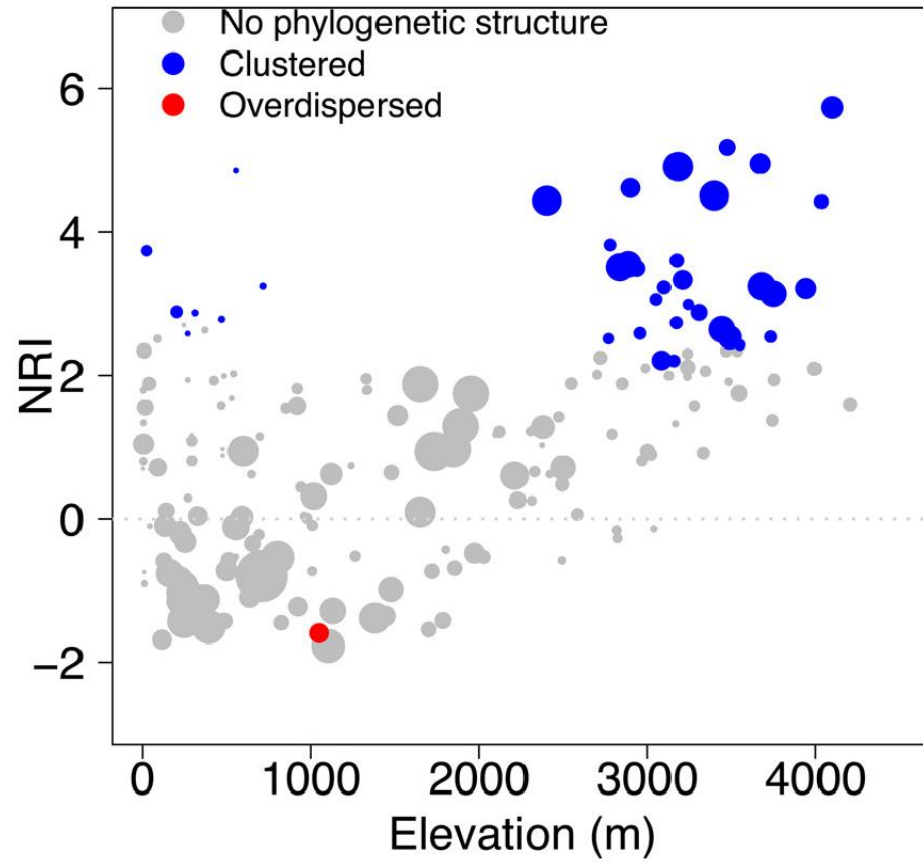
Catherine H. Graham<sup>a,1,2</sup>, Juan L. Parra<sup>a,1,2</sup>, Carsten Rahbek<sup>b</sup>, and Jimmy A. McGuire<sup>c</sup>

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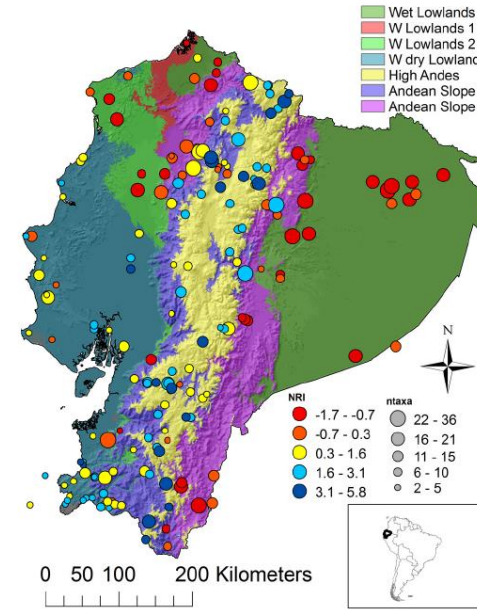
Edited by David B. Wake, University of California, Berkeley, CA, and approved July 29, 2009 (received for review March 19, 2009)

How biotic interactions, current and historical environment, and biogeographic barriers determine community structure is a fundamental question in ecology and evolution, especially in diverse tropical regions. To evaluate patterns of local and regional diversity, we quantified the phylogenetic composition of 189 humming-

birds. Here, we explore the role of biogeographic barriers and environmental filtering in structuring local community composition of hummingbirds by analyzing phylogenetic community structure, PBD and CBD using 189 hummingbird communities distributed across Ecuador. Ecuador provides an ideal setting for



**Fig. 2.** Plot of NRI versus elevation. The size of the circle is proportional to the number of species in the community.



