

Disentangling the effects of local and regional processes on biodiversity patterns through taxon-contingent metacommunity network analysis

Ana Inés Borthagaray, Mauro Berazategui and Matías Arim

A. I. Borthagaray (borthagaray@gmail.com), M. Berazategui and M. Arim, Centro Universitario Regional Este (CURE), Univ. de la República, Tacuarembó s/n, Maldonado, Uruguay. MA also at: Depto de Ecología y Evolución, Facultad de Ciencias, Univ. de la República, Iguá 4225 Piso 9 Sur, Montevideo, Uruguay.

Metacommunity theory, which has gained a central position in ecology, accounts for the role of migration in patterns of diversity among communities at different scales. Community isolation has a main role in this theory, but is difficult to estimate empirically, partly due to the taxon-dependent nature of dispersal. Landscapes could be perceived as either fragmented or connected for organisms with contrasting dispersal abilities. Indeed, the dispersal ability of a taxon, and the spatial scale at which eco-evolutionary processes shape local diversity, determine a taxon-dependent metacommunity network. In this paper, we introduce a methodology using graph theory to define this taxon-dependent metacommunity network and then to estimate the isolation of local communities. We analyzed the relative importance of local conditions versus community isolation as determinants of community richness for 25 taxa inhabiting 18 temporary ponds. Although local factors have been the foci of most previous empirical and theoretical considerations, we demonstrate that the metacommunity network is an equally important contributor to local diversity. We also found that the relative effect of local conditions and the metacommunity network depend on body size and taxon abundance. Local diversity of larger species was more affected by patch isolation, while taxon abundances were associated with positive or negative effects of isolation. Our results provide empirical support for the proposed role of metacommunity networks as determinants of community diversity and show the taxon-dependent nature of these networks.

Local processes related to biotic interactions and environmental conditions have been seen as the main determinants of community structure for more than half a century (Ricklefs and Schluter 1993). The concept of communities as isolated entities has been replaced by a paradigm that emphasizes connections to a regional species pool as additional determinants of community structure (MacArthur and Wilson 1967, Ricklefs 1987, Weiher and Keddy 1999, Hubbell 2001). More recently, the abstract concept of a regional species pool has been changed to an explicit consideration of the exchange of individuals between communities, which determines a metacommunity (Hubbell 2001, Holyoak et al. 2005, Economo and Keitt 2010, Moritz et al. 2013). Empirical evidence provides corroborative support for the important role of species exchanges in local diversity (Vanschoenwinkel et al. 2007, Economo and Keitt 2010, Logue et al. 2011), size structure (Castle et al. 2011, Borthagaray et al. 2012), species turnover (Losos and Ricklefs 2009, Carrara et al. 2012), and the stability of populations (Huxel et al. 2002, Holyoak et al. 2005, Hoopes et al. 2005). The flow of individuals from a metacommunity to a local community may be regarded as a process that enhances local richness by preventing local extinction or allowing

recolonization by a locally extinct species (MacArthur and Wilson 1967, Economo and Keitt 2008). However, large inputs of predators, diseases, or dominant competitors may also reduce recruitment, increase local extinctions, and reduce community diversity (Mouquet and Loreau 2003, Cadotte and Fukami 2005, Cadotte 2006). Although metacommunity theory has rapidly become a cornerstone in ecological theory, there have been few empirical analyses of the relative roles of metacommunity and local processes (Driscoll and Lindenmayer 2009, Logue et al. 2011).

Analysis of the relative roles of local versus metacommunity processes as determinants of local diversity has two shortcomings. First, the large variation among taxa in dispersal ability means that a fixed distance between pairs of patches may be experienced as a weak or strong barrier to dispersal for different taxa within the same species pool (Urban and Keitt 2001, Vanschoenwinkel et al. 2008, Chase and Bengtsson 2010, Borthagaray et al. 2012). The interaction between dispersal ability and landscape structure determine a taxa dependent landscape perception (Borthagaray et al. 2014). Secondly, the structures of communities may differ according their locations within landscapes even when local conditions (e.g. area, productivity or heterogeneity) are

similar among locations (Economio and Keitt 2008, 2010, Logue et al. 2011, White and Rashleigh 2012). Graph theory provides tools for advancing understanding of these two issues, estimating different networks for species with different dispersal abilities and providing several metrics for estimating community isolation (Fig. 1). Representing taxon-dependent metacommunity networks with graphs has been successfully used in ecology (Urban and Keitt 2001, Economio and Keitt 2008, 2010, Carrara et al. 2012, Borthagaray et al. 2012, 2014). This analysis provides general insights into the ways in which organisms with different dispersal abilities experience a landscape (Fig. 1A). In this context, a metacommunity network could be considered a set of local communities connected by dispersal paths (Fig. 1A; Economio and Keitt 2010, Borthagaray et al. 2014). Despite the recognition that landscape perception and the related metacommunity network are taxon-dependent, the means of identifying taxon-specific metacommunity networks is not evident. As a consequence, these networks have been typically identified using graph theory methods, such as the minimum spanning tree (Urban and Keitt 2001) and the percolation distance (Rozenfeld et al. 2008). These approaches provide robust estimations of metacommunity networks from a graph theory perspective. However, these metacommunity networks may significantly differ from the landscape experienced by the organisms under consideration. Here we introduce a new method that estimates metacommunity networks using local trends in community structure.

