

Patterns of co-occurrences in a killifish metacommunity are more related with body size than with species identity

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Abstract Body size may be more important than species identity in determining species interactions and community structure. However, co-occurrence of organisms has commonly been analysed from a taxonomic perspective and the body size is rarely taken into account. On six sampling occasions, we analysed patterns of killifish co-occurrences in nestedness (tendency for less rich communities to be subsamples of the richest), checkerboard structure (tendency for species segregation), and modularity (tendency for groups to co-occur more frequently than random expectation) in a pond metacommunity located in Uruguay. We contrasted co-occurrence patterns among species and body size-classes (individuals from different species were combined into size categories). The analysis was performed at two spatial scales: ponds (communities) and sample units within ponds. Observed nestedness was frequently smaller than the null expectation, with significantly greater deviations for body size-classes than for species, and for sample units than for communities. At the sample unit level, individuals tended to segregate (i.e. clump into a checkerboard pattern) to a larger extent by body size rather than by taxonomy. Modularity was rarely detected, but nevertheless indicated a level of taxonomic organization not evident in nestedness or checkerboard indices. Identification of the spatial scale and organization at which ecological forces determine community structure is a basic requirement for advancement of robust theory. In our study system, these ecological forces probably structured the community by body sizes of interacting organisms rather than by species identities.

Key words: body size, coexistence, community structure, negative co-occurrence, nestedness.

INTRODUCTION

Community biodiversity is determined by mechanisms that enhance or reduce coexistence (Morin 2011). The underlying processes have been main foci of research in ecology (Kneitel & Chase 2004; Morin 2011) and it is becoming increasingly clear that relevance of each mechanism depends on the scale at which a system is analysed (Violle *et al.* 2012). Large-scale patterns are often related to environmental filtering of species, whereas small-scale patterns are likely to be more affected by interspecific interactions (Weiher & Keddy 1999; Webb *et al.* 2002). The prevailing view is that species are basic elements that determine community structure and dynamics

(Morin 2010). However, non-taxonomic functional elements of biotic communities, such as functional feeding groups, life history strategies and habitat guilds, may be more relevant to community structuring (Marquet *et al.* 2004; Shipley 2010). Thus, groups of organisms of similar body size, but not necessarily of the same species, may in some contexts be more appropriate units for the analysis of community organization and the underlying mechanisms (Raffaelli 2007; Arim *et al.* 2010).

Body size has long been recognized as a main determinant of population and community organization (e.g. Elton 1927; Hutchinson 1959; Woodward *et al.* 2005). Size affects energetic demands, growth rates, edibilities, spectra of potential predators, home range sizes and most attributes related to the ecology of organisms (McNab 2002; Brown *et al.* 2007; Rooney *et al.* 2008; Arim *et al.* 2010). Although each

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species description includes information on body size, intraspecific variation in size may swamp interspecific differences (Woodward *et al.* 2005; Violle *et al.* 2012). Furthermore, body sizes of individuals may be more important for coexistence than species identity (Gotelli 1997). Body size has a role in direct interference interactions (Johnson 1991) and frequently determines whether or not smaller individuals will be consumed by those that are larger (Woodward & Hildrew 2002; Brose *et al.* 2006). Stronger predatory interactions are expected the larger the difference in body size between two organisms (Emmerson *et al.* 2005), but the reverse may be true for competition (Ritchie 2010). Thus, body sizes may be determinants of temporal or spatial segregation in the occurrences of organisms (Kohda *et al.* 2008). Organisms of closely similar body sizes may frequently co-occur by forming concentrations in preferred common environmental conditions with similar environmental filtering and microhabitat occurrences (Violle *et al.* 2012). Conversely, the frequency of coexistence may be reduced by intense competition (Kohda *et al.* 2008; Violle *et al.* 2012). In summary, the prevailing opinion is that community structure is often determined by processes operating among size-classes with underlying mechanisms that do not necessarily relate to species identities (Gotelli 1997). Nevertheless, patterns of organismic coexistence across communities have been analysed mostly with regard to species or higher-order levels of organization (Gotelli & McCabe 2002; Ulrich & Gotelli 2007a).

