

Hot spots of mutualistic networks

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Summary

1. Incorporating interactions into a biogeographical framework may serve to understand how interactions and the services they provide are distributed in space.

2. We begin by simulating the spatiotemporal dynamics of realistic mutualistic networks inhabiting spatial networks of habitat patches. We proceed by comparing the predicted patterns with the empirical results of a set of pollination networks in isolated hills of the Argentinian Pampas.

3. We first find that one needs to sample up to five times as much area to record interactions as would be needed to sample the same proportion of species.

4. Secondly, we find that peripheral patches have fewer interactions and harbour less nested networks – therefore potentially less resilient communities – compared to central patches.

5. Our results highlight the important role played by the structure of dispersal routes on the spatial distribution of community patterns. This may help to understand the formation of biodiversity hot spots.

Key-words: island biogeography, metacommunities, nestedness, pollination, seed dispersal, spatial networks, species–area relationship

Introduction

Biogeography attempts to describe the patterns of species distribution across geographical areas and has a long tradition in ecology and evolutionary biology, with early predecessors as influential as Alfred Russell Wallace. The publication of MacArthur and Wilson's book on island biogeography (MacArthur & Wilson 1967) constituted a formidable theoretical framework that brought a predictive ability to determine the number of species on an island given its area and isolation. This, in turn, became a useful tool in conservation biology, as for example in the problem of choosing between a single large or several small (SLOSS) reserves (Diamond 1975; Simberloff & Abele 1976; Higgs & Usher 1980; Bascompte *et al.* 2007). The bridge to real-world conservation applications has even become stronger around the concepts of metapopulations (Hanski 1998) and metacommunities (Leibold *et al.* 2004). Despite this success, traditional island biogeography dealt exclusively with species, ignoring their mutual dependencies. This approach resembles the development of the kinetic theory for ideal gases in physics, which ini-

tially also neglected interactions (Alonso, Etienne & McKane 2006; Volkov *et al.* 2007).

Almost independently of the above efforts in describing how species are distributed in space, recent progress has made explicit that species interactions are an equally important component of biodiversity. Interactions are at the core of significant ecosystem services such as pollination or biological control. The way these interactions are arranged to create networks of interacting species largely affects the persistence of these networks and the number of species they can support (Memmott, Waser & Price 2004; Burgos *et al.* 2007; Okuyama & Holland 2008; Bastolla *et al.* 2009; Thébault & Fontaine 2010). In the context of global change, species interactions have also been found to be even more susceptible than species themselves (Janzen 1980; Tylianakis *et al.* 2008; Sabatino, Maceira & Aizen 2010). The disruption of interactions may in turn foresee future species losses (Aizen, Sabatino & Tylianakis 2012).

A subsequent step, therefore, seems to be the inclusion of species interaction networks into a biogeographical framework. An early contribution in this direction has been John N. Thompson's geographic mosaic theory of co-evolution (Thompson 2005). This theory has brought a geographic dimension to studies on the co-evolution

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among free-living species. For example, it has described how the sign and strength of interactions between small groups of species depend on the local presence of other species. The influence of both the geographic mosaic and early metapopulation theory leads to the development of metacommunity theory, which addresses the spatial distribution of small sets of ecologically interacting species (Leibold *et al.* 2004). The first studies on metacommunities were mainly theoretical descriptions of trophic modules, with very few studies describing an entire, realistic ecological network. Only recently, there have been significant steps in this direction (Olesen & Jordano 2002; Brose *et al.* 2004; Fortuna & Bascompte 2006; Sabatino, Maceira & Aizen 2010; Sugiura 2010; Gravel *et al.* 2011; Pillai, Gonzalez & Loreau 2011; González-Castro, Traveset & Nogales 2012; Trøjsgaard *et al.* 2013). As deviations from the behaviour of ideal gases improved the kinetic theory (Alonso, Etienne & McKane 2006; Volkov *et al.* 2007), consideration of interactions has been shown to improve the accuracy of the predictions of the species–area relationship (Brose *et al.* 2004; Gravel *et al.* 2011). So far, however, the focus has been in correcting estimates of number of species (Brose *et al.* 2004; Gravel *et al.* 2011; Jabot & Bascompte 2012), and unifying two previously unrelated scaling laws, that is, the species–area and the interaction–species relationships (Brose *et al.* 2004; Aizen, Sabatino & Tylianakis 2012). The few studies explicitly addressing mutualistic interactions among species on a biogeographical scale have explored their dependence on island area (Sugiura 2010) or age (Trøjsgaard *et al.* 2013).

