Reports

Landscape connectivity explains interaction network patterns at multiple scales

Micaela Santos,[1,7] Luciano Cagnolo,[2] Tomas Roslin (iD),[3,4] Hugo J. Marrero,[5] and Diego P. Vázquez (iD)[1,6]

[1]*Argentine Institute for Dryland Research, CONICET, Avenida Ruiz Leal s/n, 5500 Mendoza Argentina*
[2]*Institute for Multidisciplinary Plant Biology (IMBIV), Faculty of Exact, Physical and Natural Sciences, National University of Córdoba and CONICET, Avenida Vélez Sarsfield 1611, 5000 Córdoba Argentina*
[3]*Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala Sweden*
[4]*Department of Agricultural Sciences, University of Helsinki, PO Box 27, (Latokartanonkaari 5), FI-00014 Helsinki Finland*
[5]*Center for Natural Renewable Resources of the Semi-Arid Zone (CERZOS), Camino de la Carrindanga Km. 7, 8000 Bahía Blanca Argentina*
[6]*Faculty of Exact and Natural Sciences, National University of Cuyo, Padre Jorge Contreras 1300, M5502JMA Mendoza Argentina*

Abstract. Under a metacommunity framework, the spatial configuration of habitat fragments could determine local community structure. Yet, quantifying fragment connectivity is challenging, as it depends on multiple variables at several geographical scales. We assessed the extent to which fragment connectivity and area explain patterns in interaction structure among four herbivore guilds and their host plants in a metacommunity. We propose an integrative connectivity metric including geographic distance, neighboring fragment area and similarity in resource composition as an extension of Hanski's classic metric. We then used nonlinear models to assess whether fragment connectivity and area predicted link richness and similarity in link composition. We found that link richness was always negatively related to connectivity but at different geographic scales depending on the herbivore guild. In contrast, while link composition was also related to connectivity, the direction and strength of this relationship varied among herbivore guilds and type of link composition (qualitative or quantitative). Furthermore, focal fragment area was not an important determinant of interaction diversity in local communities. Our findings emphasize resource similarity as a novel dimension of fragment connectivity relevant in explaining interaction diversity patterns in natural trophic networks.

Key words: habitat fragmentation; habitat networks; herbivore guilds; interaction diversity; landscape connectivity; trophic interactions.

Introduction

Habitat destruction, mainly due to land-use changes, is negatively affecting global biodiversity and ultimately leading to species extinction (Titeux 2018). Such environmental changes can also influence the distribution and abundance of species interactions through habitat loss and changes in habitat configuration of the remaining habitat fragments (Gonzalez et al. 2011). Currently, most natural habitats throughout the world are being increasingly fragmented, with short- and long-term consequences on community structure and ecosystem

functioning (Haddad 2015), for example, through immediate and delayed species extinctions that may affect interaction diversity and topology of ecological networks. Interaction diversity of an ecological network can be defined by simple metrics such as interaction richness (i.e., the number of distinct pairwise interactions among species), in an analogous way to species richness, or by more complex metrics involving interaction frequencies. Although interest on ecological networks is not new, we know much less about how ecological network properties, such as interaction diversity, are being affected by habitat fragmentation (Sabatino 2010) than the consequences for populations and communities belonging to particular trophic levels.

As a consequence of habitat fragmentation, natural habitats are being transformed into a set of fragments of different sizes, shapes and biological features, separated

from each other by variable geographical distances and different matrix types (Fahrig 2003). Previous studies on trophic networks have shown that decreased habitat size leads to decreased species richness and that phenotypic traits influence the rates at which species are lost from fragmented landscapes (Holt et al. 1999, Cagnolo 2009). Likewise, link richness in mutualistic networks decreases faster than species richness with decreasing habitat size (Sabatino 2010), and rare, specialized interactions are more likely to go extinct (Aizen et al. 2012). In contrast, habitat connectivity, defined by Taylor et al. (1993) as *the functional relationship among habitat patches due to their spatial distribution and the movement of organisms in response to landscape structure,* seems to be a more complex predictor because it may depend on neighboring distances and areas within a spatial scale (Moilanen and Neiminen 2002), which is related to species life-history traits, such as dispersal ability (Jones et al. 2015), niche breadth, and reproductive rate (Öckinger 2010). Although some theoretical (Economo and Keitt 2010), experimental (Chisholm et al. 2011), and observational studies (Kaartinen and Roslin 2011, Borthagaray et al. 2015) have shown that habitat spatial configuration has significant effects on local community structure, the extent to which habitat size and connectivity simultaneously influence species interaction patterns is still unclear.