Once a metacommunity network has been configured, graph theory provides several metrics for estimating the relative isolation of single patches within the network (Fig. 1A). In an ecological context, centrality indices are inversely related with isolation of a local community (Economio and Keitt 2010). Centrality potentially reflects the relative flow of individuals through a local patch, and then throughout the entire system (Estrada and Bodin 2008, Jordán et al. 2008). Different centrality metrics are available (Fig. 1A) that highlight the potential movement of individuals between neighboring patches (degree or eigenvector centrality), the entire metacommunity (closeness centrality), or the role of a patch connecting all other patches in the metacommunity (betweenness centrality). The centrality of a community is not a fixed attribute; it is sensitive to the scale of organism movement (Holt and Hoopes 2005). The same patch may be isolated from the metacommunity for short-distance dispersers, a central stepping-stone connecting the whole system for intermediate-distance dispersers, or part of a large set of local patches for long-distance dispersers. In this sense, several studies congruently indicate that, from whole metacommunity and local community perspectives, there is no single metacommunity network; the dispersal abilities of different taxa will determine different networks for members of a species pool inhabiting a given landscape (Keitt et al. 1997, Urban and Keitt 2001, Economio and Keitt 2008, 2010). Based on the observed relationship between individual dispersal ability and the experimented metacommunity network, we postulate that 1) the metacommunity network and community centrality change systematically with the dispersal ability of a taxa – local patch linkage distance (Fig. 1B); 2) the association between community centrality and local diversity changes systematically with the link-

age distance used to estimate the metacommunity network (Fig. 1C); 3) the local diversity–community centrality association will have an extreme value at the linkage distance congruent with the distance affecting organism flow and community diversity (Fig. 1C). This metacommunity network, which has a maximum correlation between local diversity and community isolation, could differ from metacommunity networks estimated from graph theory methods such as minimum spanning tree and percolation distance.

Here, we empirically evaluate the interplay between the spatial structure of the metacommunity network and local diversity along an environmental gradient. To this end, we analyzed 18 ponds from a metacommunity of 52 temporary ponds embedded in a matrix of grasslands in Uruguay. In this landscape, we estimated metacommunity networks for 25 taxa based on the postulates of the previous paragraph (Fig. 1). As expected from metacommunity theory, we detected a main role of isolation shaping community structure. In addition, body size and the abundance of the specific taxon determined the relative roles of local versus metacommunity processes.

Methods

Study site

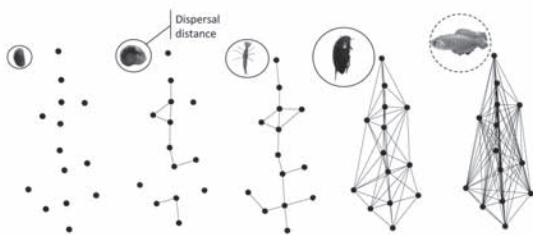
We analyzed a metacommunity of 52 temporary ponds embedded in a matrix of grasslands in Uruguay (34°25'47''S, 53°58'10''W; 5–8 m a.s.l.). Ponds varied locally in area, volume, heterogeneity, productivity, and degrees of isolation within the metacommunity (Arim et al. 2010, 2011, Piñeiro-Guerra et al. 2014). During earlier months of 2008, 52 of the ponds were water-filled, but only 18 contained water in October 2008; the biological database assembled for the present study refers to these 18 ponds. We estimated the metacommunity network for all 52 ponds because every pond community has the potential to affect others through migration. Sampled individuals were classified at high taxonomic resolution, and unclassified organisms were assigned to morphospecies. Local diversity was estimated for each pond as the number of species in higher level taxa, usually at the ordinal level (with the exception of all plants and six groups of invertebrates that we classified at the level of class or phylum) (Table 1). Ponds were characterized by the following local conditions: primary productivity (photosynthetically active standing biomass), vegetation richness depth, volume, heterogeneity (number of small 'islands' per meter of major diameter), the coefficient of variation for depth, and shape (ratio between major and minor diameters of the pond). We used quadratic terms for depth and volume when first examinations of the data revealed non-linear trends (Neter et al. 1996).

Pond isolation in the metacommunity network structure

Identifying a metacommunity network structure for each of the 25 taxa in the metacommunity was a major challenge for our analysis. Our premise was that for each taxon a network structure of ecological relevance would be one that

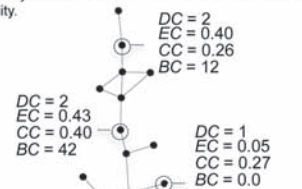
(A) Two shortcomings of empirically evaluating metacommunity theory

i. Metacommunity networks for species with different dispersal abilities and resource requirements, which are related to body size (McCann 2012).



A metacommunity network is a set of local communities connected by migration paths between patches (e.g., corridors). Metacommunity configuration is the spatial arrangement of local communities on the landscape. A network, which represents the species' perception of the landscape (Urban and Keitt 2001), is determined by metacommunity configuration and linkage distance (e.g., mean or maximum dispersal distance).

ii. Relative isolation or centrality of communities should determine the local structure of a metacommunity.



Network theory provides confident and complementary measures of community isolation and centrality. Alternative networks that represent species' perceptions of the landscape provide estimates of community isolation and centrality from the point of view of the taxa under consideration. We considered four metrics: degree centrality (DC), the number of direct paths to a community; eigenvector centrality (EC), which introduces the effect of communities that are not directly connected; closeness centrality (CC), the reciprocal of the average length of the shortest path between the reference community and all others; betweenness centrality (BC), which describes how often the reference community acts as a mediator on the shortest path between two other communities in the network (see also Economo and Keitt 2010).

