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Context-dependency and anthropogenic effects on individual plant–frugivore networks

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Anthropogenic activities, such as grazing by domestic animals, are considered drivers of environmental changes that may influence the structure of interaction networks. The study of individual-based networks allows testing how species-level interaction patterns emerge from the pooled interaction modes of individuals within populations. Exponential random graph models (ERGMs) examine the global structure of networks by allowing the inclusion of specific node (i.e. interacting partners) properties as explanatory covariates. Here we assessed the structure of individual plant–frugivore interaction networks and the ecological variables that influence the mode of interactions under different land-use (grazed versus ungrazed protected areas). We quantified the number of visits, the number of fruits removed per visit and the interaction strength of mammal frugivore species at each individual tree. Additionally we quantified ecological variables at the individual, microhabitat, neighborhood and habitat scales that generated interaction network structure under the different land uses. Individual plant–frugivore networks were significantly modular in both land uses but the number of modules was higher in the grazed areas. We found interaction networks for grazed and ungrazed lands were structured by phenotypic traits of individual trees, by the microhabitat beneath the tree canopy and were affected by habitat modifications of anthropogenic origin. The neighborhood surrounding each individual plant influenced plant–frugivore interactions only at the grazed-land trees. We conclude that anthropogenic land uses influence the topological patterns of plant–frugivore networks and the frugivore visitation to trees through modification of both habitat complexity and the ecological traits underlying interactions between individual plants and frugivore species.

Keywords: ecological networks, intrapopulation heterogeneity, land uses

Introduction

Species participating in ecological interactions, e.g. mutualism, antagonism and commensalism, are influenced by both biotic and abiotic factors, leading to widespread context-dependency in interaction outcomes and network structure (Bronstein

2015). These interactions are often embedded in mega-diverse networks (Bascompte and Jordano 2014). Recent efforts are assessing how the characteristics of the nodes (partner species) influence the density and strengths of the links (interactions) leading to distinct interaction modes (Rodríguez-Rodríguez et al. 2017) and, finally, determine network structure. Ultimately, the interaction pattern at the species-level described in most complex networks emerges from the pooled interaction modes shown by individuals within populations (Bolnick et al. 2011, Tur et al. 2014). Yet we are far from understanding how individual traits and ecological variables mold interaction patterns in nature.

The study of ecological interaction networks emerged as a way to visualize entire communities and compare complex interaction systems in different environments (Bascompte and Jordano 2014). In particular, bipartite networks depict multiple plant and animal species (nodes) that interact between them and are connected by links (Bascompte et al. 2006). These species-level links, actually emerge from individual-based networks (e.g. interactions among individual plants and their pollinators), given that trait variation among individuals might shape the structure of species-level ecological interactions (Carlo et al. 2007, Valverde et al. 2016, Rodríguez-Rodríguez et al. 2017). In this context, variation in interactions at the intraspecific level has the potential to affect ecological processes or community organization at different levels of biological organization (Bolnick et al. 2011). Thus, the heterogeneity of traits among individuals within populations and the biotic interactions they are involved in may have different implications for population dynamics and persistence (Carlo 2005, Gómez and Perfectti 2012).

Topological network properties such as nestedness and modularity are useful indexes to describe the architecture of mutualistic interactions (Dormann et al. 2009, Bascompte and Jordano 2014) and also to compare multiple networks across communities (Jordano et al. 2003). However, models of food webs and interaction networks have been routinely built on averaged estimators for species, implicitly ignoring variation in patterns and outcomes among individuals (Melián et al. 2014). Thus, a persisting challenge has been to predict interaction patterns from the traits of interacting partners, in a way that the multiple influences on outcomes can be teased apart. For example, both spatial arrangement (i.e. structure of fruiting neighborhoods) and individual traits such as size, plant architecture and fecundity, or flower shape and fruit size determine distinct modes of interaction with pollinators and frugivores that ultimately influence the position of individual plants within the population mating network or in the ranked contributions to seed rain (Carlo 2005, Valverde et al. 2016, Rodríguez-Rodríguez et al. 2017). Yet the use of modeling frameworks for testing specific hypotheses about the influences of intrinsic and extrinsic traits of nodes on network topology and structure is still very limited in ecology.