Habitat networks are powerful tools to represent spatially explicit landscapes and to quantify spatial processes (Dale and Fortin 2010). In a habitat network, migration and dispersal pathways are represented as links between habitat fragments that may have different weights (e.g., dispersal rates) and features (e.g., dispersal direction), and habitat fragments are represented as nodes that may also have different weights (e.g., fragment size) and features (e.g., resource composition). Although island biogeography theory (MacArthur and Wilson 1967) assumes dispersal from a mainland or continuous habitat to islands or habitat patches as a regional mechanism to predict local diversity, it does not consider among-patch dispersal explicitly (Prugh et al. 2008). In contrast, the metacommunity approach (Leibold and Chase 2018, Leibold 2004) posits that local communities are linked by dispersal of multiple potentially interacting species, highlighting the relevance of individual flow among neighboring patches on local community structure (Economo and Keitt 2010). Therefore, dispersal represents a spatial process that prevents local extinction and allows recolonization of locally extinct species from neighboring patches, and not only from a continuous habitat (Thompson et al. 2017). Furthermore, the network conceptualization allows modeling these more realistic landscapes to evaluate simultaneously the effects of links and nodes on local communities (Chisholm et al. 2011, Urban and Keitt 2001).

The geographic position of a fragment in a landscape defines which fragments are its neighbors. Several connectivity metrics have been proposed, defining it as either independent from organisms (structural metrics; e.g., distance to nearest patch using Euclidean distances) or dependent on them (functional metrics; e.g., least-cost paths using distances weighted by matrix composition). How structural and functional components are related is key to improve our understanding of habitat connectivity for whole communities and their potential consequences (Öckinger et al. 2018). Geographical distance is the most obvious component of structural connectivity in a habitat network, while non-geographical distance, such as compositional distance in terms of shared resources among fragments, will determine functional connectivity. Species establishment in a community is related to local resources, so that patches with similar resources usually contain similar consumer assemblages (Tilman 1982). Until now, local resources have been considered a surrogate or modulator of fragment area (e.g., resource richness or diversity and effective area; Schooley and Branch 2011) but, to our knowledge, not as a component of local connectivity. Here we propose to expand the concept and measurement of habitat connectivity by adding resources shared among habitats (i.e., similarity in resource composition) as a component of habitat connectivity, thus modulating the effects of geographical distance and fragment area on connectivity.

Our aim is to assess the extent to which fragment area and connectivity, including geographical distance, area of neighboring fragments and among-fragment similarity in plant composition, explain the diversity of interactions between plants and four herbivore guilds in a fragmented landscape. We define connectivity as a function of geographical distance to neighboring fragments weighted by their area and the similarity in resource composition between fragments, thus extending previous connectivity metrics (Hanski and Thomas 1994, Steffan-Dewenter 2003). We assume that there are discrete trophic guilds within which species have similar ecological requirements and, consequently, relate to the landscape in a similar way (e.g., in their use of dispersal pathways). Thus, we expect that for each trophic guild we can define a characteristic habitat network based on a specific connectivity model (Borthagaray et al. 2015).

Materials and Methods

Study area

To assess the extent to which fragment connectivity and area explain interaction diversity in local communities, we targeted an area of ~50,000 ha of a fragmented dryland habitat in Valle de Uco, Mendoza Province, central-western Argentina. This area is characterized by an intense, recent habitat modification, which has resulted in strong fragmentation, degradation, and loss of the native Monte Desert ecosystem since ~20 yr ago. Remnant fragments are mostly surrounded by vineyards and to a lesser extent by other types of agriculture (e.g.,

walnut orchards; Appendix S1: Fig. S1), usually with grass and herbs under crops. This type of matrix may be considered highly homogeneous and not totally inhospitable, as it may provide additional resource or refuge to insects. The natural vegetation is predominantly xerophytic, including several shrubs (e.g., *Larrea divaricata*, *Prosopis alpataco*, *Accantholippia seriphioides*, and *Lycium chilense*), cacti (e.g., *Opuntia sulphurea*), and some perennial (e.g., *Sphaeralcea miniata*) and annual herbs (e.g., *Plantago patagonica*). In this setting, we defined a natural fragment as any patch of remnant native vegetation with more than 70% of its perimeter surrounded by strongly modified habitat (e.g., agricultural land, roads, human settlements) and without indication of strong human disturbance (e.g., vegetation clearing). We identified 19 natural fragments within the target region, 14 of which were sampled with permission from land owners; the other five sites were left unsampled because of logistical constraints, but were included in our estimates of fragment connectivity in spatial analysis for the sake of completeness (Appendix S1: Fig. S2). We used QGIS software to measure fragment area and geographical distance among all fragments (the shortest edge-to-edge distance between fragments).