(B) The dominant scale for a metacommunity

Ecological processes operate at relatively narrow spatial scales (Holling 1992, Keitt et al 1997). Each scale determines a distance of influence between local communities and a metacommunity network.

a. Local scale:



Isolated communities are weakly affected by the metacommunity network.

b. Intermediate scale:



Variation in centrality determines the effect of the metacommunity vs. local processes.

c. Regional scale:



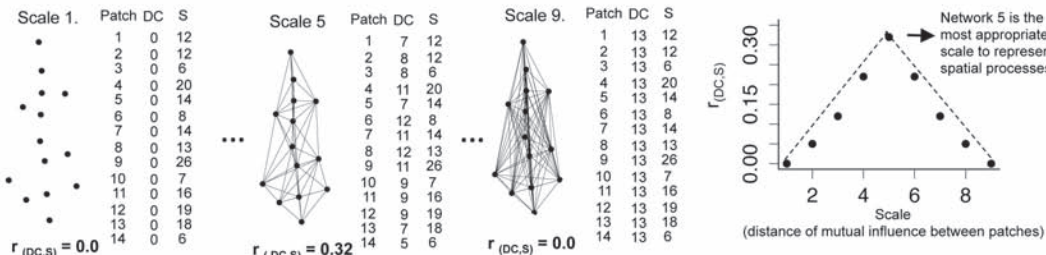
The effect of community centrality is overshadowed by connections within the entire system.

(C) Empirical detection of scales

a. Each potential scale (e.g., dispersal distance) determines a "distance of influence" between local communities.

b. The linkage distance that best represents the scale of the main mechanism (e.g. migration, environmental correlation) will determine the metacommunity network. The attribute of the metacommunity network and the relative location of local communities in the metacommunity network will determine the observed local pattern.

c. Along a gradient of scales for potential mechanisms, the association between community centrality and local conditions should be maximised for the centrality estimated from the metacommunity network at the proper scale (the scale at which the processes are operating).



(D) An empirical example: odonates

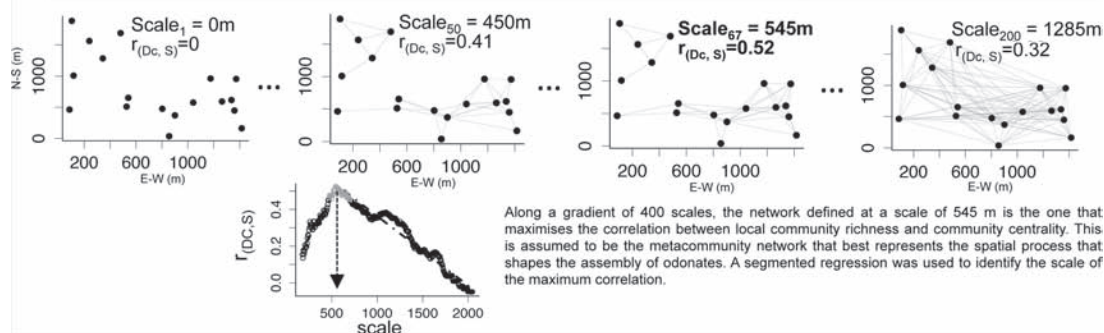


Figure 1. Schematic representation of the use of graph theory for metacommunity analysis: (A) estimating landscape perceptions for different taxa, and local community centrality; (B) changes in the metacommunity network with the scale at which the mechanisms shaping local communities operates; (C) detection of the scale at which ecological processes operate, and the associated metacommunity network; and (D) an empirical example using odonates.

Table 1. Generalized linear models constrained to two variables and ranked according to the Akaike (AIC) criterion for the 25 taxa in the metacommunity. In each case, only the best model is presented. Variables included in the final model and with significant coefficients are highlighted in grey. Positive and negative effects of local variables are indicated by + and -, respectively. Negative effects of centrality indices are indicated with a black box. The linkage distances in meters (spatial scale), selected to estimate the metacommunity network for each index, are presented within the indices columns. Abbreviations are as follows: P_i : vegetation; S^{veg}_i : vegetation richness; D_i : depth; CV_i : coefficient of variation in depth; V_i : volume; H_i : heterogeneity; PV_i : productivity volume; Sh_i : shape; DC_i : degree centrality; EV_i eigenvector centrality; BC_i : betweenness centrality; CC_i : closeness centrality. (See the text for details on the meaning and calculation of each variable).