Coexistence patterns have frequently been analysed in relation to nestedness and negative co-occurrence structure (Ulrich & Gotelli 2007a), and more recently in terms of modularity (Olesen *et al.* 2007). Nestedness describes the tendency of species composition in less rich communities to be subsamples of the richest communities (Ulrich *et al.* 2009). Negative co-occurrence index analysis attempts to quantify the tendency of species segregation patterns in space to develop occurrence structures that resemble checkerboards or patchworks (Ulrich & Gotelli 2007a). Modularity refers to the existence of groups of species or size-classes that co-occur with each other more frequently than random expectation. While systematic associations among nestedness, checkerboard structure and modularity are to be expected, they reflect complementary attributes of metacommunity structure (Ulrich & Gotelli 2007a; Fortuna *et al.* 2010).

In this study, we analysed spatial co-occurrences in a metacommunity of killifishes in temporary ponds; co-occurrences were considered in terms of (i) taxonomic identity and (ii) body size. Taking into account the putative effect of spatial scale on mechanisms determining coexistence, we conducted the analysis at

two contrasting spatial scales: (i) ponds and (ii) sample units within ponds.

METHODS

Study area

We surveyed 52 ephemeral ponds between Consejo Stream and Sarandi del Consejo Stream (34°15'19"S, 53°58'56"W) in the Castillos Lagoon basin, Rocha Department, Uruguay. These ponds occurred in grassland ground-depressions and had maximum depths of 30 cm. They were full of water in autumn and winter, and quickly dried out with increasing temperatures in spring. The organisms in this set of temporary ponds may be viewed as a metacommunity in which the spatial location of ponds was constant among years, local communities were related to local conditions and movement of individual organisms allowed migration among communities (Laufer *et al.* 2009; Arim *et al.* 2011; Ziegler *et al.* 2013). The ponds supported a diversity of vertebrates: four amphibian species (as larvae) and ephemeral populations of killifish species (*Cynopocilus melanotaenia*, *Austrolebias luteoflammulatus*, *A. viarius*, and *A. Cheradophilus*, Cyprinodontiformes, Rivulidae). Detailed descriptions of the study area and the vertebrate community are provided by Laufer *et al.* (2009) and Arim *et al.* (2011). Killifish eggs are drought resistant stages that survive through the dry period (summer). Other fishes occurred in the system, but were rarer (less than 1% of the individuals collected).

Biological sampling

Temporary ponds were sampled eight times for killifishes in the period May 2006 to August 2012 (see Table 1). Samples were taken with five equidistant hand-net sample units (15 × 20 cm, 1 mm mesh) along two transects within each pond (laid out across the maximum and minimum diameters of the ponds). At each sample position, the hand-net was moved thrice horizontally following a straight line and thrice vertically from the pond bottom to the surface. The distance between sample units increased with increasing pond size. The numbers of samples in small ponds were smaller than the numbers of sample units in larger ponds because we always located sample sites in small ponds at least 2 m apart in order to reduce interference among sample units (Krebs 1999). In larger ponds, sample sites were no more than 10 m apart; this sampling criterion was adopted to capture the elevated heterogeneity in larger ponds (Krebs 1999). Killifishes were euthanized with a lethal dose of 2-phenoxyethanol and preserved in formalin solution (10% vol/vol). Fishes were classified to the species level following Costa (1995, 2006). We measured the lengths from snout to peduncle, body depths and body widths to estimate biovolumes. Standard lengths (STL) were measured only on individuals collected in 2006. The biovolumes of the fish were estimated with an allometric relationship derived from measurements of individuals

Table 1. Standardized Nestedness (ZNODF), Checkerboard Structure (ZCS), and Modularity (ZMOD) for species (Tax = taxonomic identity) and body size-classes (Size) analysed at the community (Comm) and sample unit levels (SU)