This exciting progress, therefore, still leaves unanswered the question of how interactions and the networks they form are distributed across heterogeneous landscapes. A question that, if answered, will provide insight into the relative role of regional and local processes in shaping biodiversity. This would allow us, for instance, to achieve a better understanding of where and how regional biodiversity hot spots are formed and maintained.

Here we tackle this problem by using a metanetwork approach where species interaction networks inhabit a spatial network of habitat patches (Fig. 1). We first present a general framework based on extensive simulations. This allows controlling both the structure of local interactions and that of spatial sites. We then compare these broad predictions with the results for a particular case study formed by 12 pollination networks from untilled hills or 'sierras' raising in the Pampa region in Argentina (Sabatino, Maceira & Aizen 2010). This will show to what extent patterns predicted by our theoretical framework are found in nature. In this context, we change the emphasis of biogeography from species to their interactions and look into the biogeographical patterns of such interactions.

We ask whether interactions are relevant enough to modify conservation policies. For that, we begin by answering the question of how many patches need to be

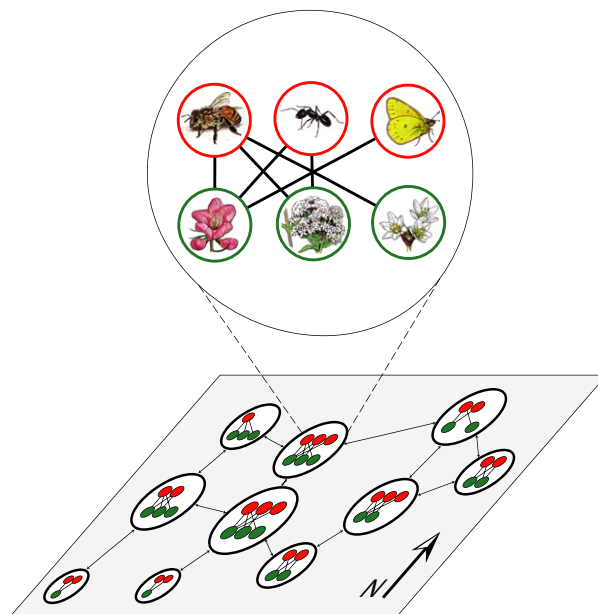


Fig. 1. Schematic representation of the theoretical framework developed in this manuscript. Each patch of the spatial network (bottom) harbours a local mutualistic network (top). The figure depicts a subset of the metaweb described in Sabatino, Maceira & Aizen (2010). Pollinator species are, from left to right, *Apis mellifera*, *Camponotus* sp. and *Colias lesbia*. Plant species are, from left to right, *Gerardia genistifolia*, *Stevia satureifolia* and *Nothoscordum bonariense*. Drawings by J. López Rojas.

conserved to register a given fraction of species or interactions. Next, we explore how these interactions are distributed across different habitat patches. This has the potential to be used as a prioritization tool. Finally, we scale all the way up to interaction networks to describe how network structure changes across the landscape. This later scale of resolution will allow us to assess the interplay between spatial and local dynamics in shaping regional patterns of biodiversity.

Materials and methods

DISPERSAL, COLONIZATION AND SURVIVAL

Metacommunity dynamics are simulated by a random process where species can colonize empty patches and be driven locally extinct. Every time step is divided into a colonization and an extinction phase. Roughly speaking, we use a spatially explicit version of the model described in Fortuna & Bascompte (2006). A patch is either empty or occupied. The model has two parameters, a colonization and an extinction probability. Patches where a certain species is absent can be colonized by that species with a probability c . Similarly, a species present in a certain patch can go extinct with a probability e .

The probability of a patch p being colonized by species s is given by the following equation:

$$C(p, s) = 1 - (1 - c)^a, \quad \text{eqn 1}$$

where the exponent a depends on whether species s is an animal or a plant. If it is an animal, a is equal to the number of adjacent patches where that animal is present. Adjacent patches are those with a direct dispersal route to the focal patch p . Nevertheless, animals only live where they can find food. Therefore, if in patch p there were none of the plant species on which animal s feeds, the probability of animal s to colonize patch p would be zero. If species s is a plant in a plant–pollinator network, the exponent a is equal to the number of adjacent patches where that plant is present.