	Pond's local conditions										Centrality Index				p-value	R^2
	P_i	S^{veg}_i	D_i	CV_i	V_i	H_i	PV_i	Sh_i	V_i^2	D_i^2	DC_i	EV_i	BC_i	CC_i		
Coleoptera	0	0	0	0	+	0	0	0	0	-	0	NA	0	NA	0.000	0.522
Hemiptera	0	0	0	0	0	0	0	0	0	0	1061	0	890	0	0.008	0.371
Diptera	0	0	+	0	0	0	0	0	0	0	0	1552	NA	0	0.004	0.429
Pulmonata	+	0	0	0	0	0	0	0	0	0	0	0	NA	0	0.069	0.244
Cyclopoida	0	0	0	0	0	0	0	+	0	0	0	0	0	706	0.035	0.352
Hymenoptera	0	0	0	0	0	0	0	0	0	0	NA	NA	1786	540	0.001	0.545
Trichoptera	0	0	0	0	0	0	0	-	0	0	0	807	0	0	0.059	0.409
Araneae	0	0	0	0	+	0	0	0	-	0	NA	NA	0	0	0.000	0.589
Order Ephemeroptera	0	0	0	0	0	-	0	0	0	0	0	1650	0	0	0.080	0.401
Odonata	0	0	+	0	0	0	0	0	0	-	0	0	0	0	0.001	0.685
Architaenioglossa	0	0	0	0	0	+	0	0	0	0	0	1792	0	0	0.026	0.317
Collembola	0	0	0	0	0	+	+	0	0	0	0	0	0	0	0.009	0.489
Decapoda	0	0	0	0	0	0	0	0	0	-	0	1408	NA	0	0.064	0.222
Calanoida	0	0	0	0	0	0	0	-	0	0	657	0	0	0	0.000	0.784
Diplostraca	0	0	0	0	0	0	0	-	0	0	NA	NA	NA	NA	0.078	0.124
Lepidoptera	0	+	0	0	0	0	0	-	0	0	NA	NA	NA	NA	0.011	0.473
Anura	0	0	0	0	0	0	0	0	0	0	812	0	0	0	0.041	0.393
Cyprinodontiformes	0	+	0	0	0	0	0	0	0	0	1140	0	NA	0	0.158	0.503
Hirudinea*	0	0	0	0	0	0	0	0	0	0	NA	1396	573	NA	0.001	0.478
Oligochaeta*	0	0	0	0	0	0	0	0	0	-	624	0	0	0	0.014	0.605
Class Acari*	+	0	0	0	0	0	0	0	0	-	NA	NA	NA	NA	0.001	0.515
Ostracoda	+	-	0	0	0	0	0	0	0	0	NA	NA	0	0	0.008	0.597
Bivalvia	0	0	0	+	+	0	0	0	0	0	NA	NA	NA	NA	0.025	0.388
Phylurr Nematoda	+	0	0	0	0	0	0	0	0	-	0	0	0	NA	0.001	0.561
Vascular plants	0	0	0	0	+	0	0	0	0	0	0	0	1591	0	0.003	0.435

*Hirudinea, Oligochaeta and Acari corresponds to subclasses.

maximizes the (positive or negative) association between pond centrality and local diversity. To this end, we proceeded stepwise as follows: 1) we constructed a set of metacommunity networks representing a gradient of dispersal ability (linkage distances), i.e. one network for each of the 400 distances considered; 2) we calculated pond centrality metrics for each network; 3) we calculated the association between pond centrality and local diversity in each metacommunity network; and 4) identified linkage distance and the related metacommunity network using a maximum biodiversity-metacommunity network association (Fig. 1C–1D). Details of the four steps are presented in the Supplementary material Appendix 1. After completing steps 1–4, we determined the metacommunity network that maximized the association between centrality measures and local diversity for each taxon. We obtained four vectors of centrality, one for each of the centrality metrics we considered. The four metrics of patch centrality were incorporated as potential explanatory variables in statistical models accounting for local diversity.

Occurrences of positive or negative associations between community centrality and diversity were analyzed by logistic regression. Trophic status (carnivore, herbivore, detritivore or filters feeder), biovolume and numerical abundance were treated as potential independent variables. The final statistical model, identified using the best subset model selection,

was limited to two independent variables, and was ranked according to the Akaike information criterion (AIC) for each one of the 25 taxa analysed. The best model is the one with the lowest AIC (Hillborn and Mangel 1997). Differences greater than two units in AIC values between models are statistically significant (Richards 2005). When models with differences smaller than two units were detected, we retained the simplest one. The maximum of two independent variables was determined by the number of available observations (Neter et al. 1996). Analyses were implemented by the bestglm package in R software (McLeod and Xu 2010).

Determinants of local diversity

The relative importance of community isolation (centrality) and the local conditions in ponds (variables previously introduced) on community species richness was analyzed with a generalized linear model (GLM) with the same procedure of previous analyses. When the species richness distribution was 0–1 or there were no more than 3 individuals per species, we selected a GLM with binomial or Poisson error distribution, but in other cases we used a Gaussian family. A best subset glm was implemented for each taxon. Finally, a logistic regression was used to evaluate associations between the presence of a metacommunity network effect and trophic

status (carnivore, herbivore, detritivore or filters feeder), biovolume and numerical abundance of the taxon. All models and statistical analysis were performed using R software (<www.r-project.org/>).

Results

Metacommunity networks

For most taxa, we identified a metacommunity network that had the maximum absolute value of correlation between its centrality measures and local diversity (Fig. 2, Supplementary material Appendix 1 Fig. A1). This outcome indicates the existence of a linkage distance that may reflect the abilities of organisms to disperse between local communities. Among the 25 taxa considered, two of the orders (Lepidoptera and

Diplostraca) and two of the classes (Acari and Bivalvia) had no associations between community centrality and diversity (Supplementary material Appendix 1 Fig. A1). In general, the centrality metrics that performed best were degree centrality and eigenvector centrality; there was a clear agreement in the spatial scale identified by these two metrics. Moreover, among taxa with significant metacommunity effects, there was a maximum association at linkage distances of 500–700 m or 1200–1500 m. Negative roles of community centralities on local diversity were significantly associated with intermediate to high abundances (Fig. 3).

Determinants of local diversity

In most taxa, local diversity was associated with community isolation (centrality) and local conditions in ponds, such as vegetation biomass, depth, volume and shape (Table 1).