		2006 May		2006 June		2008 August		2009 June		2011 August		2012 August		Mean (SD)	
Total ponds (N_P) and Killifishes (N_K)		$N_P = 14$ $N_K = 498$		$N_P = 22$ $N_K = 172$		$N_P = 18$ $N_K = 1070$		$N_P = 10$ $N_K = 166$		$N_P = 26$ $N_K = 303$		$N_P = 25$ $N_K = 763$			
Z-Index	Scale	Tax	Size	Tax	Size	Tax	Size	Tax	Size	Tax	Size	Tax	Size	Tax	Size
Nestedness	Comm	1.17	-0.92	0.47	-3.1 R	-0.22	0.00	0.68	-2.33	-2.2 C	-1.02	-0.35	-2.1 C	-0.08 (1.19)	-1.58 (1.13)
	SU	0.85	-7.2	0.75	-5.7 C	2.3 R	-7.89	-2.7 C	-2.6 C	-0.82	-0.25	-4.2 C	-3.6 C	-0.64 (2.44)	-4.54 (2.92)
Checkerboard	Comm	-0.94	1.59	0.8	1.31	1.69	0.00	-0.62	2.45	2.24	2.3	2.32	0.62	0.92 (1.42)	1.38 (0.95)
	SU	-0.82	5.3	-0.84	5.96	0.86	11.3	2.29	4.09	0.88	5.97	4.48	2.26	1.14 (2.02)	5.81 (3.03)
Modularity	Comm	-0.41	-0.95	-1.32	0.24	0.46	-2.5	NA	-0.1	-0.5	-0.38	0.43	NA	-0.27 (0.74)	-0.74 (1.08)
	SU	2.38	0.51	1.10	-0.08	0.63	-0.16	0.2	-0.06	2.57	-0.14	0.51	NA	1.23 (1.01)	0.01 (0.28)

N_P = total number of ponds with killifishes, N_K = total number of killifish sampled. **C** and **R** indicate cases where nestedness was only significant in columns or rows, respectively. Grey cells indicate significant Z values at $P < 0.05$.

collected on other occasions (biovolume = 0.0124 × STL^{3.166}; $F_{1,2663} = 9.6e + 04$; $P < 0.0001$; $R^2 = 0.973$).

Co-occurrence patterns

To analyse the effect of organism size on community structure, we sorted all individuals by biovolume and then grouped them into a number of size-classes that exactly matched the number of species observed in each sample. For each sampling occasion, we constructed four presence (1)/absence (0) matrices. Two matrices arranged ponds (communities) in columns and species identities in rows, or body size-classes in rows independently of species identity. Body size-classes were constructed by rank ordering from the smallest to the largest individual and assigning an equal number of individuals to each size-class. The total number of size-classes was equal to the total number of species identified. Two additional matrices were constructed with the same structure but with sample units arrayed in each row rather than ponds (communities).

For each matrix type and sampling occasion, we estimated checkerboard structure, nestedness and modularity. Checkerboard structure, which is the degree of negative co-occurrence among species or size-classes, was estimated with the C-score index (CS) (Stone & Roberts 1990). Nestedness was estimated with the NODF index, which is an acronym for 'nestedness metric based on overlap and decreasing fill' (Almeida-Neto *et al.* 2008; Almeida-Neto & Ulrich 2011). The fixed row–fixed column null model algorithm (FF) (sequential swap) was used to estimate significance levels for co-occurrence and nestedness indices to minimize Type I and II error rates (Ulrich & Gotelli 2007a,b). We calculated a standardized effect size (a Z-transformed score of 1000 index values from the simulated matrices) (Ulrich & Gotelli 2007a) to quantify the direction and degree of deviation from the null model. Indices and related null models were calculated with the Bipartite and vegan packages in the R-software package (<http://www.r-project.org/>), running 2000 random communities, burning the first 200 simulations and with a thin parameter of 10 (Dormann & Gruber 2009; Oksanen *et al.* 2011). A large positive value of ZCS indicates that more

organisms are segregated in their occurrences, and a large positive value of ZNODF indicates a strong pattern of nestedness (see Ulrich & Gotelli 2007a,b; Ulrich *et al.* 2009).