**Phylogenetic overdispersion** in lowlands suggests importance of inter-specific competition in absence of stress factors

**Phylogenetic clustering** in the mountains suggests importance of environmental filtering in environments which are metabolically and aerodynamically more demanding



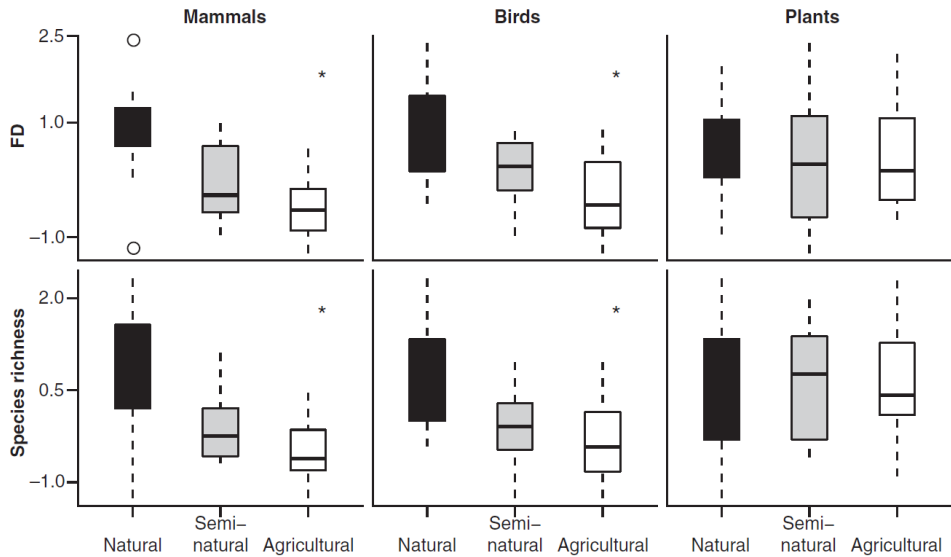
# Is all that important for nature conservation?

Ecology Letters, (2009) 12: 22–33

doi: 10.1111/j.1461-0248.2008.01255.x

## LETTER

### Loss of functional diversity under land use intensification across multiple taxa



**Figure 2** Petchey and Gaston's FD (top row) consistently declines with greater land use intensity for mammals and birds, and remains flat for plants. Species richness (bottom row) demonstrates similar responses to land use intensification. (\* $P \leq 0.05$ , Kruskal–Wallis test).

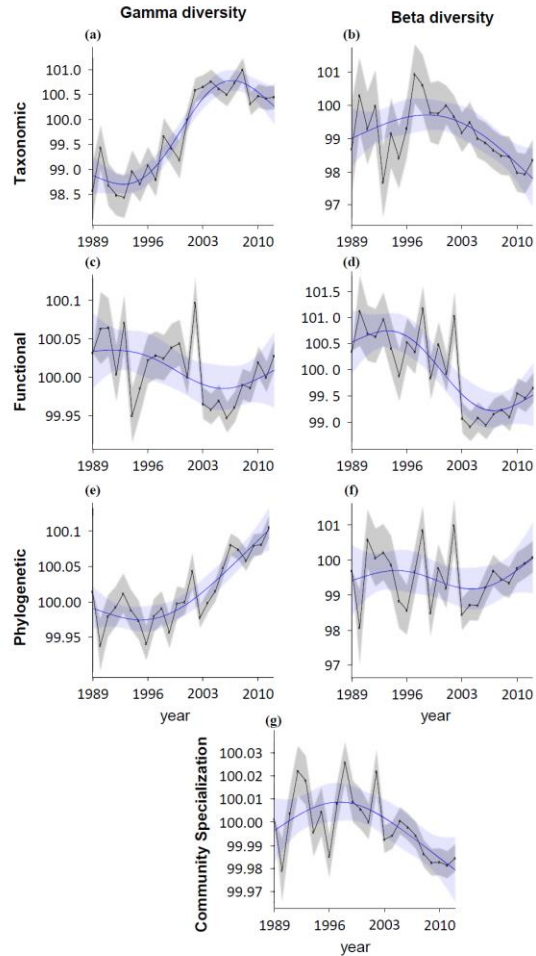


Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2014) 23, 780–788

## RESEARCH PAPER

### Asynchrony of taxonomic, functional and phylogenetic diversity in birds

Anne-Christine Monnet<sup>1</sup>, Frédéric Jiguet<sup>2</sup>, Christine N. Meynard<sup>3</sup>, David Mouillot<sup>4</sup>, Nicolas Mouquet<sup>1</sup>, Wilfried Thuiller<sup>5</sup> and Vincent Devictor<sup>1\*</sup>

