Modularity along organism dispersal gradients challenges a prevailing view of abrupt transitions in animal landscape perception

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A common property of landscapes and metacommunities is the occurrence of abrupt shifts in connectivity along gradients of individual dispersal abilities. Animals with short-range dispersal capability perceive fragmented landscapes, but organisms moving across critical thresholds perceive continuous landscapes. This qualitative shift in landscape perception may determine several attributes of local communities and the dynamics of whole metacommunities. Modularity describes the existence in some communities of relatively high numbers of mutual connections favoring the movement of neighboring individuals (even when each individual is able to reach any patch in the landscape). Local patch linkages and metacommunity connectivity along gradients of dispersal ability have been reported frequently. However, the intermediate level of structure captured by modularity has not been considered. We evaluated landscape connectivity and modularity along gradients of individual dispersal abilities. Random landscapes with different degrees of cell aggregation and occupancy were simulated; we also analyzed ten real ecosystems. An expected, a shift in landscape connectivity was always detected; modularity consistently decreased gradually along dispersal gradients in both simulated networks and empirical landscapes. Neutral metacommunities within simulated landscapes demonstrated that modularity and connectivity may reflect landscape traits in the shaping of metacommunity diversity. Average beta-diversity was strongly associated with modularity, particularly with low migration rates, while connectivity trends tracked changes in beta-diversity at intermediate to high migrations rates. Consequently, while some species are able to perceive abrupt transitions in the landscape, many others probably experience a gradual continuum in landscape perception, contrary to predictions from previous analyses. Furthermore, the gradual behavior of modularity indicates that it may represent an exceptional early-warning tool that measures system distance to tipping points. Our study highlights the multiple perceptions that different species may have of a single landscape and shows, for the first time, a theoretical and empirical relationship between landscape modularity, and metacommunity diversity.

Understanding the effect of landscape structure on the persistence of biodiversity has become a pressing theoretical issue because of increasing structural modifications of ecosystems through fragmentation and habitat loss (Ritchie 2010, Economo 2011). A first advance toward progress on this topic has been the recognition that the structure of communities is strongly affected by processes occurring at scales larger than the communities themselves (Ricklefs 1987, Weiher and Keddy 1999, Logue et al. 2011, Winegardner et al. 2012). Individual dispersal through landscapes is a main determinant of the connection between local communities and processes operating at metacommunity and higher levels of organization (Hubbell 2001, Holyoak et al. 2005). There has been a recent focus on landscape connectivity as a key topological attribute for better understanding of the ways in which regional processes determine spatial patterns

of biodiversity (Economo and Keitt 2010, Economo 2011, Logue et al. 2011, Carrara et al. 2012). However, there has been less stress on the fact that individuals in a community vary in the spatial scales at which they experience the same landscape (With and Crist 1995, Keitt et al. 1997, Borthagaray et al. 2012).

In gradients of individual attributes or landscape structure, the potential for organisms to move among patches typically fits a pattern of abrupt transitions from movements on local scales to movement that allows access to nearly all patches in the community mosaic. Such transitions have been reported in gradients of organism dispersal (Keitt et al. 1997, Urban and Keitt 2001), space occupancy and fragmentation (O'Neill et al. 1988, With and Crist 1995, Solé 2011); they are considered to be a pervasive property of ecosystems (Scheffer 2009, Solé 2011). At the same time,

most metrics widely used to represent landscape cohesion, e.g. connectedness, diameter, correlation length, number of components and order of the largest components, all have tipping points in the landscape structure (With and Crist 1995, Keitt et al. 1997, Borthagaray et al. 2012). Such transitions occur at critical thresholds where small changes in gradients produce qualitative shifts in ecosystems (Scheffer 2009, Solé 2011). Two classes of mobility traits have been proposed for animals living in such landscapes. In the first, animals are able to move across critical thresholds and thus perceive a continuous landscape, which is not the case for a second class of organisms with more restricted movement abilities (Keitt et al. 1997, Urban and Keitt 2001, Borthagaray et al. 2012).