Modularity was estimated with the R-Package igraph using the function spinglass.community (Csardi & Nepusz 2006). Standardized deviations from null expectation in modularity (ZMOD) were estimated with a null model that randomized occurrences, but retained total number of species in sites and the total number of sites in which species were observed (i.e. a fixed-fixed null model). The randomization proceeded as follows: a matrix was constructed with two columns indicating species and sites (communities or sample units); each occurrence was represented in a row of the matrix with site and species identification in the corresponding columns. In this matrix, each site was represented as many times as the number of species it contained, and each species was represented as many times as the number of sites in which it was observed. The randomization of one column provided a random co-occurrence structure preserving the number of species per site and the number of sites per species. Null expectations in modularity and standard deviation were estimated from 2000 simulations. The existence of systematic differences in deviations from null expectations between taxonomic and body size-class matrices and between community and sample unit scales of analyses were evaluated with two-way analyses of variance for the three co-occurrence indices considered (Sokal & Rohlf 1995).

RESULTS

A total of 3073 killifish were collected across all sample dates. Across all dates, 9–26 of the 52 ponds contained water (Table 1). Only those ponds with killifishes were considered in the analyses. Z-transformed nestedness was always negative, which indicates a lower degree of nestedness than that expected by chance (Table 1). The degree of nestedness was significantly greater for body size than for species identity ($F_{1,20} = 10.214$;

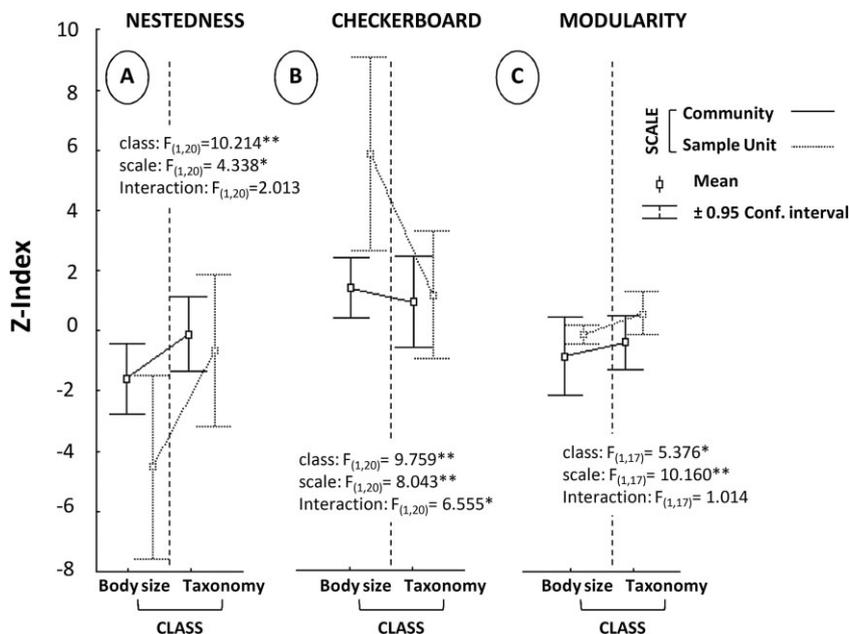


Fig. 1. Comparison of coexistence patterns measured by Z values for (A) Nestedness, (B) Checkerboard Structure, and (C) Modularity (Z-Index, values of the normalized index) considering the effect of two factors and their interaction: (i) the classes of individuals (body size *vs.* taxonomic identity), and (ii) the survey scale (sample unit *vs.* community level). ANOVA summary statistics are given for each index. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