Sampling

To describe plant composition in habitat fragments, in austral spring (October) 2015 and summer (December) 2016, we sampled vegetation at the centroid of each fragment using the point-intercept method along four 50-m transects defining a square whose center was the fragment's centroid, with sampling points every 2 m (Bullock 1996). With these data, we estimated species' abundance as the number of points in a fragment in which the species was present. To describe interaction diversity, at the centroid of each fragment we also sampled plant–herbivore interactions along two 50 × 2 m transect bands during the spring and summer of two consecutive years (2015–2016 and 2016–2017). We applied the same sampling effort in all fragments regardless of their area to maintain sampled area constant among fragments. To describe plant–herbivore interactions in the study fragments, in each transect band, we identified and estimated the abundance of all galls on leaves and stems, mined leaves, aphid colonies (family Aphididae), and scale insects (superfamily Coccoidea) on shrubs and herbs. We identified galls and mines in the field based on host plant identity and on their position, shape, color, and size. To confirm whether galls and mines collected in the field were correctly identified, we kept them in the laboratory for 1 yr after collection to allow for the emergence of adult gallers and miners. Based on adult morphology, we identified all emerged insects associated with mines and galls to the lowest possible taxonomic level (Appendix S1: Table S1). Scale insects and aphids were identified to the morphospecies level based on external morphology.

Interaction diversity metrics

We described interaction diversity of each plant-herbivore network using three different metrics: (1) interaction richness, calculated as the number of links per fragment (one value per guild and fragment); (2) quantitative (frequency-based) similarity in interaction composition, calculated as the sum of the Bray-Curtis similarity index (i.e., one minus Bray-Curtis dissimilarity) from four quantitative matrices (one for each guild) with plant–herbivore interactions in columns, fragments in rows, and abundance of each individual interaction in cells (number of galls, mines, scale insects, and aphid colonies); and (3) qualitative (presence–absence) similarity in interaction composition, calculated as the sum of the Jaccard similarity index (i.e., one minus Jaccard dissimilarity) from the same four matrices described above but as qualitative matrices, i.e., with plant–herbivore interactions in columns, fragments in rows, and 1–0 as presence–absence of each individual interaction in cells. As these three metrics describe different components of biodiversity (Borcard et al. 2011), they gave us complementary information about how many different interactions there are, how abundant they are and who they are to assess the distribution and abundance of trophic interactions on fragments. Similarity indices were calculated with the *vegan* package of R statistical software (Oksanen 2019).