The network approach provides a powerful set of tools for representing complex landscapes and quantifying emergent properties at the whole network scale (Keitt et al. 1997, Urban and Keitt 2001, Estrada and Bodin 2008, Dale and Fortin 2010, Economo and Keitt 2010). In this context, modularity refers to the degree to which some groups of habitat patches have a higher probability of mutual flow of individual organisms than other patches (Newman and Girvan 2004). Modularity was proposed as a chief metric of networks more than 40 yr ago (May 1972). Since then, several metrics have been developed to identify modules and compartments (see Bodin and Norberg 2007 and Olesen et al. 2007 for a very brief treatment of this topic), but only after recent development of robust modularity-detecting algorithms (Newman and Girvan 2004, Guimerà and Amaral 2005) have modules and compartments been widely detected in ecological networks (Stouffer and Bascompte 2011, Dupont and Olesen 2012). Modularity has been identified as a major structural property of ecological networks; it has been used to explore spatial structure in populations identified by degree of genetic isolation (Fortuna et al. 2009), colonization in metacommunities (Bellisario et al. 2010), interaction networks (Olesen et al. 2007, Rezende et al. 2009), and biogeographical boundaries (Carstensen et al. 2012). However, few studies have explored changes in modular structure in relation to spatio-temporal variability (Ramos-Jiliberto et al. 2011, Dupont and Olesen 2012).

In comparison with alternative metrics, modularity probably has better potential in discerning the environment that is effectively perceived by organisms (Newman and Girvan 2004). In this sense, modularity may function as a measure of the extent to which structural (landscape) networks approach the functional networks in which biological processes operate (Tischendorf and Fahrig 2000). The landscape network represents the routes through which organisms move among patches (Urban and Keitt 2001). This movement represents a flow of genes, and hence the course of evolution (Fortuna et al. 2009), a flow of individuals, which determines metapopulation dynamics and synchrony (Liebhold et al. 2004), and a flow of species, with consequent impacts on local diversity (Holyoak et al. 2005). These flows may determine the mechanisms of patch dynamics, mass effects, species sorting, and/or neutral dynamics within metacommunities (Holyoak et al. 2005). Among these four mechanisms, neutral dyamics are particularly suited to the analysis of interplays between landscape networks

and community structures (Economo and Keitt 2010). Neutral models emphasize the effect of migration rate from the metacommunity to local communities on biodiversity structure (Hubbell 2001), a rate that is determined by patch and landscape structures (Economo and Keitt 2010). As a consequence, neutral metacommunities may reflect the basic effects of landscape on biodiversity regardless of organism attributes.

In the present study, we explored modularity of landscapes as an indicator of structures perceived among organisms differing in dispersal abilities. The postulated behavior for modularity was an abrupt transition, as reported for other metrics (O'Neill et al. 1988, With and Crist 1995, Keitt et al. 1997, Urban and Keitt 2001). Furthermore, we explicitly analyzed the functional effect of landscape networks on metacommunity diversity, relating the average beta diversity of metacommunities to modularity and connectivity.

Methods

In the present work, we used the network approach to analyze the relationship between landscape structure and its perception by animals. Within this conceptual framework, a landscape is represented as a graph defined by a set of nodes connected by links. Typically, nodes correspond to habitat patches and links indicate functional relationships among them (Keitt et al. 1997, Urban and Keitt 2001). The structure (topography) of the graph reflects the spatial arrangement of the patches in the landscape and also the scales at which animals interact with this arrangement (Keitt et al. 1997, Economo and Keitt 2010, Borthagaray et al. 2012).

Landscape structures

We generated different random fractal landscapes with varying degrees of spatial autocorrelation in occupancy using the Hurst parameter (H, from 0 to 0.8) and the proportion of space occupied (p, from 0.1 to 0.9) (Supplementary material Appendix 1). Fractal landscapes of 50×50 cells were generated using the fieldsim algorithm proposed by Brouste et al. (2007) and implemented in R software (FieldSim package, R Development Core Team). The algorithm generates landscapes of cells with auto-correlated values between 0 and 1. These landscapes were transformed to occupied and empty cells, assigning a value of 1 or 0 to each cell when values were below or above the proportion of occupancy simulated, respectively (Ferrero 2010). Using a graph-theoretical approach, we estimated a network of p occupied cells with H degree of spatial autocorrelation for each fractal landscape. High values of p and H indicated a high proportion of occupancy and extreme aggregation, and low values of p and H indicated a low proportion of occupancy and low aggregation.