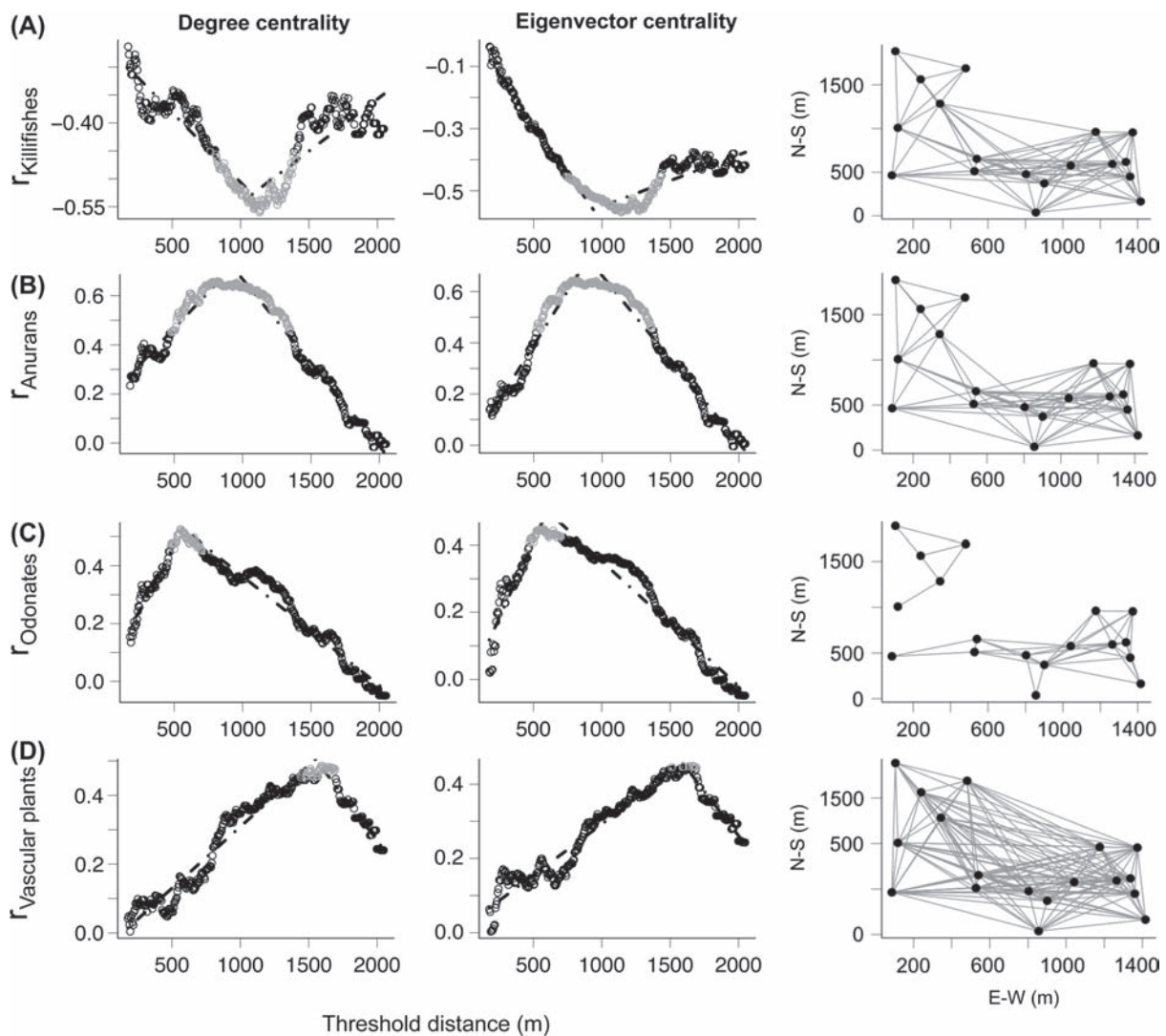


Figure 2. Estimated metacommunity networks for (A) killifishes, (B) anurans, (C) odonates and (D) vascular plants. The associations (Pearson correlation) between community diversity and local community centrality (degree and eigenvector) were calculated for 400 linkage distances for each taxon. Gray dots represent associations that were statistically significant at $p = 0.05$. Fitted lines and breaking points were obtained from segmented regressions. A minimum in (A) and maxima in (B–D) are observable for both centrality indexes. The third column of graphs shows the metacommunity networks associated with each taxon, which was calculated for linkage distances that maximize the association between centrality and diversity. The results for the 25 taxa and the four indices of centrality are presented in the Supplementary material Appendix 1 Fig. A1.

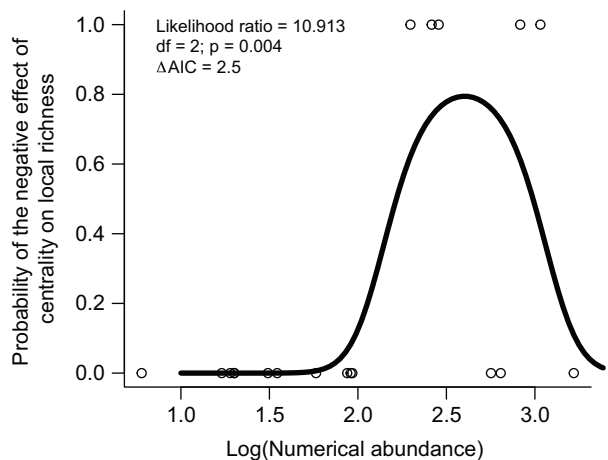


Figure 3. Probability of the negative effect of community centrality on species richness as a function of taxon abundance. Intermediate to high abundances were associated with the detection of a negative effect of community centrality on local richness. Δ AIC refers to the difference between the best-fitting model and the second best one.