Besides each animal species having a certain probability of becoming locally extinct, they go deterministically coextinct if every plant species they feed on has become extinct in that habitat patch.

The extinction probability for animals is the same for all species and all patches $E(p,s)=e$. Regarding plants in plant–pollinator metacommunities, their extinction probability depends on their number of pollinators present in that given patch b . This is encapsulated in the following equation for a plant's extinction probability:

$$E(p,s) = e/b. \quad \text{eqn 2}$$

Note that all probabilities are taken from a uniform distribution.

Despite the extreme simplicity behind these simulations, the model reproduces qualitatively the patterns observed in nature. Thus, we can argue that these simple rules are just enough to encapsulate the essence of the metacommunity dynamics.

SPATIAL NETWORKS

We compare four different spatial structures of increasing heterogeneity in the number of links per habitat patch: a regular lattice, a random network (Erdős & Rényi 1959), an exponential network (following Barabasi & Albert 1999) with uniformly random attachment, and a scale-free network (following Barabasi & Albert 1999) with preferential attachment. All theoretical results presented in main text correspond to the random network, while we reproduce the equivalent results for the other spatial topologies in the Appendix S1 (Supporting information). This comparison serves to test to what degree spatial structure affects the patterns here described. The advantage of using large theoretical networks relies in the statistical power they provide and in our ability to control for spatial heterogeneity.

The empirical data set consists of 12 patches out of 18 from which we know the local plant–pollinator networks. The spatial network in this case is constructed by using a threshold distance under which two patches are considered to be linked through dispersal (Urban & Keitt 2001). Here we use the thresholds that maximize the signal between the measured property and patch centrality (see Appendix S4, Supporting information for details and an assessment of the robustness of our analysis to this particular choice). In the construction of the empirical spatial network, we include all the 18 fragments. Although we do not sample the other 6, they can be part of one or many dispersal routes.

As a measure of the importance of a habitat patch within the spatial network, we focus on its betweenness centrality. A patch's betweenness centrality measures the number of times such a patch acts as a bridge along the shortest path between two other patches (Freeman 1977). This measure is intimately linked to dispersal within the network. Note that this encapsulates the con-

cept of isolation in MacArthur and Wilson's theory of island biogeography. Thus, our work expands the few recent papers addressing networks in a biogeographical dimension by adding a patch's isolation and spatial dynamics to the previous focus on island area (Sugiura 2010) and age (Trøjsgaard *et al.* 2013).

ECOLOGICAL NETWORKS

The pampean plant–pollinator networks were surveyed from 12 isolated 'sierras', ranging between 12 and 2147 ha and immersed in an intensively used agricultural matrix. The number of plant species, animal species, and interactions ranged between 17 and 39, 48 and 79, and 132 and 243, respectively. Further details can be found in Sabatino, Maceira & Aizen (2010), and Aizen, Sabatino & Tylianakis (2012). For the simulations, we use the metaweb of these local networks, composed by 172 pollinators and 96 plants.

In our simulations, each patch of the spatial network harbours an empirical plant–pollinator network. It depicts the mutualistic interactions between plants and the animals that pollinate their flowers. The characteristics of those networks are described in Bascompte & Jordano (2007). In particular, at the beginning of the simulation, we populate each habitat fragment with the metaweb from Sabatino, Maceira & Aizen (2010).

To see whether our results affect only plant–pollinator networks, or they are general to mutualistic interactions, we have also simulated the dynamics of plant–seed dispersers. Both the details of the simulations and the results can be found in the Appendix S2 (Supporting information). All qualitative results shown here hold for this other set of simulations.

As a measure of overall network structure, here we focus on nestedness. In a nested network, specialists interact with species that form well-defined subsets of the species interacting with the most generalists (Bascompte *et al.* 2003). This is a pervasive property of the architecture of mutualistic networks, with potential implications for their persistence (Memmott, Waser & Price 2004; Burgos *et al.* 2007; Bastolla *et al.* 2009).