For each landscape, we constructed a gradient of distances with 50 break points from the closest to the most distant patches. Thus, we examined 50 networks defined by threshold distance for each of the fractal landscapes. Network links were estimated using centroid to centroid

Euclidean distances between cells (Urban and Keitt 2001). Two cells in a network were connected by a link when the separation between them was below a critical distance (one of the 50 break points under consideration) (Keitt et al. 1997, Urban and Keitt 2001). Considering all combinations of the Hurst parameter, the proportion of space occupied and the gradient of distances connecting pairs of cells, we constructed a total of 4050 networks. In addition, 10 empirical landscapes were analyzed using the same procedure. This approach has been used successfully to identify critical scales in network metrics as connectedness or correlation length (Keitt et al. 1997, Urban and Keitt 2001).

Modularity

Modularity was estimated for each of the networks along the distance gradient using an algorithm based on simulated annealing implemented in the R software (igraph package, Csardi and Nepusz 2006, R Development Core Team, Supplementary material Appendix 2). Simulated annealing is a stochastic optimization technique that identifies modules in a graph by maximizing a function of modularity (Newman and Girvan 2004, Guimerà and Amaral 2005, Reichardt and Bornholdt 2006). This algorithm has better sensitivity and computational cost performances that are better than alternative approaches (Danon et al. 2005). To determine modularity, the algorithm requires that the network is connected. Therefore, at each distance the largest component was selected and its modularity estimated (Bodin and Norberg 2007). Four non-linear models were evaluated to describe the association between modularity, m, and threshold distance, d_t, used to connect cells in simulated landscapes: 1) $m = a + cd_t + bd_t^2$; 2) $m = (a + cd_t)e^{bd_t}$; 3) $m = a^{e(bd_t)}$ and 4) $m = ad_t^b$, with model selection determined by the lowest Akaike's information criterion value (AIC). The parameters a, b and c represent maximum modularity, main trend, and attenuation in the slope, respectively. The parameters of the models fitted were compared along the gradient of proportion of occupancy (p) and aggregation (H).

For each network, we also computed landscape connectedness (the proportion of all pairs of patches mutually connected) using the connectedness function implemented in the package sna in R software (Butts 2013, R Development Core Team). As a complement, we estimated the minimum distance at which the whole network was connected, i.e. the percolation point (following Rozenfeld et al. 2008), and plotted the landscape network at this distance.

Metacommunity dynamics

We evaluated the effect of landscape structure on metacommunity diversity with a neutral model (Hubbell 2001). Each occupied cell of the landscape was inhabited by a community of 100 individuals (starting with a uniform distribution of abundances) belonging to 20 species. Each iteration involved the following steps: 1) all communities were randomly sorted to update diversity; 2) one individual was randomly removed from a focal community (the community in which biodiversity was updated); 3) the metacommunity from which individuals were able to immigrate was determined by the sum of species abundances among local communities directly connected to the focal community; 4) an individual removed was replaced with another from a random sample of the same community with a probability of 1-m, or from the metacommunity with a probability of m; 5) steps 1–3 were repeated for all local communities. After 500 iterations, we computed a Jaccard index of beta diversity among all pairs of local patches using the 'vegdist' function of the vegan package in R (Oksanen et al. 2011, R Development Core Team). Average beta diversity among all pairs of local communities was calculated as a measure of spatial structuring. This neutral model was simulated with 39 (0 to 1) migration rates for a landscape with a Hurst parameter of 0.4 and an occupancy of 0.20. Results from previous calculations demonstrated that this landscape correctly represented the main patterns emerging from the whole set of landscapes.

For each migration rate value, we used the mean beta diversity of the metacommunity and the threshold dispersal distance to construct landscape network relationships. To examine the predictive ability of each network metric, we fitted a linear regression to the plot of mean beta diversity on modularity (or connectivity). Finally, we related the variances explained by these regression models to the migration rate of the neutral model.

Results

Landscape modularity decreased and connectedness increased along the gradient of threshold distances in all simulated and empirical landscapes (Fig. 1, 2 and Supplementary material Appendix 2). However, landscape modularity tracked a gradual decrease without a single transition, and this was also the case for connectedness. Moreover, at the critical threshold distance (percolation point), the habitat network was still fragmented (in most cases) into several modules (modularity values ≥ 0.6), even when connectedness indicated a fully connected network (Fig. 1).