Several taxa show more than one model equally congruent with observations (less than two unit of AIC of difference between models). However, the difference between these models usually involves substitutions among local variables or among centrality metrics, not affecting the interpretation of a local versus metacommunity effect. Congruent with their performances in associations between local diversity and isolation, degree centrality and eigenvector centrality were the two metrics most frequently incorporated into the generalized linear models. The occurrence of a metacommunity network effect was related to body sizes of taxa under consideration. Specifically, we found a significant sigmoidal relationship between the probability of a regional effect on local diversity and body size (Fig. 4).

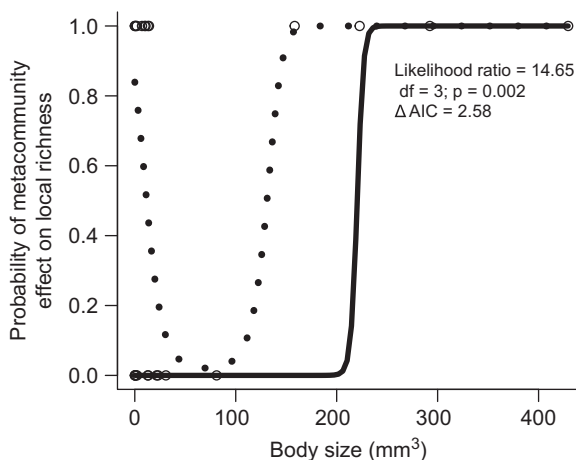


Figure 4. Probability of a metacommunity effect on local diversity and body size. The dotted and solid lines correspond to the models with and without the interaction effect between body size and the detritus category of diet, respectively. Δ AIC refers to the difference between the best-fitting model and the second best one.

Discussion

Local diversity has long been considered as a result of the interplay between local and regional processes (MacArthur and Wilson 1967). However, the relative importance assigned to these processes and the mechanisms by which they are connected has changed significantly through time (Chesson 2000, Hubbell 2001, Holyoak et al. 2005). Currently, different theories consistently point to the flow of individuals among local communities as a chief determinant of community structure (Hubbell 2001, Holyoak et al. 2005). This flow determines real metacommunity structures that go beyond abstract idealizations of species pools (MacArthur and Wilson 1967, Weiher and Keddy 1999) to spatially explicit networks (Economato and Keitt 2008). Our approach based on metacommunity network allowed us to detect significant isolation effects in 14 of 25 taxa even when local determinants were considered. Furthermore, the metacommunity effects we detected were typically large and comparable to classical local determinants of diversity, such as productivity, ecosystem size and heterogeneity (Rosenzweig 1995, Chesson 2000).

We considered four network centrality metrics (degree, eigenvector, closeness and betweenness) that describe complementary attributes of the potential flow of individual members of the metacommunity through local communities (Economato and Keitt 2010). It is essential to compute a large set of metrics that reflect community isolation in different ways. In the metacommunity we considered, degree and eigenvector centralities were systematically identified as determinant of local diversity, suggesting that individual flow in the immediate neighborhood and across the whole metacommunity impacts local diversity. Importantly, this outcome indicates the presence of ecological mechanisms operating at different scales within the same metacommunity. As a consequence, in addition to metacommunity and community scales, there are also intermediate levels of spatial aggregation at which individual flows impact local diversity (Cadotte 2006, Borthagaray et al. 2014). Incorporation of metacommunity theory into the mainstream of ecological concepts means that there is now a pressing need for the development of statistical approaches that detect the spatial scales and metacommunity networks shaping local diversity (Logue et al. 2011).

The network approach complements recent improvements in the empirical analysis of metacommunities based on variance partitioning, site-by-species incidence matrices (Meynard et al. 2013), spatial autocorrelation (Shurin et al. 2009), and multispecies occupancy models (Dorazio et al. 2010). While positive and negative effects were predicted by previous considerations, positive effects have been recorded more frequently (Economato and Keitt 2008, 2010). The principal mechanism underlying such positive effects is a reduction in local extinction rates mediated by a rescue effect and/or recolonization (MacArthur and Wilson 1967, Brown and Kodric-Brown 1977). Similar findings have been reported at the species level in real landscapes (Urban and Keitt 2001) and at the community level in theoretical simulations (Economato and Keitt 2008, 2010, Borthagaray et al. in press). On the other hand, mechanisms determining a negative association between community centrality and

local diversity have been subjects of less attention (but see Chase and Shulman 2009). We found that a negative effect of flow from and to a metacommunity is likely to occur in groups with intermediate to high abundances. This pattern may be related to biological attributes connected to abundance, such as competitive and predatory abilities. Large flows of dominant competitors, efficient predators or intraguild predators are expected to increase the abundances of these organisms with concomitant reductions in local diversity in more connected patches (Holt and Huxel 2007). However, these attributes may also determine large intra-taxon interactions and dominance by a few species from the available pool. When dominant species have a high rate of migration to local communities (determined by high network centralities) the local effect is expressed as a reduction in taxon diversity.