MEASURE OF NESTEDNESS

Nestedness is measured as in Bastolla *et al.* (2009), which has the advantage of being related to network dynamics. Although there are other nestedness measures such as NODF (Almeida-Neto *et al.* 2008), they are all highly correlated and do not qualitatively change our results (Bascompte & Jordano 2014). To measure relative nestedness, we randomized the network a thousand times using the probabilistic model described in Bascompte *et al.* (2003). Relative nestedness was then calculated as a z -score between the observed value and the randomizations:

$$z = \frac{N - \bar{N}_r}{\sigma_{N_r}}, \quad \text{eqn 3}$$

where N is the nestedness value of the observed network, and \bar{N}_r and σ_{N_r} are the average and standard deviation of nestedness values across randomized network replicates.

Results

Our results show that one needs to sample a larger number of patches to record interactions than would be necessary to record an equal proportion of species (Fig. 2).

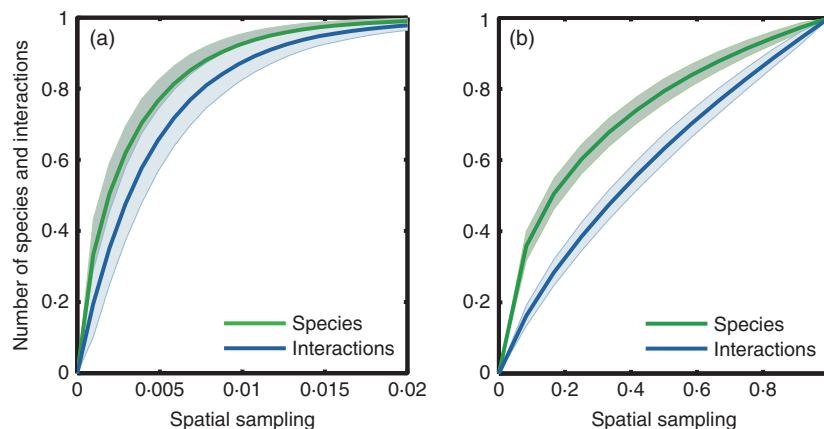


Fig. 2. Rarefaction curves of species (green) and interactions (blue) for the metacommunity simulations (a), and for the empirical case study (b). Spatial sampling is measured as the proportion of sampled patches. Here we use the proportion of sampled species and interactions, respectively, in order to obtain comparable magnitudes. To obtain panel (a), the model runs in a spatial network with a random degree distribution, 1024 nodes, and an extinction-to-colonization ratio of 2.2. After 10 000 time steps, we randomly sample the patches and count the new species and interactions found. Panel (b) corresponds to the empirical case study. The empirical network has 18 nodes. The habitat patches are also selected randomly. Shaded areas represent the 95% confidence interval.

This difference is largely modulated by both environmental stochasticity – here represented by the extinction-to-colonization ratio – and spatial heterogeneity – here represented by the degree distribution of the spatial network (Appendix Fig. S1). Specifically, the larger the environmental stochasticity, the larger the number of habitat fragments that have to be sampled to achieve an equivalent proportion of interactions (Appendix Fig. S2). This difference also grows with the heterogeneity of the spatial network. Thus, for the random spatial network (Appendix Fig. S1), one would need to sample 1.7 times more patches at the highest value of environmental stochasticity. This difference grows up to 2.5 times more patches for the scale-free network (Appendix Fig. S2). In agreement with these theoretical results, the study of the empirical data set shows that – for this particular setting – one would need to sample twice the number of patches to record 60% of the interactions than to record 60% of the species (Fig. 2).

Once we have shown how the total number of interactions scales up with number of patches – that can be taken as surrogate of area in our model – we next move to mapping how the number of interactions is distributed across the spatial network. This will inform us on how the number of interactions depends on patch isolation. Our results show first that more central patches – that is the more important ones in terms of dispersal across the network (see Materials and methods for a proper definition) – have more interactions and more species than more isolated patches (as noted by the positive slopes in Fig. 3). Secondly, the proportion of interactions in a patch – compared with the total number of interactions in the metaweb – is always lower than the equivalent proportion of species (as noted by the relative position of the two fitted lines in Fig. 3). This consistent pattern explains the previous result, that is the fact that the rarefaction curve of species lies above the rarefaction curve of inter-

actions. This pattern is observed both in the simulations and the analysis of the empirical data set.