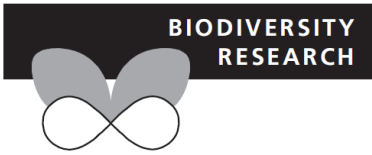


**Figure 2** Temporal trends of diversity facets over 1989–2012. Taxonomic (a) γ-diversity and (b) β-diversity. Functional (c) γ-diversity and (d) β-diversity. Phylogenetic (e) γ-diversity and (f) β-diversity. (g) Community specialization index (CSI). Yearly changes in diversity indices (and their standard error, in the grey band) were obtained from a model accounting for spatial gradients and temporal autocorrelation. Variations in (γ or β) functional and phylogenetic diversities and in CSI were adjusted to variations in (γ or β) taxonomic diversity. The y-axis represents the relative variation of the facet considered compared with its value in 2001 set to 100 as a reference. We also added a nonlinear regression (smoothed line) to describe the major temporal trajectory of each index during the period.



# Multifaceted diversity–area relationships reveal global hotspots of mammalian species, trait and lineage diversity

Florent Mazel<sup>1\*</sup>, François Guilhaumon<sup>2</sup>, Nicolas Mouquet<sup>3</sup>, Vincent Devictor<sup>3</sup>, Dominique Gravel<sup>4</sup>, Julien Renaud<sup>1</sup>, Marcus Vinicius Cianciaruso<sup>5</sup>, Rafael Loyola<sup>5</sup>, José Alexandre Felizola Diniz-Filho<sup>5</sup>, David Mouillot<sup>2,6</sup> and Wilfried Thuiller<sup>1</sup>



# Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe

Laure Zupan<sup>1\*</sup>, Mar Cabeza<sup>2</sup>, Luigi Maiorano<sup>3</sup>, Cristina Roquet<sup>1</sup>, Vincent Devictor<sup>4</sup>, Sébastien Lavergne<sup>1</sup>, David Mouillot<sup>5</sup>, Nicolas Mouquet<sup>4</sup>, Julien Renaud<sup>1</sup> and Wilfried Thuiller<sup>1</sup>