Variation in the outcome of interspecific interactions due to biotic and abiotic contexts (i.e. context-dependence) has been documented in a number of studies (Thompson 1988, Agrawal et al. 2007, Chamberlain and Holland 2009, Valverde et al. 2016, Rodríguez-Rodríguez et al. 2017). In particular, plant–pollinator and plant–frugivore interactions are greatly context-dependent (Carlo 2005, Carlo and Yang 2011, Rodríguez-Rodríguez et al. 2017), mainly because they largely involve generalized interactions among partners instead of highly specialized ones (Schleuning et al. 2012). One of the main drivers of the context variation in interaction networks can be anthropogenic disturbances, such as species introduction and changes in land use managements, by modifying natural habitats and population abundances (Tylianakis et al. 2008, Dirzo et al. 2014, Potts et al. 2016, Vanbergen et al. 2017). Alteration of mutualisms by anthropogenic drivers may in turn affect the maintenance of biodiversity and the ecosystem services provided (Tylianakis et al. 2008, Kiers et al. 2010, Díaz et al. 2013). Changes in landscape patterns occurring at both local and larger scales (forest loss and fragmentation, mosaics of vegetation, shrub encroachment, etc.) may lead to changes in mutualistic assemblages and thus impact the outcomes of interactions in a number of ways (Tscharntke et al. 2012). These influences can be properly assessed within complex interaction networks with the help of generalized linear models (ERGM). Such models explicitly account for both the attributes of the nodes, i.e. characteristics or properties of species or individuals that covary with the modes of interaction and their outcomes, and the full structure of the network (Wasserman and Pattison 1996, Snijders et al. 2010).

The social sciences have an extended tradition of causal modeling approaches to decipher correlates of complex social interactions (Saul and Filkov 2007). Recent social network studies have extensively used exponential random graph (ERGMs) and probability (p*) models to account for the global structure of social networks as a function of their "local" features, i.e. properties of the interacting nodes (Wasserman and Pattison 1996, Wang et al. 2013). ERGMs model the probability distribution function (pdf) for interactions within a given class of graphs (Snijders et al. 2010). Given an observed graph and a set of explanatory variables on that graph the pdf is estimated. The pdf provides a concise summary of the class of graphs to which the observed graph belongs, i.e. the pdf can be used to calculate the probability that any given graph is drawn from the same distribution as the observed graph. When comparing the observed network structure with modeled networks that include or exclude specific covariates of node attributes, inferences can be made about causal influences determining how interactions are distributed among nodes in the network (Kolaczyk and Csárdi 2014).

In this study we assessed the effect of land use management (protected areas and surrounding grazed lands) and the heterogeneity of individual tree traits on the structure and organization of plant–frugivore networks. We used an individual-based approach and a plant-based perspective to evaluate the strength and frequency of plant–frugivore interactions and their context-dependency at the scale of

individual trees within distinct types of landscape. The study plant is *Prosopis flexuosa* (Fabaceae: Mimosoideae), a key tree species in its natural distribution area (Campos and Velez 2015). We hypothesized that frugivory networks will vary at two scales, the local or individual context determined by the ecological traits of each individual plant (e.g. tree size, fruit crop, physiognomy of the growing site, neighborhood effects) (García et al. 2001, Carlo 2005, Bolnick et al. 2011), and at a broader context influenced by the large-scale anthropogenic land use where interactions take place. Specifically, we: 1) evaluated the topological patterns of frugivory networks among individual *Prosopis* plants and their frugivore assemblage; 2) compared the topological patterns of frugivory networks between protected areas and surroundings grazed lands; 3) related variation of frugivore visitation to trees with individual plant traits, and 4) linked topological patterns of plant–frugivore networks to the ecological variables underlying the interactions.

Material and methods

Study site

We conducted the fieldwork in the MaB Ñacuñán Reserve (ungrazed site) and in adjacent grazed lands located at Mendoza Province, Argentina (see Supplementary material Appendix Table A1 for details). The climate is semi-arid and seasonal, with hot wet summers (mean temperatures >20°C) and cold dry winters (mean temperatures <10°C). The mean annual precipitation is 325 mm (Estrella et al. 2001). Vegetation communities that occur in the area are: *Prosopis flexuosa* woodlands, creosotebush shrublands and sand dunes (Roig 1971). Open woodlands consist of a tree layer of *P. flexuosa* and *Geoffroea decorticans*, a shrub layer of *Larrea divaricata*, *L. cuneifolia* and *Condalia microphylla*, and a grass layer of *Pappophorum* spp. *Trichloris crinita* and *Digitaria californica* (Roig 1971).