$P = 0.005$) with Z deviations of 2.7 units on average (Fig. 1A). The scale of analysis significantly affected the degree of nestedness, with sample units more structured than communities ($F_{(1,20)} = 4.338$; $P = 0.050$) (Fig. 1A). The interactions between factors were not significant ($F_{(1,20)} = 2.013$; $P = 0.171$). Significantly more checkerboard structures than random expectation were identified in all sample periods for body size and for most of the taxonomic aggregations of individuals (Table 1). The degree of checkerboard structure was significantly greater for sample units than communities ($F_{(1,20)} = 8.043$; $P = 0.010$), and significantly greater for body size than for taxonomic identity ($F_{(1,20)} = 9.759$; $P = 0.005$). The interaction term was significant ($F_{(1,20)} = 6.555$; $P = 0.019$), indicating significantly larger Z-indices at the sample unit level for the body size aggregation of individuals (Fig. 1B). Finally, modularity was significantly larger at the sample unit level ($F_{(1,17)} = 10.160$; $P = 0.005$) and for taxonomic identity (class: $F_{(1,17)} = 5.376$; $P = 0.033$), but with no significant interaction ($F_{(1,17)} = 1.014$; $P = 0.328$) (Fig. 1C). However, it should be noted that in only one case was the modularity index lower than expected by chance (Table 1).

DISCUSSION

Identification of the spatial scale and organization level at which ecological processes operate is crucial to the

assignment of roles in the structuring of ecological systems (Levin 1992; Arim *et al.* 2007). Our analyses systematically indicated greater degrees of non-random co-occurrence for body size than for taxonomic identity, particularly at the sample unit level, which is a spatial scale at which biotic interactions tend to dominate (Webb *et al.* 2002; Violle *et al.* 2012). The operation of ecological processes through individual body size rather than through species identity may structure communities in ways that differ from taxonomic predictions (Naisbit *et al.* 2012). The analysis of species occurrence across different communities is a widespread and robust approach used in ecological considerations (Ulrich & Gotelli 2007a; Canavero *et al.* 2009). Species identity is viewed as the basic unit for describing community structure because binomial nomenclature summarizes the set of attributes that determine the fates of individuals arriving, recruiting, competing and surviving within communities (Kneitel & Chase 2004). However, body size may also summarize such a set of ecological attributes (Brown *et al.* 2007; Woodward *et al.* 2010).

Large ontogenetic shifts with increasing fish body size and the selection of species that are ecologically similar probably account for the predominance of body size over taxonomic identity in the present analysis. The potential ecological and evolutionary mechanisms determining non-random patterns of species co-occurrence have been extensively discussed and summarized elsewhere (Ulrich & Gotelli 2007a).

Because of their largely indeterminate growth patterns, fishes may be viewed as classic examples of organisms with a wide range of body sizes and associated ecological attributes that emerge through the process of ontogeny (Raffaelli 2007; Masdeu *et al.* 2011). Different life stages of the same species of fishes may occupy different trophic niches leading to spatial segregation by life stage (Muñoz & Ojeda 1998). The spatial segregation of organisms with different body sizes has been reported frequently for freshwater systems (Romare *et al.* 2003; Hildrew *et al.* 2007). Consistent with these earlier works, the main determinants of community structure in our study system appeared to be different niche requirements and antagonist interactions between body size-classes (Arim *et al.* 2010). Although these determinants reduced coexistence within ponds, the lack of significant structuring at the pond level indicates that the processes were not sufficiently powerful for exclusion of either species or size-classes. Furthermore, spatial segregation of individual size-classes within communities may have enhanced species coexistence by reducing intra- and interspecific interactions. However, when the intraspecific spectrum in body size is more limited and/or there are large interspecific differences in attributes, taxonomic identity is expected to have stronger effects than body size-class (e.g. Arim *et al.* 2007).