Fragment connectivity metrics

We described fragment connectivity based on the classic metric proposed by Hanski and Thomas (1994) and later modified by Steffan-Dewenter (2003): $c_i = \sum e^{-\alpha d_{ij}} A_j$, where d_{ij} is the geographic distance between fragments i and j, α is a parameter describing the decay of connectivity with distance, and A_j is the area of fragment j. To represent the greater flux of herbivores between communities with similar resources, we modified this index by adding similarity in plant resource composition (S_{ij}) as a factor affecting species dispersal probability among neighboring communities. S_{ij} was measured as Bray-Curtis' similarity index calculated from plant species composition in each fragment. Thus, this component modulates the contribution of geographic distance and area to connectivity, so that fragments are more or less connected according to their resources. Fig. 1 illustrates a spatially explicit landscape composed by three patches of different sizes and resource composition, using one hypothetical resource in patches 1, 2, and 3 with abundance 10, 1, and 7, respectively. In Fig. 1a, patch 2 has the highest connectivity owing to its geographical position in spite of being the most dissimilar, and patch 3 has the lowest connectivity in spite of being the most globally similar. A contrasting situation is shown in Fig. 1f where patches 1 and 3 are more similar to each other than to patch 2, while patch 3 is slightly more similar to patch 2, resulting
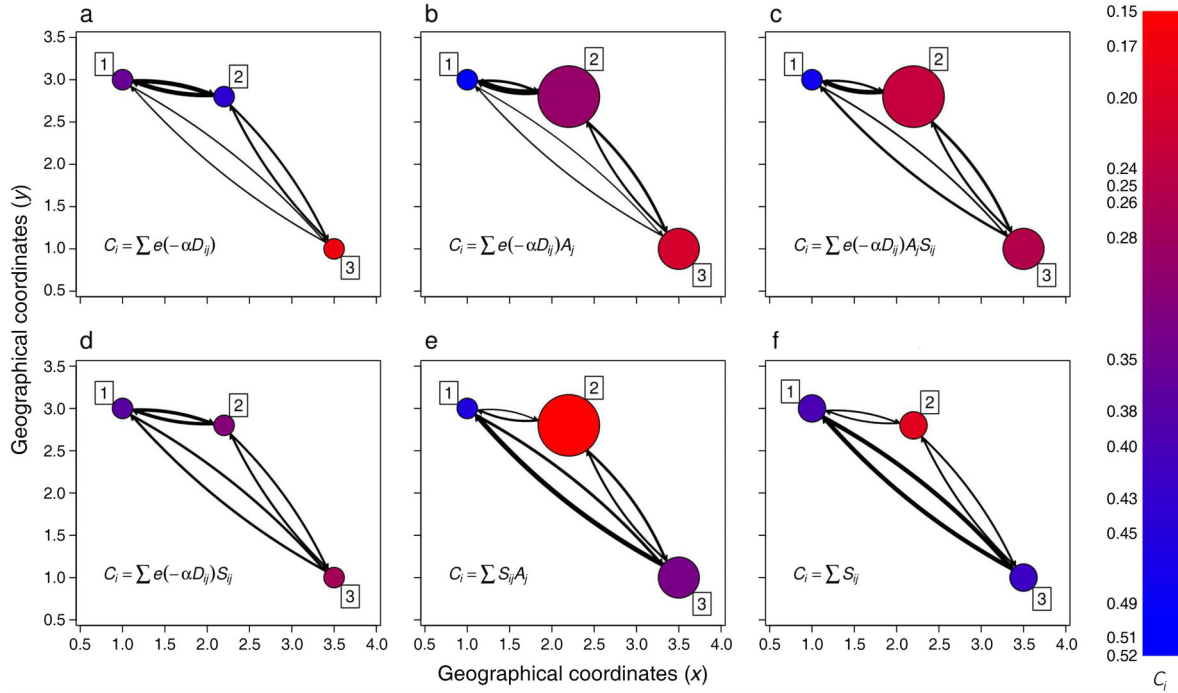
Reports

Fig. 1. An illustration of connectivity metrics. Each panel shows three habitat fragments (circles) linked by one of the six types of connectivity metrics (C_i, a–f, C_D, C_{DA}, C_{DAS}, C_{DS}, C_{SA}, C_S; see *Materials and Methods: Fragment connectivity metrics*); circle color represents patch connectivity (C_i) from low (red) to high (blue), while circle area represents patch area. Patch inputs represent C_i (focal patch connectivity) and outputs represent C_j (neighboring patch connectivity); arrow line widths are proportional to the magnitudes of C_{ij} and C_{ji}. In the equations, D_{ij} is the geographical distance between patches i and j, α is a parameter controlling the slope of the exponential decay of connectivity with distance, A_j is the area of neighboring fragments, and S_{ij} is the similarity in resource composition between fragments i and j; see *Materials and Methods* for further details. Thus, for instance, in panel c, arrows between circles 1 and 3 are thinner than between 1 and 2 and 2 and 3 because geographic distances contribute less to connectivity; circle 1 contributes less to connectivity of circles 2 and 3 (thinner arrows from 1 to 2 and 1 to 3 than in the opposite sense) because circle 1 is the smallest; and circle 2 contributes less to connectivity of 1 and 3 because it is the most dissimilar, as shown in panel f.

in greater connectivity in patch 3, even though it is the most distant patch. In addition, when geographical and non-geographical distances are weighted by neighboring area, larger neighbors weigh more (as illustrated by arrow direction and width). Thus, in Fig. 1b and e, patch 1 is the most connected, as it has at the same time the largest and nearest neighbor (patch 2) and the most similar neighbor (patch 3), which is also relatively large. In this study, we assessed six connectivity metrics with different combinations of the above three components to assess their relative contributions (Fig. 1). Overall, these metrics cover the entire gradient from strictly structural to strictly functional:

$$C_D : c_i = \sum e^{-\alpha d_{ij}}$$

$$C_{DA} : c_i = \sum e^{-\alpha d_{ij}} A_j$$

$$C_{DAS} : c_i = \sum e^{-\alpha d_{ij}} A_j S_{ij}$$

$$C_{DS} : c_i = \sum e^{-\alpha d_{ij}} S_{ij}$$

$$C_{SA} : c_i = \sum S_{ij} A_j$$

$$C_S : c_i = \sum S_{ij}.$$

Statistical analyses

To assess whether fragment area and/or connectivity components explained interaction diversity responses in the 14 studied habitat fragments, we used a maximum likelihood approach to select among competing models. We built all possible competing models using these two predictors (area and connectivity metric C_D, C_{DA}, C_{DAS}, C_{DS}, C_{SD}, and C_S), which resulted in 19 models, including (1) a series of full models, composed by area, one connectivity measure, and their interaction; (2) a series of additive models composed by area and one connectivity measure; and (3) a series of individual models composed by either area or one connectivity measure. This set of models was built for each trophic guild. To find the most relevant geographic scale describing fragment connectivity (metrics C_D, C_{DA}, C_{DAS}, and C_{DS}), we also

Reports

estimated the α value that best fit the data. We allowed α to vary from positive to negative values, so that connectivity could decrease or increase, respectively, with increasing distance. We then ranked models using Akaike's Information Criterion (AIC) and calculated Akaike weights (AIC weights) and evidence ratio for each model (Appendix S1: Table S2). The best-fitting model was that with the lowest AIC (defined as having ΔAIC = 0), selecting all models with ΔAIC ≤2. Analyses were carried out with the *bbmle* package in R (Bolker 2007).

RESULTS

Interaction diversity

We identified a total of 40 host species of shrubs and herbs, which we found to interact with 40 morphospecies of stem and leaf galls on 23 plant species, 25 miner morphospecies on 22 plant species, aphid morphospecies on 21 plant species, and scale insect morphospecies on 30 plant species (Appendix S1: Table S3). Furthermore, we identified some emerged adults from galls as the most likely gall inductors belonging to families Cecidomyiidae, Tanaostigmatidae, Cynipidae, and Psyliidae, while others were classified as gall inquilines rather than gallers sensu stricto. In 32% of galls, we found no herbivore emerged adults. although in most of them, we detected parasitoids or an exit hole that confirms the emergence of insects. Emerged adults from mines were identified as leaf miners belonging to families Agromyzidae, Gelechiidae, Bucculatricidae, Nepticulidae, and Gracillariidae, or as parasitoids, which represent 76% of all collected mines. Aphids (family Aphididae) and scale insects (superfamily Coccoidea) were not identified to any lower taxonomic level (Appendix S1: Table S1).

Fragment connectivity and fragment area as drivers of interaction diversity in trophic networks

Link richness was negatively related to connectivity for the four herbivore guilds, so that link richness tended to be greater for the least connected fragments (Fig. 2a–d; Appendix S1: Table S4). However, the connectivity metric included in the best-fitting model varied among guilds: while connectivity included only geographical distances for aphids, it included geographical distances weighted by similarity in resources for scale insects and only similarity in resources for gallers and miners. Furthermore, for those guilds for which the best-fitting model included geographic distance as part of the connectivity metric, the decay of connectivity with geographic distance also varied markedly among guilds (Fig. 2b, d).

In contrast, interaction composition was negatively or positively related to connectivity when similarity in composition was based on qualitative information (Jaccard's index) and quantitative information (Bray-Curtis index),

depending on the guild (Fig. 2e–l; Appendix S1: Table S4). Likewise, the connectivity metric included in the best-fitting model varied among guilds and qualitative or quantitative indices. Connectivity included geographical distances weighted by resource similarity for aphids (qualitative and quantitative composition) and leaf miners (only quantitative composition), resource similarity weighted by neighboring area for scale insects and gall makers (qualitative information in both), and only resource similarity for scale insects and gall makers (quantitative composition in both) and leaf miners (qualitative composition). Furthermore, for those guilds for which the best-fitting model included geographic distance as part of the connectivity metric, as found for interaction richness, the decay of connectivity with geographic distance also varied markedly among guilds (Fig. 2g, h, l).

DISCUSSION

Focusing on the interactions between plants and four herbivore guilds, we found that interaction diversity was related to fragment connectivity, suggesting an important role for both spatial distance per se and functional distances based on shared resources. This result was evident in terms of different connectivity models related to link richness and composition. Surprisingly enough, fragment area had no detectable imprint on interaction richness and composition.

An imprint of shared resources

A landscape can be described in many alternative ways. Here, we proposed to model the landscape as a habitat network where the connectivity is a function of geographic distance to neighboring fragments weighted by their area, as well as the similarity in resource composition between habitat fragments. We found that similarity in plant composition contributes more than the other components of connectivity to explain local interaction diversity between plants and herbivores, which suggests that traits of herbivore species determine their colonization and persistence in local communities regardless of the type of feeding habits, i.e., endophagous for leaf miners and gall makers or ectophagous for aphids and scale insects. According to basic mechanisms proposed for metacommunity dynamics, this finding suggests that species sorting may be at play, whereby species distributions and abundances can be related to the environmental or biotic conditions in a particular habitat (Leibold and Chase 2018). Thus, regional distribution of resources (regional heterogeneity), and not only local resources, seem to be important to explain local species interactions.