The gradual reductions in modularity were consistent across all simulated landscapes, and degrees of patches aggregation and density did not affect this general trend (Fig. 1 and Supplementary material Appendix 2). Furthermore, for all landscapes analyzed, the best model was $m = (a + cd_t)e^{bd_t}$, which described a decreasing linear and then exponential relationship between modularity and threshold distance, except in landscapes with $p = 0.8$ and $p = 0.9$ (Supplementary material Appendix 2). As the same function described the change in modularity with dispersal distance in most of the simulated landscapes, it was therefore possible to explore the existence of systematic trends in the parameters of this function in response to landscape structure (p and H). While clear trends were observable (Fig. 3), the whole function was consistent among all simulated landscapes. The main differences in parameters occurred only at high levels of patch aggregation (H) involving more gradual or sudden declines in modularity in landscapes with high or low patch densities (p), respectively (Fig. 3).

Large values of mean beta diversity occurred in the absence of migration from neighboring patches (Fig. 4a). Migration lead to an abrupt reduction in beta diversity as
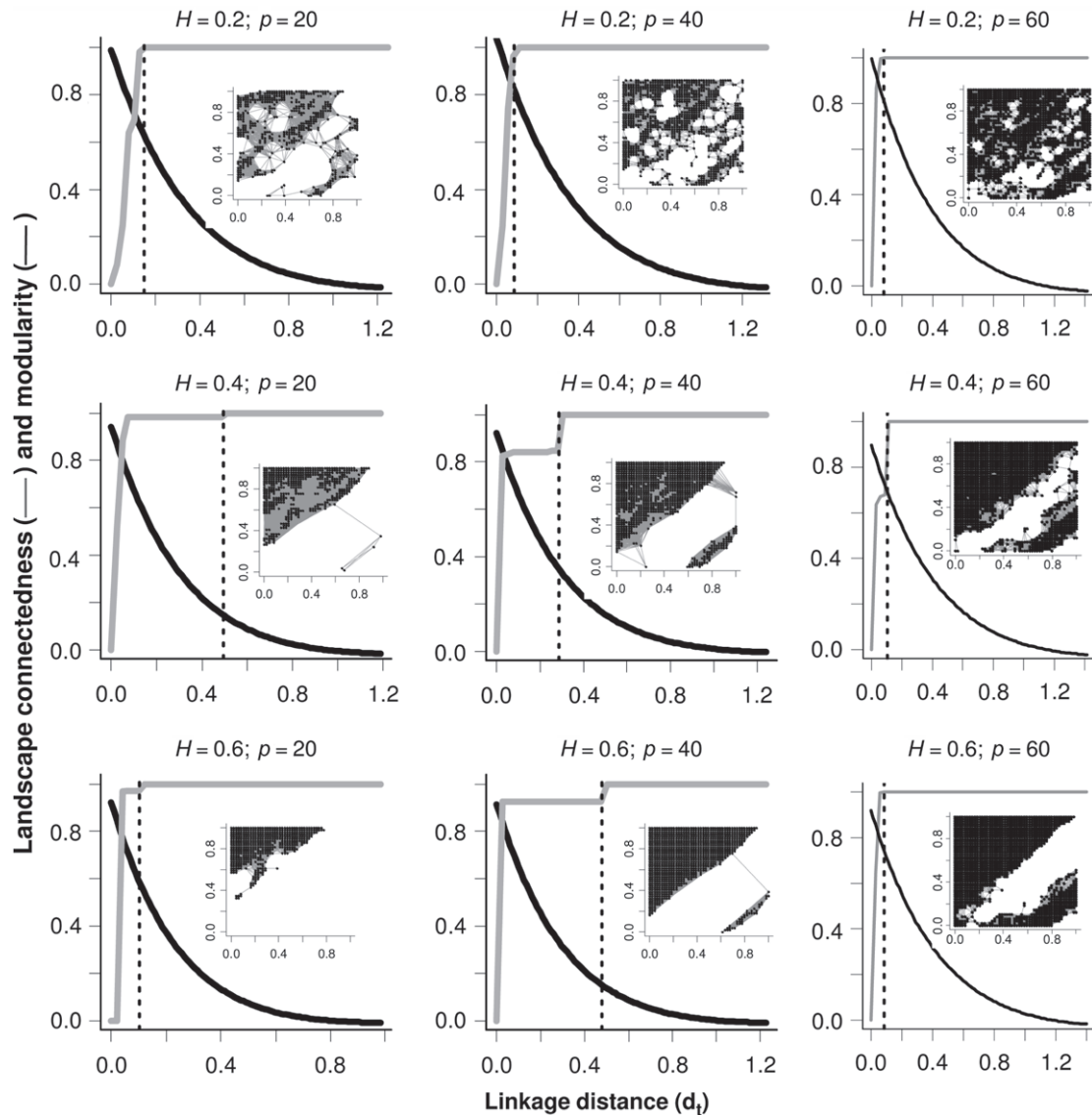
Figure 1. Landscape connectedness (gray line) and modularity (black line) along gradients of dispersal ability in simulated landscapes, e.g. threshold distances to link patches. Networks at the percolation point are depicted within each plot and the percolation distance is indicated by a vertical dotted line. Plots correspond to simulated landscapes at three levels of spatial aggregation ($H = 0.2$; $H = 0.4$; $H = 0.6$) and three proportions of occupancy ($p = 0.2$; $p = 0.4$; $p = 0.6$). In Supplementary material Appendix 1 presents a full set of spatial aggregations and spatial occupancies.