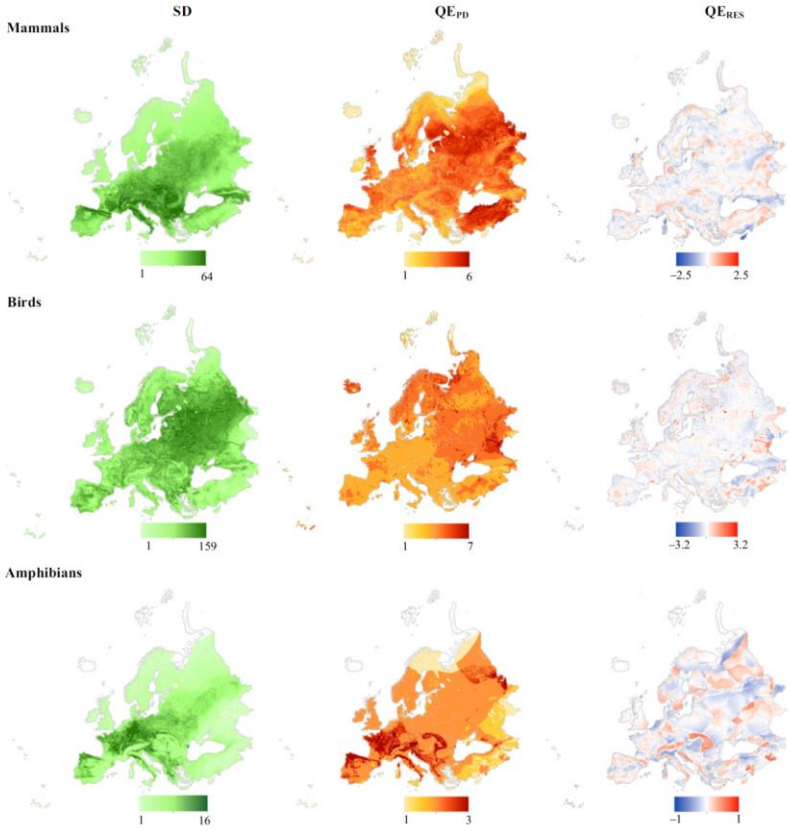
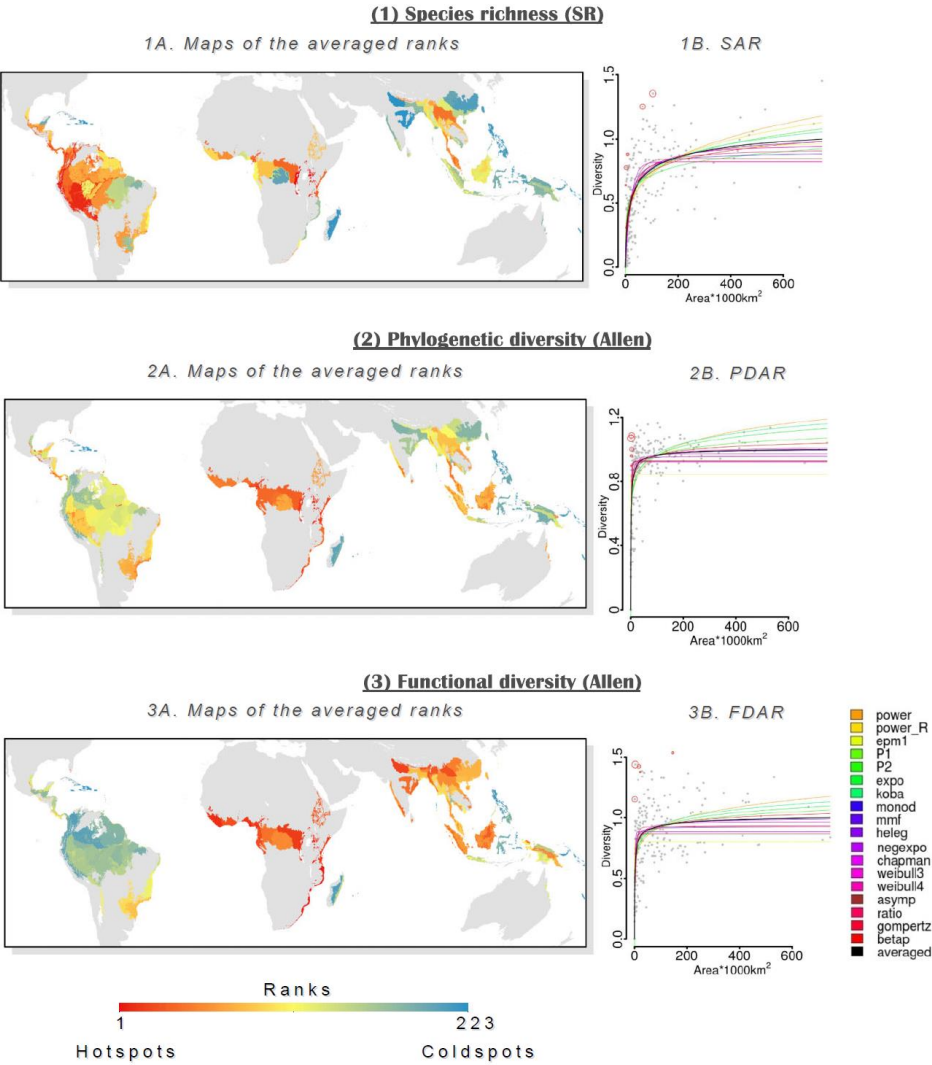


Figure 2 Spatial distribution patterns of species diversity (SD, left column), phylogenetic diversity (QEPD, middle column) and the residuals (QERES, right column) from the spatial regression between QEPD and SD for mammals (upper line), birds (middle line) and amphibians (lower line). For SD, low to high values are represented by a green colour gradient from soft to dark green, the QEPD follows a yellow to red gradient for increasing values of QEPD and for QERES values, the blue colours depict negative values of residuals (lower diversity than expected by the relationship between QEPD and SD) while the red colours depict positive residuals (higher QEPD than expected).