Negative effect of connectivity on link richness

Surprisingly, we found that link richness in the four plant–herbivore networks was negatively related to
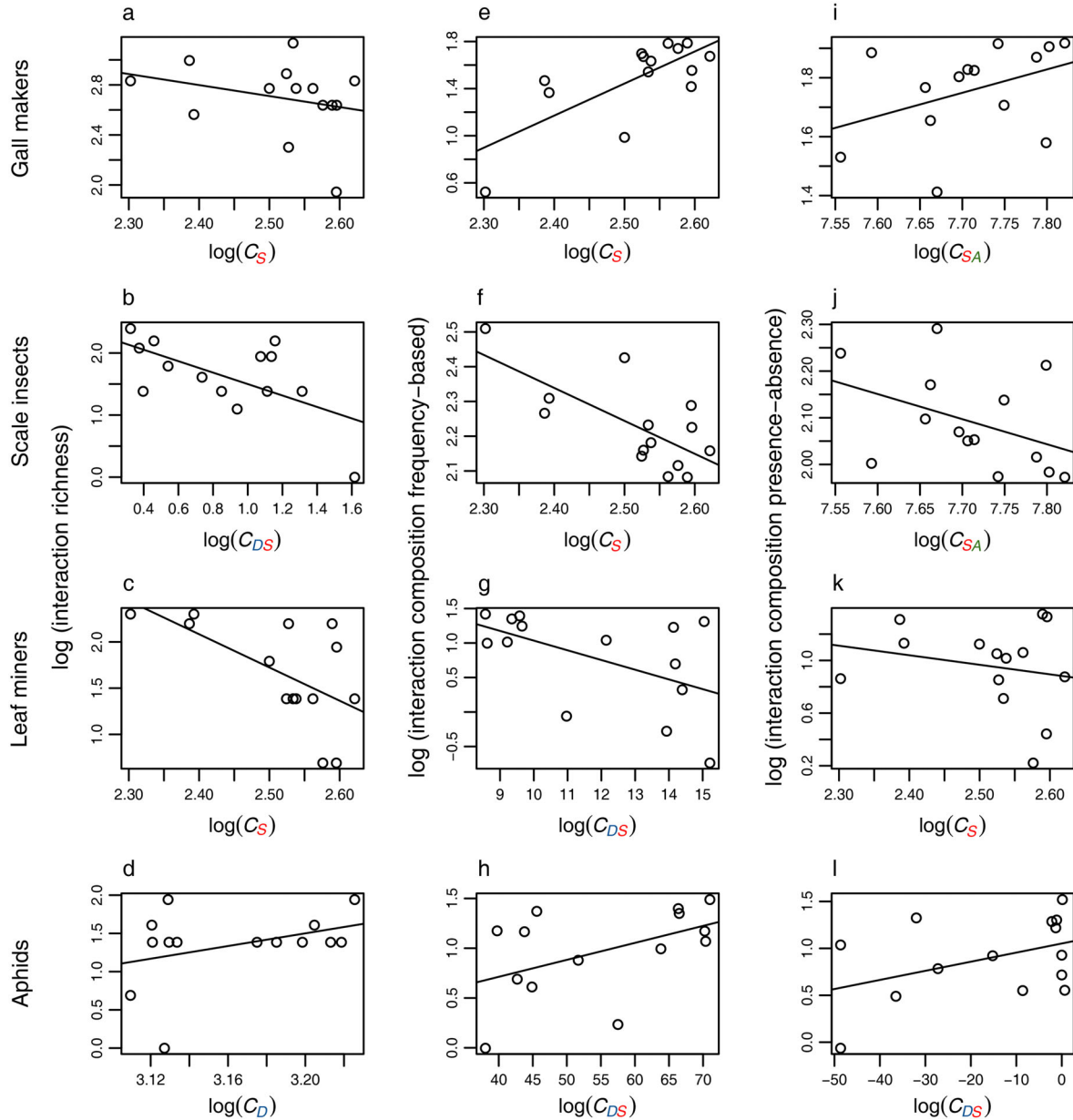
Reports