The association of dispersal ability with body-size probably determines the perception of landscape structure by organisms in a metacommunity (Borthagaray et al. 2012, 2014). In this sense, individual flows between patches are suggested to be an essential ingredient in the persistence of large-bodied species (Arim et al. 2010, McCann 2012). Consequently, local diversity of these large taxa would be sensitive to the spatial arrangement of patches in the network reflected in the centrality values. In contrast, landscape structure is more likely to be disconnected for species with small bodies; this relationship would increase the prevalence of local conditions over metacommunity effect (Borthagaray et al. 2012). The association between metacommunity effect and body size could also be related to other attributes such as trophic position, resource requirements, range of prey consumed, growth rate, and abundance (Peters 1983, Arim et al. 2010). However, in the case of abundance, no association between population density and body size has been observed in this system (Arim et al. 2011).

Recent attention to metacommunity dynamics is emphasizing the role of community networks in local and regional biodiversity (Chase and Bengtsson 2010, Logue et al. 2011). The methods we used in our present analysis were appropriate for the identification of a plausible metacommunity network for most taxa and in this sense they represent an advance in the construction of metacommunity networks, but further development work is certainly required. Specifically, the interplay between landscape structure, local community environment, and biological attributes may promote connections between distant patches; the reverse may be true for closer patches (Vanschoenwinkel et al. 2009). Further, under several circumstances, a weighted network concept may be more appropriate than one based on topology (Moritz et al. 2013). Finally, the identification of a metacommunity network for each taxon implicitly assumes that intertaxa differences in landscape perception are much larger than intraspecific differences. This is a classic assumption in most community studies (Violle et al. 2012, Canavero et al. 2014), but is not always met. This could be a significant source of variation in the performance of centrality measures as determinants of local diversity that deserves further research.

In this study we focused on the relative effects of landscape structure and local conditions on biodiversity. In most cases, we observed a major role for the metacommunity network

in determining local diversity. Nevertheless, most previous attention has been focused on local conditions as agents of biodiversity regulation (Chesson 2000; Borthagaray et al. 2012). Improved knowledge of the ways in which animals perceive landscape structure will contribute greatly to ecological understanding of the mechanisms determining species coexistence and biodiversity patterns (Pillai et al. 2011, McCann 2012). Theoretical and experimental developments demonstrate that landscape structure varies along gradients of dispersal abilities; this relationship between structure and dispersal presents challenges for researchers seeking to identify networks comprised of many species that coexist in metacommunities (Economio and Keitt 2008, 2010). In this study we empirically demonstrated 1) a strong gradient in landscape structure determined by the spatial scale at which communities interact, and 2) several scales of landscape perception among different taxa, which in turn affected local diversity patterns. We believe that our work contributes to advancing our understanding of animal perception of landscape structure and its effect on local and regional biodiversity.

Acknowledgements – This work was supported by a postdoctoral fellowship CONICYT – FONDECYT no. 3130360 (Chile) and a grant from Comisión Sectorial de Investigación Científica (CSIC) 2011-463 (Uruguay) to AIB, and Fondo Clemente Estable 2011-2-7117 and 2007-054 to MA. AIB thanks CONICYT: Anillo en Complejidad Social SOC-1101. Authors thank PROBIDES and Establecimiento Barra Grande for field assistance and Anthony Chapman for English edition.

References

- Arim, M. et al. 2010. Food web structure and body size: trophic position and resource acquisition. – *Oikos* 119: 147–153.
- Arim, M. et al. 2011. Determinants of density–body size scaling within food webs and tools for their detection. – *Adv. Ecol. Res.* 45: 1–39.
- Borthagaray, A. I. et al. 2012. Connecting landscape structure and patterns in body size distributions. – *Oikos* 121: 697–710.
- Borthagaray, A. I. et al. 2014. Modularity along organism dispersal gradients challenges a prevailing view of abrupt transitions in animal landscape perception. – *Ecography* 37: 564–571.
- Borthagaray, A. I. et al. in press. Effects of metacommunity network on local communities structure: from theoretical predictions to empirical evaluations. – In: Belgrao, A. et al. (eds), *Aquatic functional biodiversity: an eco-evolutionary approach*. Elsevier, USA.
- Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. – *Ecology* 58: 445–449.
- Cadotte, M. W. 2006. Dispersal and species diversity: a meta-analysis. – *Am. Nat.* 167: 913–924.
- Cadotte, M. W. and Fukami, T. 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. – *Ecol. Lett.* 8: 548–557.
- Canavero, A. et al. 2014. Patterns of co-occurrences in a killifish metacommunity are more related with body size than with species identity. – *Austral Ecol.* 39: 455–461.
- Carrara, F. et al. 2012. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. – *Proc. Natl Acad. Sci. USA* 109: 5761–5766.
- Castle, M. D. et al. 2011. Predicted effects of behavioural movement and passive transport on individual growth and