the network became more connected at larger threshold distances. At low migration rates, beta diversity resembled the pattern for modularity; at higher migration rates, the pattern resembled the inverse of the trend in connectivity. These qualitative trends were confirmed in the relationship between the proportion of variation explained by the linear models of connectivity and modularity along a gradient of linkage distance (Fig. 4b).

Discussion

The existence of abrupt transitions between disconnected and connected landscapes in gradients of dispersal abilities is viewed as a major property of landscapes and metacommunities, which is robust across different methodological approaches and systems analyzed (O'Neill et al. 1988, With

and Crist 1995, Urban and Keitt 2001, Laita et al. 2011). However, the patterns of landscape modularity in gradients of dispersal ability have not been subjected to detailed scrutiny. We have demonstrated here for the first time that, in spite of potential access to all parts of the landscape beyond the critical threshold distance, when high levels of modularity persist, landscape perception by organisms may still be fragmented and affect biodiversity patterns. Furthermore, the continuous nature of changes in modularity, in contrast to other metrics, suggests that it may be used to determine how far systems are from tipping points (Scheffer 2009). Importantly, development of the detection abilities of this kind of metric, which might be used in early warning analyses, is now a pressing imperative in ecology and conservation biology (Scheffer 2009, Solé 2011, Barnosky et al. 2012).