In general, biological filtering is more important at large scales, while biotic interactions dominate at small scales within communities (Webb *et al.* 2002). The detection of lower nestedness than expected by chance, more checkerboard structure and a tendency towards zero significant modularity point towards intra-community spatial segregation of size-classes as the dominant pattern in the structure of the killifish guild we examined. Furthermore, the larger deviation from null models at the sample unit scale indicates that biotic interactions among size-classes acted as strong forces in the system studied. Size dependent predation is widespread in aquatic communities, and was especially marked in those we examined (Arim *et al.* 2010, 2011). Small organism preference for habitats with refuges (Meerhoff *et al.* 2007) in which predation pressure from larger guild members may be avoided (Laufer *et al.* 2009) is a main driver of spatial segregation by size-class (Muñoz & Ojeda 1998). The reduction in predation risk by growth into larger size-classes allows organisms to access new resources present in different microhabitats (Arim *et al.* 2010). Also relevant in this context is the fact that thermoregulation in fishes depends on microhabitat selection on thermal gradients, which may be particularly important in ponds with little heat buffering capacity (Angilletta 2009). There is a large variation in body heating and cooling times across the range of killifish sizes we encountered, and this may be a driving factor

in the differentiation of spatial distributions (Angilletta 2009). Thus, predation, antipredator behaviours, resource accessibility and thermoregulation are all related to body size, and probably account for the patterns we resolved.

The larger degree of spatial structuring by body size rather than by taxonomic identity most probably did not stem from methodological artefacts. The performances of co-occurrence indices depend on matrix size, fill and the algorithms selected in the randomization procedure (Ulrich & Gotelli 2007a; Almeida-Neto *et al.* 2008; Almeida-Neto & Ulrich 2011). The null model selected (fixed-fixed with quasi-swap) has low Type I and II error rates (Ulrich & Gotelli 2007a,b; Ulrich *et al.* 2009) and was used in all our analyses. In the construction of size-class matrices we ensured that the numbers of rows and columns matched those in the taxonomic counterpart. Matrix fills were similar between taxonomic and size-class matrices. Any fill differences were sufficiently small that they were very unlikely to have been a significant source of bias (Ulrich & Gotelli 2007a; Almeida-Neto *et al.* 2008). In summary, the use of one null model, and the construction of matrices of the same size with similar fills lend support to our contention that systematic differences between taxonomic and size-classes matrices were a robust outcome of the present study.

Taxonomic identity is usually considered a reflection of a unique set of attributes determining the potential coexistence of individuals with their competitors and predators in particular environmental conditions (Morin 2011). However, in some ecological and evolutionary contexts, body size may be a better indicator of this suite of attributes (Raffaelli 2007). Our results suggest that the analysis of community structure as a function of species segregation would probably be enriched by the inclusion of other perspectives, such as body size, trophic category, functional group or other biological meaningful clustering of individuals into categories (Marquet *et al.* 2004). Community ecology has been pursued mainly from a species perspective on the assumption that interspecific interactions are the major mechanisms determining structure (Chase & Leibold 2003). Clearly, this view is too limited and should be expanded by the recognition of body size and other attributes as major determinants of community structure.