The Ñacuñán Reserve (34°02'S, 67°58'W) is the only fenced protected area in the Monte Desert Biome free from livestock since 1961 (Ojeda et al. 1998). Around the reserve, grazing by domestic animals (predominantly cattle) is the main land use. The production system is extensive with an average stocking density of 27 ha per animal unit (Guevara et al. 2009). *Prosopis flexuosa* is the only tree species (mean height = 5 m) in the plant community that produces large-sized fruits (length = 14 ± 2 cm; number of seeds = 15 ± 2; individual fruit dry mass = 2.47 ± 0.68 g) with a sugary mesocarp attractive to animals (Roig 1971, Kingsolver et al. 1977, Mooney et al. 1977). The *Prosopis* assemblage of frugivores includes mammal species ranging from antagonistic (seed predators) to mutualistic species (legitimate seed dispersers; Campos and Ojeda 1997, Campos et al. 2008, 2017, Giannoni et al. 2013). Previous studies showed that the species is visited by a restricted set of frugivore species (Campos et al. 2016, Miguel et al. 2017).

Plant–frugivore interactions

The study was conducted during the *P. flexuosa* fruiting season in the years of 2015 and 2017. We selected two replicated areas inside the ungrazed site and three adjacent grazed sites (n sites = 4), and following internal roads we randomly chose and individually tagged adult *P. flexuosa* trees (diameter ground level >7.5 cm; Álvarez et al. 2006). To avoid spatial pseudoreplication, we defined a pairwise average distance among trees of 400 m. The number of selected trees was 70 for the ungrazed (with subgroups of trees located in two different areas inside the site) and 120 (three subgroups of trees located in different sites) for the grazed lands (n= 190; Supplementary material Appendix 1 Fig. A2).

We placed an infrared camera trap on a branch of every tree at 1.5 m above the ground to quantify the number of visits and the number of fruits removed by frugivore species at each focal tree. Cameras were vertically-oriented (De Bondi et al. 2010) and faced to a bait station of 20 *Prosopis* fruits under the tree crowns. Before placing the fruits we removed all other ripe fruits on the ground under the tree crowns. To prevent false triggers, we cleared the vegetation in an area of 0.07 m^2 where fruits were placed (Smith and Coulson 2012). Each camera was set up to take 3 consecutive photographs every 30 s, triggered by movement at high sensitivity to detect small mammal species (<100 g), during 48 h (total hours recorded = 9120). A total of 40 cameras (20 per site) were operating simultaneously at randomly-selected trees. We downloaded photographs captured by cameras and analyzed images individually to identify frugivores at the species level following species descriptions (Braun and Ojeda 2000, Giannoni et al. 2001, Tognelli et al. 2001).

The sequence of three consecutive photographs by a frugivore species was defined as a visitation event, and the frequency of interactions was calculated by summing all the independent visits of each frugivore species to every focal tree. To determine the number of removed fruits by each frugivore species per visit we subtracted the number of final fruits (number of fruits left after each frugivore visit) from the number of initial fruits and summed all removed fruits per frugivore species at every tree to determine the intensity of interactions.

Plant traits

For each focal tree we obtained a set of intrinsic and extrinsic ecological variables (Jordano and Schupp 2000). The intrinsic variables include individual tree traits: total tree height, number of unripe fruits on crown and number of ripe fruits on ground beneath tree crown. In order to count all the fruits on the canopy and the ground beneath, two observers scanned each *Prosopis* tree before the installation of the camera trap.

As extrinsic tree variables we characterized two scales, the immediate surroundings of each tree and the broader, mesoscale characteristics of the habitat surroundings. Thus, the extrinsic variables include the number of interspecific

and intraspecific tree neighbors surrounding each focal tree within a circle of 10 m radius (hereafter neighborhood). To describe the microhabitat beneath each *Prosopis* tree canopy, we measured the vegetation cover beneath tree crowns using the modified point quadrat method (Passera et al. 1983). Under each tree canopy we quantified the height and cover of plant species every 0.3 m at four 3 m-long transects (oriented to the cardinal points). We estimated the mean and standard deviation of: total vegetation cover, bare ground cover, litter cover and vegetation cover classified at three height stratum (lower: 0.2 to 0.4 m; medium: 0.6 to 0.8 m and high stratum: 1.1 to 1.4 m). To summarize data for each vegetation stratum we obtained the Shannon–Wiener diversity index for each tree (H'= $-\Sigma\ p_i \log p_i$) (Magurran 2004). We also recorded the geographical location (UTM coordinates) for every focal *Prosopis* tree.