The above two results were based on counting the number of interactions and presenting this result as either an aggregated or a patch-by-patch amount. We next consider the patterning of these interactions in the context of how the nested structure of the local mutualistic networks changes across space (Fig. 4). As shown by our results, central patches sustain communities whose interactions are significantly nested, while peripheral patches harbour less nested communities with interactions organized in a way that does not differ significantly from a random assembly. Indeed, the more central the habitat patch is, the more significantly nested is its mutualistic community (Fig. 4). The same pattern is found in the empirical metacommunity. In the Appendix S3 (Supporting information), we show that the relationship between nestedness and patch centrality is not mediated by the relationship between network size and patch centrality. As also shown in the Appendix S5 (Supporting information), patch centrality is a better predictor of the number of interactions and of network structure than patch area. However, the number of species in a patch is more correlated with patch area than with patch centrality.

Discussion

A predictive theory of how interactions are distributed in space may be relevant in the context of understanding how habitat fragmentation will erode the architecture of biodiversity and the services it provides. Specifically, knowing how this network structure changes across the landscape can provide insight into how resilient these networks will be. Similarly, it can guide efforts aimed at reversing this destructive trend, such as in reserve design.

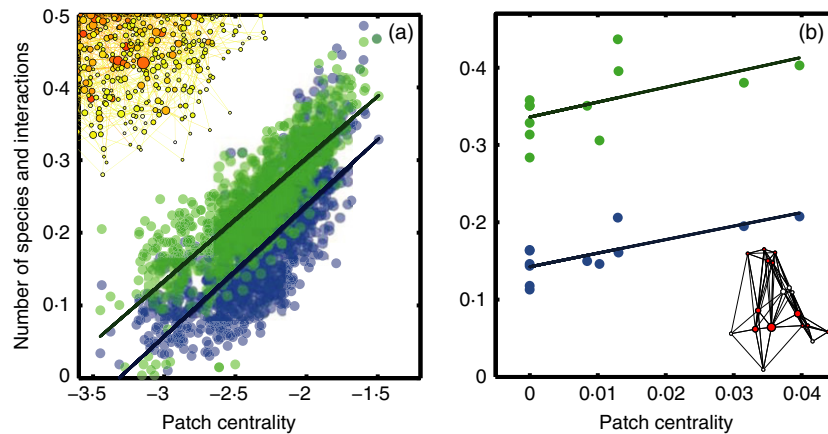


Fig. 3. Spatial distribution of species and interactions for the simulated (a) and empirical (b) metacommunities. (a) The normalized number of species (green) and interactions (blue) is significantly correlated with the log betweenness centrality of the patch where the community is harboured (Spearman correlation, $P < 0.001$, $r = 0.80$ for interactions; and $P < 0.001$, $r = 0.85$ for species). In the top-left corner is shown a fragment of the theoretical network of 1024 patches with a random degree distribution, and an extinction-to-colonization ratio of 2:2. The size of the nodes is proportional to their betweenness centrality, the color is redder, and the larger is the number of interactions found in that patch. (b) The same result for the empirical case study ($P = 0.016$, $r = 0.67$ for interactions; and $P = 0.019$, $r = 0.66$ for species). The spatial network of the 18 patches with a threshold distance of 17 km is represented in the bottom-right corner. Patches that were actually sampled are represented in red. The normalized number of species and interactions is calculated comparing the number found in the focal patch with the number of species or interactions found in the metaweb (Sabatino, Maceira & Aizen 2010). Fitted lines are only meant to guide the eye.