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REFERENCES

- Almeida-Neto M., Guimarães P., Guimarães P. R., Loyola R. D. & Ulrich W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227–39.
- Almeida-Neto M. & Ulrich W. (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environ. Modell. Softw.* **26**, 173–8.
- Angilletta J. M. J. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Arim M., Abades S., Laufer G., Loureiro M. & Marquet P. A. (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos* **119**, 147–53.
- Arim M., Berazategui M., Barreneche J. M., Ziegler L., Zaruki M. & Abades S. R. (2011) Determinants of density–body size scaling within food webs and tools for their detection. *Adv. Ecol. Res.* **45**, 1–40.
- Arim M., Marquet P. A. & Jaksic F. M. (2007) On the relationship between productivity and food chain length at different ecological levels. *Am. Nat.* **169**, 62–72.
- Brose U., Jonsson T., Berlow E. L. *et al.* (2006) Consumer–resource body-size relationships in natural food webs. *Ecology* **87**, 2411–17.
- Brown J. H., Allen A. P. & Gillooly J. F. (2007) The metabolic theory of ecology and the role of body size in marine and freshwater ecosystems. In: *Body Size: The Structure and Function of Aquatic Ecosystems* (eds A. G. Hildrew, D. Raffaelli & R. Edmonds) pp. 1–15. Cambridge University Press, New York.
- Canavero A., Arim M. & Brazeiro A. (2009) Geographic variations of seasonality and coexistence in communities: the role of diversity and climate. *Austral Ecol.* **34**, 741–50.
- Chase J. M. & Leibold M. A. (2003) *Ecological Niches. Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago.
- Costa W. J. E. M. (1995) Revision of the Neotropical annual fish genus *Cynopoeilus* (Cyprinodontiformes: Rivulidae). *Copeia* **2**, 456–65.
- Costa W. J. E. M. (2006) The South American annual killifish genus *Austrolebias* (Teleostei: Cyprinodontiformes: Rivulidae): phylogenetic relationships, descriptive morphology and taxonomic revision. *Zootaxa* **1213**, 1–162.
- Csardi G. & Nepusz T. (2006) The igraph software package for complex network research. *Int. J. Compl. Syst.* **1695**.
- Dormann C. F. & Gruber B. (2009) Indices, graphs and null models: analyzing bipartite ecological network. *Open Ecol. J.* **2**, 7–24.
- Elton C. (1927) *Animal Ecology*. University of Chicago Press, Chicago.
- Emmerson M. C., Montoya J. M. & Woodward G. (2005) Body size, interaction strength, and food web dynamics. In: *Dynamic Food Webs, Multiple Species Assemblages, Ecosystem Development and Environmental Change* pp. 167–78. Elsevier, San Diego. (eds P. C. de Ruiter, V. Wolters & J. C. Moore).
- Fortuna M. A., Stouffer D. B., Olesen J. M. *et al.* (2010) Nestedness versus modularity in ecological networks: two sides of the same coin? *J. Anim. Ecol.* **79**, 811–17.
- Gotelli N. J. (1997) Competition and coexistence of larval ant lions. *Ecology* **76**, 1761–73.
- Gotelli N. J. & McCabe D. J. (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* **83**, 2091–6.
- Hildrew A. G., Raffaelli D. G. & Edmonds-Brown R. (2007) *Body Size: The Structure and Function of Aquatic Ecosystems*. Cambridge University Press, New York.
- Hutchinson G. E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–59.
- Johnson D. M. (1991) Behavioral ecology of larval dragonflies and damselflies. *Trends Ecol. Evol.* **6**, 8–13.
- Kneitel J. M. & Chase J. M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.* **7**, 69–80.
- Kohda M., Shibata J. Y., Awata S. *et al.* (2008) Niche differentiation depends on body size in a cichlid fish: a model system of a community structured according to size regularities. *J. Anim. Ecol.* **77**, 859–68.
- Krebs C. J. (1999) *Ecological Methodology*. Addison-Wesley Educational Publishers, Boston.
- Laufer G., Arim M., Loureiro M., Piñeiro-Guerra J., Clavijo-Baquet S. & Fagundez C. (2009) Diet of four annual killifishes: an intra and interspecific comparison. *Neotrop. Ichthyol.* **7**, 77–86.
- Levin S. (1992) The problem of pattern and scale in ecology. *Ecology* **73**, 1943–67.
- McNab B. K. (2002) *The Physiological Ecology of Vertebrates*. Cornell University Press, Ithaca.
- Marquet P. A., Fernández M., Navarrete S. A. & Valdovinos C. (2004) Diversity emerging: toward a deconstruction of biodiversity patterns. In: *Frontiers of Biogeography: New Directions in the Geography of Nature* (eds M. Lomolino & L. R. Heaney) pp. 191–209. Sinauer Associates, Sunderland.
- Masdeu M., Teixeira-de Mello F., Loureiro M. & Arim M. (2011) Feeding habits and morphometry of *Iheringichthys labrosus* (Lütken, 1874) in the Uruguay River (Uruguay). *Neotrop. Ichthyol.* **9**, 657–64.
- Meerhoff M., Iglesias C., Teixeira de Mello F. *et al.* (2007) Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biol.* **52**, 1009–21.
- Morin P. J. (2010) Emerging frontiers of community ecology. In: *Community Ecology: Processes, Models, and Applications* (eds H. A. Verhoef & P. J. Morin) pp. 193–201. Oxford University Press, Oxford.
- Morin P. J. (2011) *Community Ecology*, 2nd edn. Wiley Blackwell, Oxford, UK.
- Muñoz A. A. & Ojeda F. P. (1998) Structure of carnivorous intertidal fishes of the Chilean coast: implications of ontogenetic dietary shifts. *Oecologia* **114**, 563–73.
- Naisbit R. E., Rohr R. P., Rossberg A. G., Kehrl P. & Bersier L.-F. (2012) Phylogeny versus body size as determinants of food web structure. *Proc. Roy. Soc. Lond. B Biol.* **279**, 3291–7.
- Oksanen J., Blanchet F. G., Kindt R. *et al.* (2011) Community Ecology Package. *R package version 2.0-2*.