FIG. 2. Best-fitting models linking connectivity and fragment area to three plant–herbivore network properties: interaction richness, quantitative (frequency-based) similarity in interaction composition, and qualitative (presence–absence) similarity in interaction composition for four herbivore guilds (rows) on 14 habitat fragments in the study area in Valle de Uco (Mendoza, Argentina). The fragment connectivity metric (C) in each panel is expressed in terms of their components: D, geographical distances (in blue), A, neighboring area (in green), S, similarity in plant composition (in red); see Fig. 1 and *Materials and Methods* for details. Connectivity units are not standardized.

fragment connectivity when it included a strictly structural component (geographical distance), a functional component (similarity in resource composition), or both. Taken at face value, this result may seem counterintuitive, since we would expect that dispersal prevents local extinction and allows recolonization of locally extinct species from neighboring patches (Leibold 2004). Sampling stochasticity could have played a role in

determining link richness found in the fragments, mainly because detection of interactions involving rare species is less likely than interactions between common species, for example because they depend on where the sampling points and transects were placed. Yet, the pattern could also be attributed to landscape effects on another trophic level. Why a plant–herbivore interaction occurs in a local community depends not only on host plant

availability but also on the presence of natural enemies, namely the arrival of natural enemies with higher dispersal rates and wider home-range than herbivores (Grainger et al. 2017) and of competitively superior herbivore species (Meester et al. 2016); this may be truer for ectophagous insects such as scale insects and aphids, which are naturally more exposed to predators and parasitoids and have a tendency to be sedentary and build up large populations in a short time. In our study system, there are several superhost shrub species that harbor high herbivore richness of multiple guilds. Therefore, these superhosts may be a target for both dominant herbivore species and natural enemies, resulting in decreased interaction richness. In addition, when the effect of similarity in resource composition was stronger than the unique spatial effect or of both components combined, we infer that interaction richness is limited by common plants at intermediate abundances, and thus a significant number of interactions could occur between rare plants and rare herbivores actually present in more dissimilar fragments. Furthermore, an abundant superhost plant in a dissimilar fragment could be a target of higher richness of herbivore or natural enemies than in similar fragments where their abundance is lower. In addition, if specialist parasitoids are extirpated first from a landscape, releasing their target herbivores, leading to increased plant–herbivore link richness. This mechanism may be stronger in isolated fragments with highly dissimilar plant composition, where rare plants are more represented; this may be especially important for endophagous insects such as leaf miners and gall makers, which are highly specialized guilds and can benefit from an abundant superhost or specific rare hosts.

Positive and negative effects of connectivity on similarity in link frequency and composition

The observed negative effect of similarity in resource composition on similarity in link composition may be related to priority effects of some herbivore competitors (i.e., differences in the timing of species arrival in the community; Leibold and Chase 2018), which could contribute to define final community composition. Alternatively, if different species of rare herbivores interact with rare plants in different fragments, as we argued above for link richness, similarity in link composition should be negatively related to similarity in plant resources. Furthermore, when neighboring fragment area is also relevant, a mass effect could also be at play, which means that excess of individuals in the regional pool may disperse to less suitable habitat and survive even if their local growth rate is negative (Amarasekare and Nisbet 2001).

No effect of area per se?

Our results indicate that fragment area itself may not be a relevant determinant of local interaction diversity of plant–herbivore networks. A plausible explanation of this result is that current plant resource configuration in our study area is the result of recent habitat fragmentation (around 20 yr), which could imply that small, geographically isolated patches do not necessarily have lower plant species abundances and richness, because they are actually exhibiting their pre-fragmentation structure: an extinction debt (Helm et al. 2006). We found evidence for an extinction debt in our study system (Appendix S1: Fig. S3). Therefore, although we should expect that habitat loss and fragmentation lead to changes in plant community structure in the long run for the whole landscape, time since fragmentation in our system may simply be too short. Thus, local resources and plant–herbivore interactions are unlikely to have resulted from decreased area in fragments, but a detectable influence of fragmentation in the oldest fragments appears to be already on progress.

Conclusions

The long-term consequences of habitat fragmentation and habitat loss on ecological networks are poorly understood. Understanding how species and their interactions change across time and space is essential to mitigate the negative effects of habitat transformation and guarantee ecosystem functioning. Overall, two main factors may be driving plant–herbivore interaction diversity regardless of herbivore guild in this recently fragmented landscape: a so far unpaid extinction debt, especially involving shrubs, which are perennial and were the most represented life forms, and predation/parasitism pressure, which is likely strong and exerted mainly by generalists. Future studies should start from the premise that fragmentation consequences are not the same for all species (or species guilds); the challenge is to understand how these differences in spatial and presumably temporal scales among organisms are affecting local communities.