To describe the habitat at the mesoscale in the proximity of each *Prosopis* tree (hereafter habitat), we used the modified point quadrat method (Passera et al. 1983) with 100 sample stations along ten 50 m length transects in each of the ungrazed and grazed sites (n sample stations per site= 1000) and obtained the same vegetation measures explained in the paragraph above for the transects under tree crowns. In order to relate habitat structure with focal *Prosopis* trees we associated trees to the nearest vegetation transect. For doing so, we considered a middle distance point at each transect and associated its data to the nearest tree(s) using the geographical positions of trees and transects. In cases with more than one transect located near to only one tree, we averaged covers of those transects and associated the averaged data to the tree.

Data analysis

Individual-based network analysis

We constructed weighted bipartite networks between *P. flexuosa* individual trees and frugivore species (i.e. individual-species networks) for both land uses (ungrazed and grazed sites), by defining an adjacency matrix among 190 plants as rows and frugivore species as columns. Matrix elements were > 0 if a plant–frugivore interaction occurs and zero otherwise (Bascompte and Jordano 2014). For each individual plant we obtained the number of visits per animal species (frequency of interaction) and the number of removed fruits per visit (intensity of interaction). We obtained the interaction strength (total effect) by multiplying frequency and intensity of interactions (Vázquez et al. 2005). Individual *Prosopis* plants and frugivore species were represented as nodes in weighted bipartite networks with links representing the interaction strength between them. We discarded data from trees in which camera traps did not work (n=8). In addition, we dropped from further analyses (except visualization of the networks) those trees for which no interaction was recorded during the sampling (n=9 and n=14 trees in the ungrazed and grazed areas, respectively).

We used the nonparametric Spearman's rank-order correlation test to compare the ranks in intensity of frugivore interactions across species at both land uses. To describe

and compare the topological structures between plant–frugivore weighted networks we estimated three parameters, modularity (M) by applying the Beckett algorithm (Beckett 2016), the Hamming distance (HD), and the graph structural correlation (gscor). Modularity is the tendency of a network to be organized in clusters, in which a modular network is organized into highly inter-connected subsets of nodes being less connected to other nodes (Olesen et al. 2007, Dupont et al. 2009). In our study modules represent groups of individual plants in the populations that shared higher number of interactions of similar frugivore species. The Hamming distance between two network graphs measures the minimum number of link substitutions required to change one network into the other, or the minimum number of link additions/deletions that could have transformed one network into the other (Butts and Carley 2005). The overall structural congruence between the two network graphs was tested with the structural graph correlation (gscor; 'sna' package in R).

The significances of both modularity and Hamming distance were assessed by randomization, based on null models with 999 iterations each. Significance of the Hamming distance between the two networks compared is obtained by estimating the distance between one of the observed networks and each of n=999 randomized versions of the other. An observed distance above a 95% significance percentile indicates a significant difference in the overall structure of the two networks. The Hamming distance estimation requires networks of the same size. Given that the grazed area had a larger sample of trees (n=106) compared to the ungrazed area (n=61), we subsampled the grazed dataset (n=999 random subsamples without replacement) to samples of n=61 trees and run the Hamming distance estimation algorithm at each iteration. We averaged the observed distance estimation and compared its value to the average of the total 998 001 randomizations obtained during the runs. The significance for the gscor estimate was obtained by a similar repeated subsampling of the larger network, as explained above. We used the 'ggplot2' and 'igraph' R packages for networks fitting and visualization (Csárdi and Nepusz 2006, Wickham 2009) and the 'bipartite' and 'sna' packages for network analysis and comparisons (Handcock et al. 2008, Butts 2016).

Frugivore visitation to trees

To test for relationships between frugivore visitation and plant traits we performed canonical correlation analysis (CCA; Borcard et al. 2011). Thus, we compared two multivariate data sets of the same length (same number of rows, the number of studied trees, n=120), in which one included plant traits (tree traits, neighborhood, microhabitat and habitat) while the other data set included data of frugivore species-specific visitation to trees. Before performing CCA, we tested for multicollinearity (VIF factors) among predictor variables, setting a conservative threshold of 2 (package 'vif' in R) and excluding redundant variables.