- Olesen J. M., Bascompte J., Dupont Y. L. & Jordano P. (2007) The modularity of pollination networks. *Proc. Natl Acad. Sci. USA* **104**, 19891–6.
- Raffaelli D. (2007) Food webs, body size and the curse of the latin binomial. In: *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems* (eds N. Rooney, K. S. McCann & D. L. G. Noakes) pp. 53–64. Springer, Dordrecht.
- Ritchie M. E. (2010) *Scale, Heterogeneity, and the Structure and Diversity of Ecological Communities*. Princeton University Press, Princeton.
- Romare P., Berg S., Lauridsen T. & Jeppesen E. (2003) Spatial and temporal distribution of fish and zooplankton in a shallow lake. *Freshwater Biol.* **48**, 1353–62.
- Rooney N., McCann K. S. & Moore J. C. (2008) A landscape theory for food web architecture. *Ecol. Lett.* **11**, 867–81.
- Shipley B. (2010) *From Plant Traits to Vegetation Structure. Chance and Selection in the Assembly of Ecological Communities*. Cambridge University Press, Cambridge.
- Sokal R. R. & Rohlf F. J. (1995) *Biometry*. Freeman and Co., New York.
- Stone L. & Roberts A. (1990) The checkerboard score and species distributions. *Oecologia* **85**, 74–9.
- Ulrich W., Almeida-Neto M. & Gotelli N. J. (2009) A consumer's guide to nestedness analysis. *Oikos* **118**, 3–17.
- Ulrich W. & Gotelli N. J. (2007a) Disentangling community patterns of nestedness and species co-occurrence. *Oikos* **116**, 2053–61.
- Ulrich W. & Gotelli N. J. (2007b) Null model analysis of species nestedness patterns. *Ecology* **88**, 1824–31.
- Violle C., Enquist B. J., McGill B. J. *et al.* (2012) The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* **27**, 244–52.
- Webb C. O., Ackerly D. D., McPeck M. A. & Donoghue M. J. (2002) Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* **33**, 475–505.
- Weiherr E. & Keddy P. A. (1999) *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge.
- Woodward G., Ebenman B., Emmerson M. C. *et al.* (2005) Body size determinants of the structure of and dynamics of ecological networks: scaling from the individual to the ecosystem. In: *Dynamic Food Webs. Vol. 3. Multispecies Assemblages, Ecosystem Development and Environmental Change* (eds P. C. de Ruiter, V. Wolters & J. C. Moore) pp. 179–97. Elsevier, Amsterdam.
- Woodward G., Perkins D. M. & Brown L. E. (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Phil. Trans. Roy. Soc. B* **365**, 2093–106.
- Woodward G. U. Y. & Hildrew A. G. (2002) Food web structure in riverine landscapes. *Freshwater Biol.* **47**, 777–98.
- Ziegler L., Berazategui M. & Arim M. (2013) Discontinuities and alternative scalings in the density–mass relationship of anuran larvae. *Hydrobiologia*. doi: 10.1007/s10750-013-1553-2.