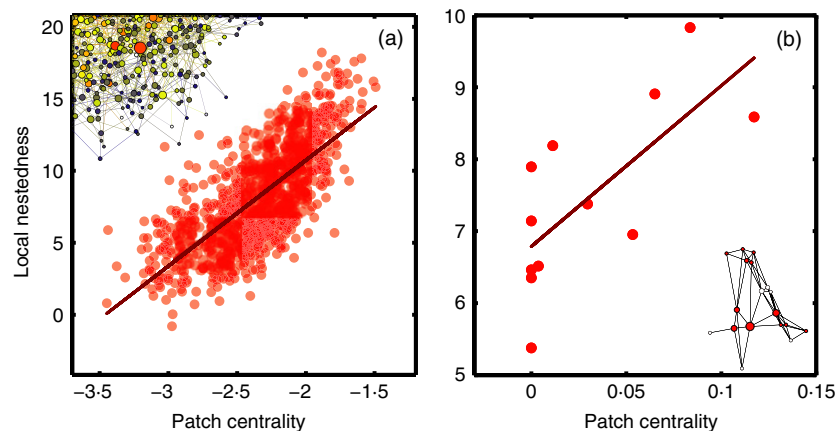


Fig. 4. Spatial distribution of network structure for the simulated (a) and empirical (b) metacommunities. The average relative nestedness of a local community is significantly correlated with the log betweenness centrality of the patch where the community is harboured (a) (Spearman correlation, $P < 0.001$, $r = 0.74$). The results in here represent a random spatial network of 1024 patches with an extinction-to-colonization ratio of 2:2. In the top-left corner, we show a fragment of that spatial network. The size of the nodes is proportional to their betweenness centrality. White colour indicates non-significantly nested networks ($z\text{-score} \in [-1.96, \dots, 1.96]$). Blue/yellow/red scale represents significantly nested communities. The redder the node, the larger the nestedness of the community it harbours. (b) The same result for the empirical case study (Spearman correlation, $P = 0.005$, $r = 0.75$). The spatial network of the 18 patches with a threshold distance of 12 km is represented in the bottom-right corner. Patches that were actually sampled are represented in red. Fitted lines are only meant to guide the eye.

The species–area relationship has been a cornerstone of a predictive conservation biology in the sense of exploring how different re-arrangements of the habitat would translate into different numbers of coexisting species. This can provide a rule of thumb in terms of how much area should be protected if we were interested in conserving a minimum number of species. In line with this, here we show that we may need more than twice the number of habitat patches in order to preserve a given proportion of

total interactions, especially in most fluctuating environments. This means that a reserve arrangement designed on the basis of species presence and absence may not be enough to protect interactions and therefore will fail in protecting ecosystem functioning (Tylianakis *et al.* 2009).

In spatial networks of habitat patches, however, not all patches are equally relevant in order to preserve interactions. We have shown that there is considerable variability in the importance of a given patch in terms

of harbouring interactions and species. That importance depends on the patch location in relation to the rest of the patches. Therefore, this result should be interpreted in the light of the differential rescue effect across the landscape, which is linked to patch position. Even when the extinction rate of a species was the same, the rescue effect by which a local patch can be recolonized from a nearby patch is much lower in peripheral patches (Gilarranz & Bascompte 2012). However, not only is the distribution of species heterogeneous across the landscape. As recently pointed out, in real landscapes, there is not a random loss of interactions; while interactions between generalist species are ubiquitous, interactions involving specialist species are much more vulnerable (Aizen, Sabatino & Tylianakis 2012). Interestingly enough, this type of result can only be understood when integrating information on local network structure and landscape dynamics. This relates to two major theories bringing analytical tractability to multispecific co-evolutionary studies: network theory (Bascompte & Jordano 2007) and the geographic mosaic theory of co-evolution (Thompson 2005).

Beyond differences in the number of interactions across the landscape, different patches are also playing different roles in terms of how their interactions are assembled. Thus, the nested structure of the local network varies across the landscape. Given the importance of nestedness for maintaining network size (Bastolla *et al.* 2009) and robustness (Mommott, Waser & Price 2004; Burgos *et al.* 2007; Thébault & Fontaine 2010), local differences in nestedness are likely to translate into differences in the persistence of these local networks. The higher stability of communities in central patches is twofold. First, we have shown that central patches tend to harbour more nested communities. Other things being equal, nested communities tend to be more persistent (Bastolla *et al.* 2009). Secondly, this goes along the tendency for such central patches to be involved in a large number of dispersal routes and therefore to have a higher incidence of rare species due to a higher recolonization rate.

Network persistence, therefore, is a combination of local and regional processes that cannot be understood independently from each other. The positive or negative feedbacks between patch isolation and network structure may help to explain the spatial distribution of biodiversity hot spots. These results pave the road for a deeper understanding of how spatial structure and dispersal simultaneously affect local community structure, the geographic distribution of ecosystem services and co-evolutionary processes.

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Data accessibility

The plant–pollinator interaction matrices for each of the sampled Sierras, the metaweb, and the area and coordinates of each Sierra, are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.cr3ft> (Gilarranz *et al.* 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Plant–pollinator interactions.

Appendix S2. Seed disperser interactions.

Appendix S3. Nestedness increases with patch centrality independently of network size and connectance.

Appendix S4. Criteria to create the empirical spatial network.

Appendix S5. Influence of patch centrality and area.