Network modularity and connectivity provide complementary metrics of the landscape structure that shape
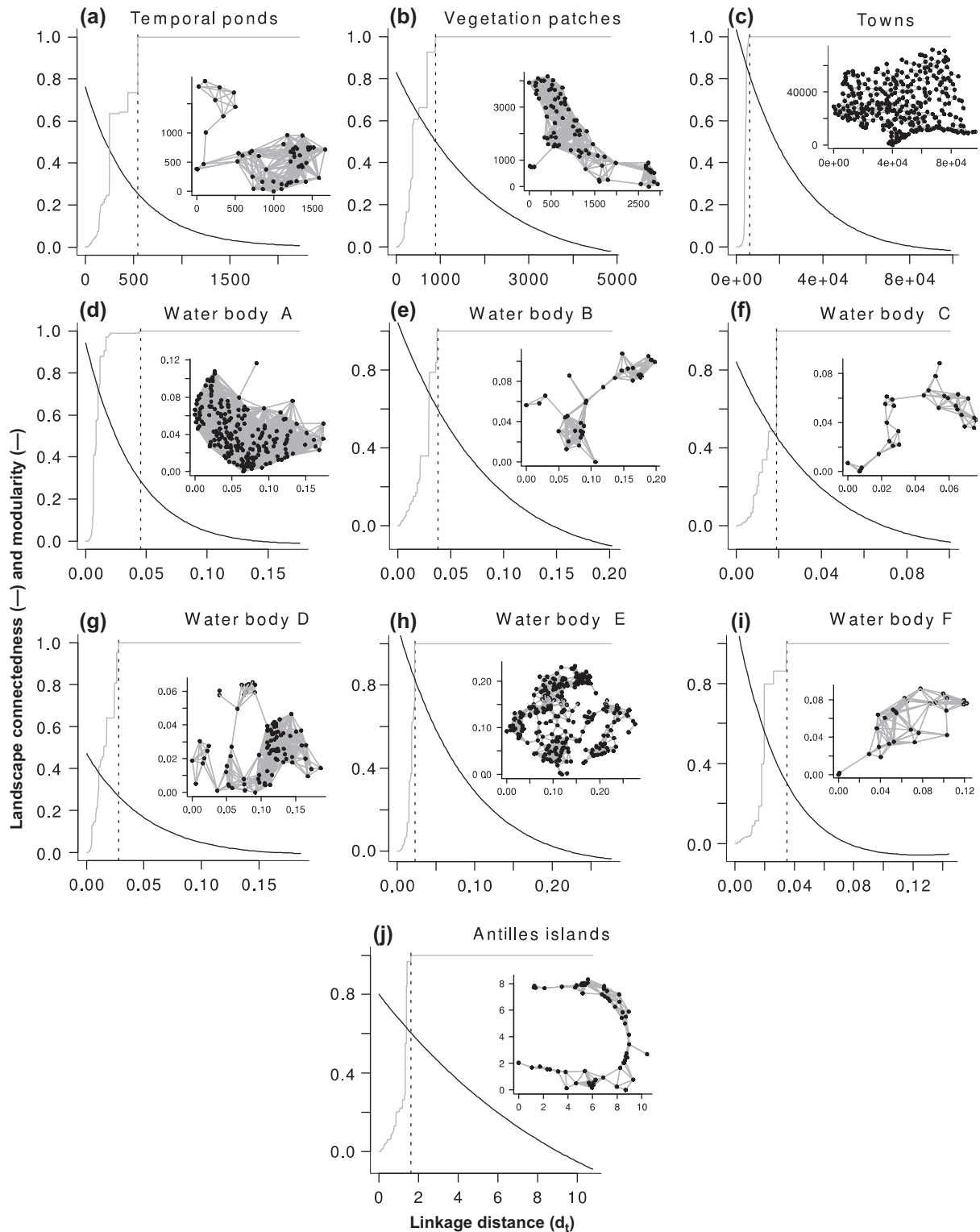
Figure 2. Landscape connectedness (gray line) and modularity (black line) along a gradient of threshold distances connecting patches on real landscapes. Vertical dotted lines indicate percolation distances; inset networks were estimated at these distances. Empirical landscapes were: (a) temporary ponds in Uruguay (34°25″47″S, 53°98″10″W), (b) patches of vegetation in the Atacama Desert, Chile (Chile (20°29″S–20°26″S), (c) towns in Canelones, southern Uruguay (34°13″S–34°50′S, 55°30′–56°30′W), (d–i) water bodies located near Mar del Plata, in eastern Argentina (A: 38°2′41.95″S; 58°33′13.97″W; B: 37°58′45.63″S, 58°27′45.06″W; C: 38°1′27.89″S, 58°24′14.13″W; D: 38°7′49.45″S, 58°6′45.02″W; E: 38°0′56.75″S, 58°13′39.27″W; F: 38°3′19.88″S, 57°46′46.04″W), and (j) Antilles islands, east of Hispaniola (14°42′N, 62°42′W).
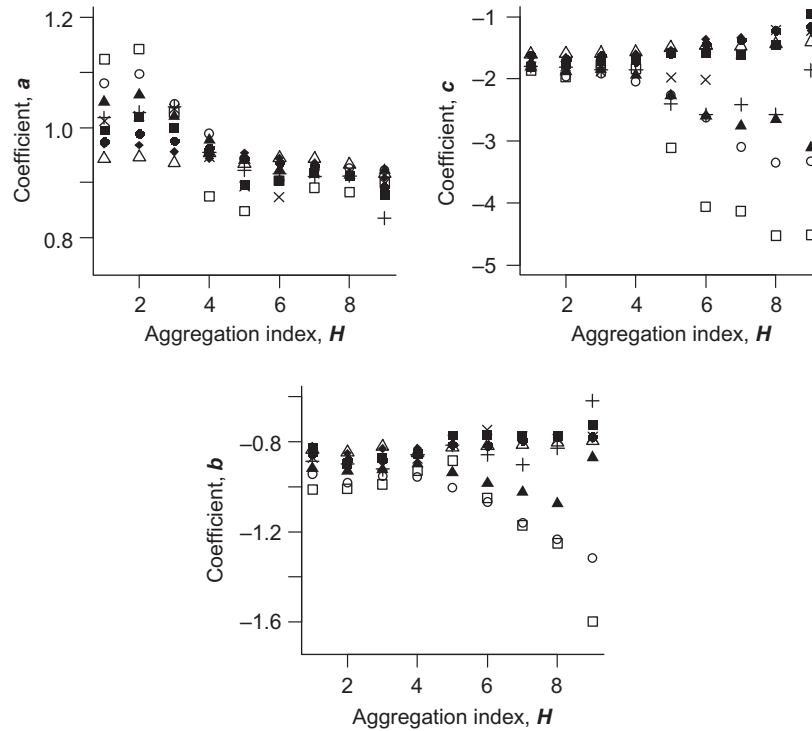
Figure 3. Response of landscape modularity (m) to a gradient of linkage distance (d_t). The model $m = (a + cd_t)e^{bd_t}$ best fit the simulations. a, b and c are parameters representing maximum modularity, main trend, and attenuation in the slope, respectively. Symbols indicate the proportion of occupied cells (p) in the landscape: □ $p = 0.1$; ○ $p = 0.2$; ▲ $p = 0.3$; + $p = 0.4$; × $p = 0.5$; ■ $p = 0.6$; ● $p = 0.7$; ◆ $p = 0.8$ and △ $p = 0.9$. Landscape aggregation (H) reduces maximum modularity (a) and also leads to steeper reduction in modularity with distance to linkage, but only in landscapes with low occupancy. To an infinitesimal extent, the reverse might be true for landscapes with larger occupancies.