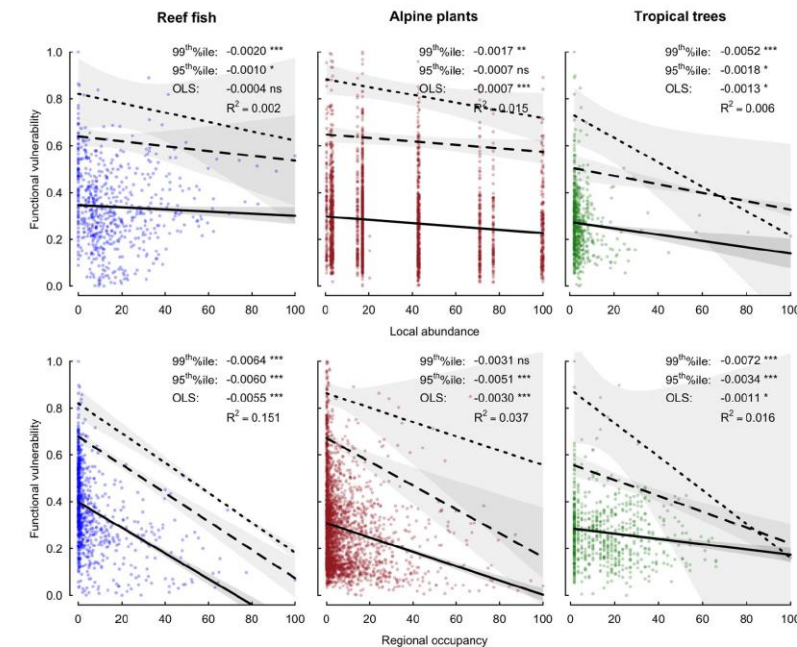


# Rare species have rare functions

In ecological systems most species are rare—that is, represented by only a few individuals or restricted to particular habitats—and are vulnerable to being lost. Yet the ecological consequences of such biodiversity loss are often overlooked and remain controversial. In the best-case scenario, the functions that these rare species provide to their ecosystems might be insured by more common species, which share combinations of functional traits with the rare species, thereby helping to maintain ecosystem functioning despite rare species loss. In the worst-case scenario, rare species would have functional traits that are distinct from those of common species; thus, the functions they support would also be vulnerable to extinction. We examined three highly diverse ecosystems (coral reefs, alpine meadows, and tropical forests) and addressed whether common species would insure against the loss of functions carried by rare species. We demonstrate that highly distinct combinations of traits are supported predominantly by rare species. It is thus not only the quantity but also the quality of biodiversity that matters. Thus, our findings highlight that we need to change how we think about biodiversity in general, and about conservation strategies in particular, by moving beyond the protection of biodiversity per se and beyond focusing on iconic, charismatic, or phylogenetically distinct species, to protecting species that support irreplaceable functional roles and associated services.

## Rare Species Support Vulnerable Functions in High-Diversity Ecosystems

David Mouillot<sup>1,2\*</sup>, David R. Bellwood<sup>2,3</sup>, Christopher Baraloto<sup>4,5</sup>, Jerome Chave<sup>6</sup>, Rene Galzin<sup>7</sup>, Mireille Harmelin-Vivien<sup>8</sup>, Michel Kulbicki<sup>9</sup>, Sebastien Lavergne<sup>10</sup>, Sandra Lavorel<sup>10</sup>, Nicolas Mouquet<sup>11</sup>, C. E. Timothy Paine<sup>12</sup>, Julien Renaud<sup>10</sup>, Wilfried Thuiller<sup>10</sup>



**Figure 2. Functional vulnerability as a function of commonness.** Species commonness is measured as in Figure 1. Functional vulnerability, scaled between 0 and 1, quantifies the lack of functional insurance provided by the rest of the pool to the focal species in terms of functional traits and regional occupancy. Solid lines represent ordinary least square regressions, whereas dashed and dotted lines represent 95th and 99th quantile regressions, respectively. Shaded areas indicate the 95% confidence intervals for each relationship. ns  $p > 0.05$ , \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ . doi:10.1371/journal.pbio.1001569.g002

Species that have low functional redundancy and are likely to support the most vulnerable functions, with no other species carrying similar combinations of traits, are rarer than expected by chance in all three ecosystems.



# SUMMARY

- Traits are related to adaptations, performance, and niche
- They help to understand mechanisms and processes behind the patterns
- There are different traits and they tell different stories
- *Functional biogeography* creates maps of traits
- *Functional diversity* uses traits to estimate ecological space and its structure
- FD might not always add something to species richness, but it often does
- Phylogenetic diversity might help if traits are conservative
- Both FD and PD provide valuable insights for nature conservationists