Literature Cited

Aizen, M. A., M. Sabatino, and J. M. Tylianakis. 2012. Specialization and rarity predict nonrandom loss of Interactions from mutualist networks. Science 335:1486–1489.

Amarasekare, P., and R. M. Nisbet. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist 158:572–584.

Bolker, B. 2007. Maximum likelihood estimation and analysis with the bbmle package. R package. Version 0.8.1.R Foundation for Statistical Computing, Vienna, Austria.

Reports

Reports

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical ecology with R. Springer, Berlin, Germany.

Borthagaray, A. I., M. Berazategui, and M. Arim. 2015. Disentangling the effects of local and regional processes on biodiversity patterns through taxon-contingent metacommunity network analysis. Oikos 124:1383–1390.

Bullock, J. 1996. Plants. Pages 111–138 in W. J. Sutherland, editor. Ecological Census Techniques: A Handbook. Cambridge University Press, Cambridge, UK.

Cagnolo, L., et al. 2009. Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. Conservation Biology 23:1167–1175.

Chisholm, C., Z. Lindo, and A. Gonzalez. 2011. Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. Ecography 34: 415–424.

Dale, M. R. T., and M. J. Fortin. 2010. From graphs to spatial graphs. Annual Review of Ecology, Evolution, and Systematics 41:21–38.

Economo, E. P., and T. H. Keitt. 2010. Network isolation and local diversity in neutral metacommunities. Oikos 119:1355–1363.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Gonzalez, A., B. Rayfield, and Z. Lindo. 2011. The disentangled bank: how loss of habitat fragments and disassembles ecological networks. American Journal of Botany 98:503–516.

Grainger, T. N., R. M. Germain, N. T. Jones, and B. Gilbert. 2017. Predators modify biogeographic constraints on species distributions in an insect metacommunity. Ecology 98: 851–860.

Haddad, N. M., et al. 2015. Habitat fragmentation and its lasting impact on earth's ecosystems. Science Advances 1: e1500052.

Hanski, I., and C. D. Thomas. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biological Conservation 68:167–180.

Helm, A., I. Hanski, and M. Parte. 2006. Slow response of plant species richness to habitat loss and fragmentation. Ecology Letters 9:72–77.

Holt, R. D., J. H. Lawton, G. H. Polis, and N. D. Martinez. 1999. Trophic rank and the species-area relationship. Ecology 80:1495–1504.

Jones, N. T., R. M. Germain, T. N. Grainger, A. M. Hall, L. Baldwin, and B. Gilbert. 2015. Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. Journal of Ecology 103:935–944.

Kaartinen, R., and T. Roslin. 2011. Shrinking by numbers: landscape context affects the species composition but not the quantitative structure of local food webs. Journal of Animal Ecology 80:622–631.

Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leibold, M. A., and J. M. Chase. 2018. Metacommunity ecology. Princeton University Press, Princeton, New Jersey, USA.

MacArthur, Robert H., and Edward O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Meester, L. D., J. Vanoverbeke, L. J. Kilsdonk, and M. C. Urban. 2016. Evolving perspectives on monopolization and priority effects. Trends in Ecology and Evolution 31:136–146.

Moilanen, A., and M. Neiminen. 2002. Simple connectivity measures in spatial ecology. Ecology 83:1131–1145.

Öckinger, E., et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters 13:969–979.

Öckinger, E., M. Winsa, S. P. M. Roberts, and R. Bommarco. 2018. Mobility and resource use influence the occurrence of pollinating insects in restored seminatural grassland fragments". Restoration Ecology 26:873–881.

Oksanen, J. et al. 2019. vegan: Community Ecology Package. R package version 2.5-2. https://CRAN.R-project.org/package= vegan

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences 105:20770–20775.

Sabatino, M., et al. 2010. Direct effects of habitat area on interaction diversity in pollination webs. Ecological Applications 20:1491–1497.

Schooley, R. L., and L. C. Branch. 2011. Habitat quality of source patches and connectivity in fragmented landscapes. Biodiversity and Conservation 20:1611–1623.

Steffan-Dewenter, I. 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conservation Biology 17:1036–1044.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Thompson, P. L., B. Rayfield, and A. Gonzalez. 2017. Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. Ecography 40:98–108.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Titeux, N., et al. 2018. Global scenarios for biodiversity need to better integrate climate and land use change. Diversity and Distribution 23:1231–1234.

Urban, D., and T. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205–1218.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2883/suppinfo