biodiversity structure. According to the predictions of random landscape and percolation-based models, sudden breakup of the landscape into smaller disconnected fragments occurs in all simulated and empirical landscapes (Keitt et al. 1997, Urban and Keitt 2001, With and Pavuk 2012). The distance at which this transition takes place is related to habitat path occupancy and aggregation (With and Crist 1995, With and King 1999). This connectivity pattern has been corroborated by increasing numbers of empirical examples in several terrestrial ecosystems (Keitt et al. 1997, Urban and Keitt 2001, Borthagaray et al. 2012, With and Pavuk 2012). The existence of a single abrupt transition in connectivity has important effects on the total amount of resources that different individuals in the same metacommunity are able to access, which in turn acts as a determinant of patterns in biodiversity (Economo and Keitt 2010), body-size distribution (Borthagaray et al. 2012) and population persistence (With and Pavuk 2012).

However, the gradual trend in modularity we detected indicates that an abrupt transition in connectivity is not the only possible outcome of these relationships. Notably, all the simulated and empirical landscapes had gradual decreases in modularity across gradients of threshold distance. Our analysis of trends in beta diversity indicates roles for both connectivity and modularity, with relative relevance of each determined by migration rate among local communities. At high migration rates, connectivity may be more associated with metacommunity diversity, while an association with modularity

dominates at low migration rates. We emphasize that even when the association between modularity and biodiversity was weaker than the association of biodiversity with connectivity, the continuous nature of modularity confers upon this index considerable potential in the analysis of natural ecosystems.

In our analysis of neutral communities all species have the same dispersal ability, representing the threshold distance the mobility of all species (Hubbell 2001). However, real communities have large variation in dispersal ability among organisms (Keitt et al. 1997, Urban and Keitt 2001). Interspecific variation in traits related to dispersal – e.g. body size – should determine that different species perceive different landscapes (Borthagaray et al. 2012). As consequence, different degrees of inter-communities differentiation – beta diversity – could be promoted by the same landscape, among species with different dispersal abilities but conforming the same metacommunity. This effect of landscape perception among organisms could impact on local interactions with non-evident consequences on local diversity and its variation among communities.