The CCA generates pairs of synthetic variables (canonical variables) by linear combinations of the two measured sets of variables in order to maximize their correlations. The analysis obtained canonical correlations (R^2) between synthetic variables that refer to the total variance from data sets explained by them. In order to assess the significance of the canonical correlation, the CCA performs a Wilk's lambda test in which the lambda value represents the total variance not explained by the full canonical model (Nimon et al. 2010). We used the CCA R package for performing the canonical correlation analysis (González and Déjean 2012).

Ecological correlates

We built exponential random graph models (ERGMs) to analyze the ecological variables that might have produced the structure of weighted plant–frugivore networks at each land use (Kolaczyk and Csárdi 2014). First we tested for multicollinearity (pearson correlation) among predictor variables and we did not include in models variables with a pairwise correlation > 0.30, considering a value of $p < 0.05$. ERGMs implement a version of Markov chain Monte Carlo maximum likelihood to estimate parameters within linear models analogous to general linear models (GLM's). The structure of an ERGM closely parallels that of a standard regression model in statistics. The presence or absence of network edges (i.e. the interaction links between a tree and the frugivore species visiting it) is taken to be the response variable, while the role of the predictor variables is played by some combination of network summary statistics (i.e. endogenous variables) and functions of node and edge attributes (i.e. incorporating exogenous effects of variables such as tree size, density of neighbors, etc.). Given that the theoretical justification for the asymptotic χ^2 and F-distributions used by ERGM to compute the significance values for the parameter estimates has not been established formally to date, our preference is to interpret these values with caution, as additional summary statistics (Kolaczyk and Csárdi 2014).

In its simplest form, the model specifications involve statistics that are functions only of the network structure (i.e. controlling for endogenous effects derived from just the pattern of links among nodes). Yet we may expect that the probability of a link joining two nodes depends not only on the status (i.e. presence or absence) of links between other pairs of nodes, but also on attributes of the nodes themselves (i.e. allowing for assessment of exogenous effects). For attributes that have been measured, we can incorporate them into the ERGM specification in the form of additional statistics in the exponential term (Snijders et al. 2010, Kolaczyk and Csárdi 2014). Thus, the presence or absence of network links and their configurations is considered as a response variable in random graph models. In addition, we considered plant node traits (tree characteristics, neighborhood, microhabitat and habitat variables) as predictor variables in the ERGM. Therefore, we first have assigned specific ecological traits to each plant node (i.e. node attributes) and then we associated

the weighted bipartite structures to these traits in order to assess the conditional contribution of each predictor variable to the overall network structure. To verify independence, we tested for spatial autocorrelation between latitudinal (X) and longitudinal (Y) coordinates of each *Prosopis* tree using the corAR1 function from the 'nlme' R package (Pinheiro et al. 2016).

We set four groups of models including different descriptor variables according to the types of effect tested: individual tree models, including variables of tree size and fecundity; neighborhood models, with variables associated with the intraspecific and interspecific neighborhood of each *Prosopis* tree; microhabitat models, including descriptors of the vegetation cover surrounding each focal tree, and, habitat models, with variables related to vegetation cover describing land uses. To compare model fits we computed analysis of variance (ANOVA) using the 'Chisq' test statistic (Handcock et al. 2017) and we followed the BIC (Bayesian information criterion) approach to model selection (Link and Barker 2006). We performed ERG models using the 'sand' and 'ergm' R packages (Hunter et al. 2008, Handcock et al. 2017, Kolaczyk and Csárdi 2017). Analyses were performed using R ($<$ www.r-project.org $>$).

Data deposition

Data and R code for the analyses are available at the GitHub repository: $<$ https://github.com/PJordano-Lab $>$ and the Dryad Digital Repository $<$ http://dx.doi.org/10.5061/dryad.1n755 $>$ (Miguel et al. 2018).

Results

Prosopis–frugivore networks at different anthropic land uses

We analyzed a total of 29 902 images from camera traps (18 271 for grazed and 11 631 for ungrazed land uses) in which 12 frugivore species were recorded interacting with a total of 167 *Prosopis* trees (Fig. 1). Also, other three species, including one bird species, *Eudromia elegans*, were recorded visiting trees but not removing fruits (Supplementary material Appendix 1 Table A2 for taxonomic details). The total number of trees without frugivore interactions recorded was 15.