- community size structure in marine ecosystems. – *Adv. Ecol. Res.* 45: 41–66.
- Chase, J. M. and Shulman, R. S. 2009. Wetland isolation facilitates larval mosquito density through the reduction of predators. – *Ecol. Entomol.* 34: 741–747.
- Chase, J. M. and Bengtsson, J. 2010. Increasing spatio-temporal scales: metacommunity ecology. – In: Verhoef, H. A. and Morin, P. J. (eds), *Community ecology*. Oxford. Univ. Press, pp. 57–68.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Annu. Rev. Ecol. Syst.* 31: 343–366.
- Dorazio, R. M. et al. 2010. Models for inference in dynamic metacommunity systems. – *Ecology* 91: 2466–2475.
- Driscoll, D.A. and Lindenmayer, D.B. 2009. Empirical test of metacommunity theory using an isolation gradient. – *Ecol. Monogr.* 79: 485–501.
- Economio, E. P. and Keitt, T. H. 2008. Species diversity in neutral metacommunities: a network approach. – *Ecol. Lett.* 11: 52–62.
- Economio, E. P. and Keitt, T. H. 2010. Network isolation and local diversity in neutral metacommunities. – *Oikos* 119: 1355–1363.
- Estrada, E. and Bodin, Ö. 2008. Using network centrality measures to manage landscape connectivity. – *Ecol. Appl.* 18: 1810–1825.
- Hillborn, R. and Mangel, M. 1997. *The ecological detective: confronting models with data*. Monographs in population biology. – Princeton Univ. Press.
- Hoehn, M. et al. 2007. The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? – *Mol. Ecol.* 16: 3299–3312.
- Holling, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. – *Ecol. Monogr.* 62: 447–502.
- Holt, R. D. and Hoopes, M. F. 2005. Food web dynamics in a metacommunity context. – In: Holyoak, M. et al. (eds), *Metacommunities. Spatial dynamics and ecological communities*. Univ. of Chicago Press, pp. 68–93.
- Holt, R. D. and Huxel, G. R. 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. – *Ecology* 88: 2706–2712.
- Holyoak, M. et al. 2005. *Metacommunities. Spatial dynamics and ecological communities*. – Univ. of Chicago Press.
- Hoopes, M. F. et al. 2005. The effects of spatial processes on two species interactions. – In: Holyoak, M. et al. (eds), *Metacommunities. Spatial dynamics and ecological communities*. Univ. of Chicago Press, pp. 35–67.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. – Princeton Univ. Press.
- Huxel, G. R. et al. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. – *Ecol. Res.* 17: 419–432.
- Jordán, F. et al. 2008. Identifying important species: linking structure and function in ecological networks. – *Ecol. Modell.* 216: 75–80.
- Keitt, T. H. et al. 1997. Detecting critical scales in fragmented landscapes. – *Conserv. Ecol.* 1: 4; <www.ecologyandsociety.org/vol1/iss1/art4/>.
- Logue, J. B. et al. 2011. Empirical approaches to metacommunities: a review and comparison with theory. – *Trends Ecol. Evol.* 26: 482–491.
- Losos, J. B. and Ricklefs, R. E. 2009. *The theory of island biogeography revisited*. – Princeton Univ. Press.
- MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography*. – Princeton Univ. Press.
- McCann, K. S. 2012. *Food webs*. – Princeton Univ. Press.
- McLeod, A. I. and Xu, C. 2010. bestglm: Best subset GLM. – <<http://cran.r-project.org/web/packages/bestglm/vignettes/bestglm.pdf>>.
- Meynard et al. 2013. Disentangling the drivers of metacommunity structure across spatial scales. – *J. Biogeogr.* 40: 1560–1571.
- Moritz, C. et al. 2013. Disentangling the role of connectivity, environmental filtering and spatial structure on metacommunity dynamics. – *Oikos* 122: 1401–1410.
- Mouquet, N. and Loreau, M. 2003. Community patterns in source-sink metacommunities. – *Am. Nat.* 162: 544–557.
- Neter, J. et al. 1996. *Applied linear statistical models*. – Irwin Press, Chicago.
- Peters, R. H. 1983. *The ecological implications of body size*. – Cambridge Univ. Press.
- Pillai, P. et al. 2011. Metacommunity theory explains the emergence of food web complexity. – *Proc. Natl Acad. Sci. USA* 108: 19293–19298.
- Piñeiro-Guerra, J. M. et al. 2014. Biodiversity–productivity relationship in ponds: community and metacommunity patterns along time and environmental gradients. – *Austral Ecol.* doi: 10.1111/aec.12149.
- Richards, S. A. 2005. Testing ecological theory using the information-theoretic approach: examples and cautionary results. – *Ecology* 86: 2805–2814.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. – *Science* 235: 167–171.
- Ricklefs, R. E. and Schluter, D. 1993. *Species diversity in ecological communities. Historical and geographical perspectives*. – Univ. of Chicago Press.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. – Cambridge Univ. Press.
- Rozenfeld, A. F. et al. 2008. Network analysis identifies weak and strong links in a metapopulation system. – *Proc. Natl Acad. Sci. USA* 105: 18824–18829.
- Shurin, J. B. et al. 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. – *Oecologia* 159: 151–159.
- Urban, D. and Keitt, T. 2001. Landscape connectivity: a graph-theoretic perspective. – *Ecology* 82: 1205–1218.
- Vanschoenwinkel, B. et al. 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. – *Oikos* 116: 1255–1266.
- Vanschoenwinkel, B. et al. 2008. Any way the wind blows – frequent wind dispersal drives species sorting in ephemeral aquatic communities. – *Oikos* 117: 125–134.
- Vanschoenwinkel, B. et al. 2009. Community structure in temporary freshwater pools: disentangling the effects of habitat size and hydroregime. – *Freshwater Biol.* 54: 1487–1500.
- Weier, E. and Keddy, P. A. 1999. *Ecological assembly rules. Perspectives, advances, retreats*. – Cambridge Univ. Press.
- White, D. and Rashleigh, B. 2012. Effects of stream topology on ecological community results from neutral models. – *Ecol. Modell.* 231: 20–24.
- Violle, C. et al. 2012. The return of the variance: intraspecific variability in community ecology. – *Trends Ecol. Evol.* 27: 244–252.

Supplementary material (available online as Appendix oik.01317 at <www.oikosjournal.org/readers/appendix>). Appendix 1.