The search for tipping-points in landscape connectivity at which sudden shifts occur has important implications for the design and management of conservation strategies. However, the ability to predict tipping points before they are reached is certainly problematic due to abrupt non-linear ecosystem responses to spatial and temporal variations (Scheffer 2009, Solé 2011). Consequently, finding suitable tools for the detection of tipping points is an elusive target in ecological
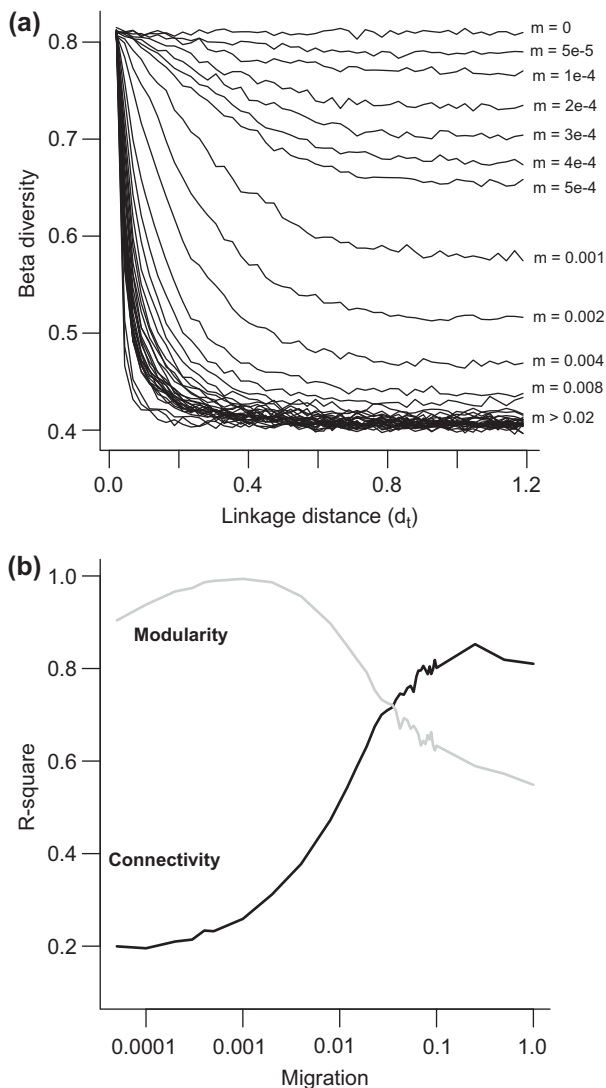
Figure 4. (a) Mean beta diversity along a gradient of linkage distance (d_t) estimated for 39 values of migration rates (from 0 to 1). (b) Explained variation for mean beta diversity by landscape connectedness (gray line) and modularity (black line), in a gradient of migration rates.

research (Solé 2011). Most methods for detecting early warnings of critical transitions need long-term datasets in order to function adequately (Dakos et al. 2012). Snapshots of landscapes or ecological networks captured in the short term may be used to estimate modularity. Examining these modularities in relation to simulated or natural gradients of habitat fragmentation, species loss, or interaction density, may provide clues to the identities of driver mechanisms; thus measures of modularity function as valuable tools in the evaluation of system distance from critical transitions. In this sense, analyses based on graph theory and metrics as modularity are complementing the set of tools for the treatment of conservation issue from a landscape perspective (Schumaker 1996, Keitt 2000, Ritters et al. 2000, Ewers et al. 2013). In this sense, modularity is probably capturing a component of landscape structure not evident from other analyses (Bodin and Norberg 2007, Fortuna et al. 2009).

Our analyses indicate that the role of landscape modularity in shaping biodiversity is probably enhanced by ongoing global changes in landscape structure and function that reduce migration rates. Fragmentation and habitat loss are widely recognized as two main drivers of landscape structure (With and King 1999, Fahrig 2003, Biswas and Wagner 2012, Cushman et al. 2012, Rubio and Saura 2012). On gradients of organism dispersal, individuals experience a gradual reduction in modularity, which represents a transition from access to local patches to access to the whole system. Migration rate is expected to interact with dispersal distances in determining a major role for modularity at low rates of organism movement among patches. Additional processes directly connected with individual movement among landscapes, such as metapopulation dynamics (Liebhold et al. 2004), species differentiation (de Aguiar et al. 2009), or disease propagation (May 2006), are expected to be dependent on the degree of modularity in patches of habitat (Fortuna et al. 2009, Bellisario et al. 2010, Carstensen et al. 2012). This study aimed at improving understanding of animal perceptions of landscape structure and should motivate further empirical and theoretical studies of the role of landscape structure on biological processes.

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