The ranked intensity of frugivore interactions across species was significantly consistent when comparing trees at the ungrazed and grazed lands (S = 122.86, p = 0.05, Spearman's rho = 0.57). However, individual frugivore species varied in their frequency, intensity and strength of interactions with *Prosopis* plants in the two land uses (Table 1). The total number of frugivore species interacting with *Prosopis* trees was 11 for grazed (two domestic species) and nine for ungrazed lands (Table 1, Fig. 1). *Microcavia australis* was the species with

Figure 1. Photos from camera traps illustrating the main frugivore species interacting with *Prosopis* trees. (A), *Graomys griseoflavus*; (B), *Dolichotis patagonum*; (C), *Microcavia australis*; (D), *Lycalopex griseus*; (E), *Conepatus chinga*; (F), *Chaetophractus vellerosus*. Infrared camera traps were suspended from the canopy, on a branch of every sampled tree 1.5 m above the ground.

the highest number of frugivory interactions recorded at both land uses.

The topologies of plant–frugivore interaction networks did not differ between land use types (Hamming distance [mean and 1st–3rd quantiles] = 77 900 [74 900–80 900]; randomized values: 95 600 [93 400–97 900]), with the observed Hamming distances being significantly below the randomized ones (p = 0.003). The overall congruency of the two network topologies and structures is further supported by the significant structural graph correlation (gscor) between them, assessed with a quadratic-assignment procedure (gscor = 0.8421, p < 0.0001).

Frugivory networks were significantly modular at both land uses and modularity values were highly significantly different of that expected from a random distribution (M_{grazed} = 0.52, z = 51.39, p << 0.0001; $M_{ungrazed}$ = 0.41, z = 26.38, p << 0.0001). The weighted bipartite networks comprised nine modules for grazed lands and five for ungrazed land use (Supplementary material Appendix 1 Fig. A1). The majority of modules included only one frugivore species interacting with either a large number of *Prosopis* trees (e.g. *M. australis* at grazed and ungrazed networks) or a low number of trees (e.g. *Dolichotis patagonum* at the ungrazed network; Fig. 2). Additionally, connectance (C) and nestedness (NODF, Almeida-Neto et al. 2008) were statistically significant for both interaction networks (C_{grazed} = 0.11, z = –10.45, p << 0.0001; $C_{ungrazed}$ = 0.16, z = –9.56, p << 0.0001; $NODF_{grazed}$ = 9.16, z = –11.87, p << 0.0001; $NODF_{ungrazed}$ = 23.68, z = –11.16, p << 0.0001).

Table 1. Number of trees visited at least once and interaction measures (frequency, intensity and total effect) between frugivore species and *Prosopis* trees of the grazed (G) and ungrazed (Ug) land uses. Frequency of interactions indicates the number of total visits of each mammal species to trees; intensity of interactions represents the number of fruits removed from trees per species, and the total effect was calculated as the product of frequency and intensity. Data indicate mean values ± 1SE.

Frugivore species	Order: Family	Anthropic land use	No. of visited trees	Frequency	Intensity	Total effect
Graomys griseoflavus	Rodentia: Muridae	G	66	5.08 ± 0.72	3.38 ± 0.53	42.09 ± 8.15
		Ug	51	16.46 ± 2.96	4.99 ± 0.80	114.81 ± 31.85
Akodon dolores	Rodentia: Muridae	G	35	2.42 ± 0.50	2.44 ± 0.53	28.67 ± 7.79
		Ug	27	8.51 ± 1.83	1.36 ± 0.42	42.39 ± 16.56
Calomys musculinus	Rodentia: Muridae	G	3	0.05 ± 0.03	0.08 ± 0.08	0.08 ± 0.08
		Ug	6	0.24 ± 0.11	0.07 ± 0.05	0.24 ± 0.16
Microcavia australis	Rodentia: Caviidae	G	67	11.61 ± 1.75	4.98 ± 0.69	157.74 ± 30.18
		Ug	47	20.23 ± 3.20	6.90 ± 0.96	270.97 ± 51.37
Dolichotis patagonum	Rodentia: Caviidae	G	6	0.49 ± 0.29	0.49 ± 0.26	8.00 ± 5.07
		Ug	4	0.27 ± 0.16	0.26 ± 0.22	1.59 ± 1.50
Ctenomys mendocinus	Rodentia: Ctenomyidae	G	0	–	–	–
		Ug	1	0.03 ± 0.03	0.09 ± 0.09	0.17 ± 0.17
Bos taurus	Artiodactyla: Bovidae	G	26	1.25 ± 0.30	1.93 ± 0.48	11.87 ± 3.61
		Ug	0	–	–	–
Equus caballus	Perissodactyla: Equidae	G	5	0.38 ± 0.17	0.54 ± 0.29	5.33 ± 2.97
		Ug	0	–	–	–
Lycalopex griseus	Carnivora: Canidae	G	28	0.80 ± 0.21	1.39 ± 0.40	8.50 ± 3.09
		Ug	9	0.23 ± 0.08	0.44 ± 0.22	0.91 ± 0.55
Conepatus chinga	Carnivora: Mephitidae	G	16	0.27 ± 0.08	0.38 ± 0.16	1.13 ± 0.52
		Ug	4	0.06 ± 0.03	0.04 ± 0.04	0.04 ± 0.04
Chaetophractus vellerosus	Xenarthra: Dasypodidae	G	9	0.10 ± 0.03	0.20 ± 0.09	0.27 ± 0.12
		Ug	7	0.10 ± 0.04	0.13 ± 0.11	0.13 ± 0.11
Tupinambis rufescens	Lacertilia: Teiidae	G	7	0.11 ± 0.05	0.10 ± 0.08	0.25 ± 0.18
		Ug	4	0.06 ± 0.03	0	0

Ecological context of frugivore visitation to *Prosopis* trees

For grazed land uses, variation in frugivore visitation to trees was significantly related with plant traits (Wilk's λ = 0.05, F = 1.62, df = 176,761, p << 0.0001; Table 2). Only the first canonical variable was significant, with a canonical correlation of $R^2 = 0.65$ (F = 1.62, p << 0.0001), explaining 46% of the total variance shared between the two original variable sets. Frugivore species with high correlations on this canonical variable included: *Tupinambis rufescens* (0.772), *Conepatus chinga* (0.520), *Akodon dolores* (0.249), *Bos taurus* (0.210), *Equus caballus* (0.215) and *Chaetophractus vellerosus* (–0.259). Regarding the plant traits, this first canonical variable was mainly correlated with traits describing trees fecundity (fruits on crown, 0.908, and fruits on ground, 0.313), interspecific neighborhood (–0.226), microhabitat variables (variation of the low height vegetation stratum, 0.195; cover and variation of the medium height vegetation stratum, –0.195 and –0.225, respectively) and habitat characteristics (litter cover, 0.271 and cover of the high height stratum 0.226; Table 2).

Contrary to what we found for grazed lands, frugivore visitation was not significantly correlated with plant traits at ungrazed land- uses (Wilk´s λ = 0.08, F = 0.88, df = 140,345, p = 0.81). The first fitted model explained 43% of the total variance shared between the two original variable sets $R^2 = 0.59$ (F = 0.88, NS; Table 2).

Correlates of individual-specific *Prosopis* traits and interaction patterns

As expected from the tree-sampling protocol, where focal trees were selected at a minimum distance of 400 m, the visitation patterns to *Prosopis* plants were not spatially correlated (L = –1194.3, df = 5, p = 1). Therefore we fitted the ERG models without any spatially-explicit information. The number of edges between nodes in the grazed-lands graph was of $L(y_g) = 1368$, while in the ungrazed-lands graph was of $L(y_{ug}) = 482$. Because of the bipartite character of these networks, triads (i.e. three nodes connected by links) were not a possible outcome, as individual plants can directly interact only with animals and not between them.

We fitted twelve candidate models for the grazed-lands graph and ten for the ungrazed-lands network graph (Supplementary material Appendix 1 Table A3). For both the grazed and ungrazed-lands graphs, the edges effects were highly significant, implying that there is an influence of the number of interactions on the probability of observing the given networks; i.e. the probability of a link is proportional to the degrees of the interacting nodes. For the grazed-lands graph the exponential random model containing twelve predictor variables (full model) was the one that better explained the variation in network connectivity. This model showed that, tree height decreases the odds of plant–frugivore (vertices) interactions by a factor of exp (–0.016847) = –1.07. Moreover, crown fruits (standing fruit crop) increases the odds of
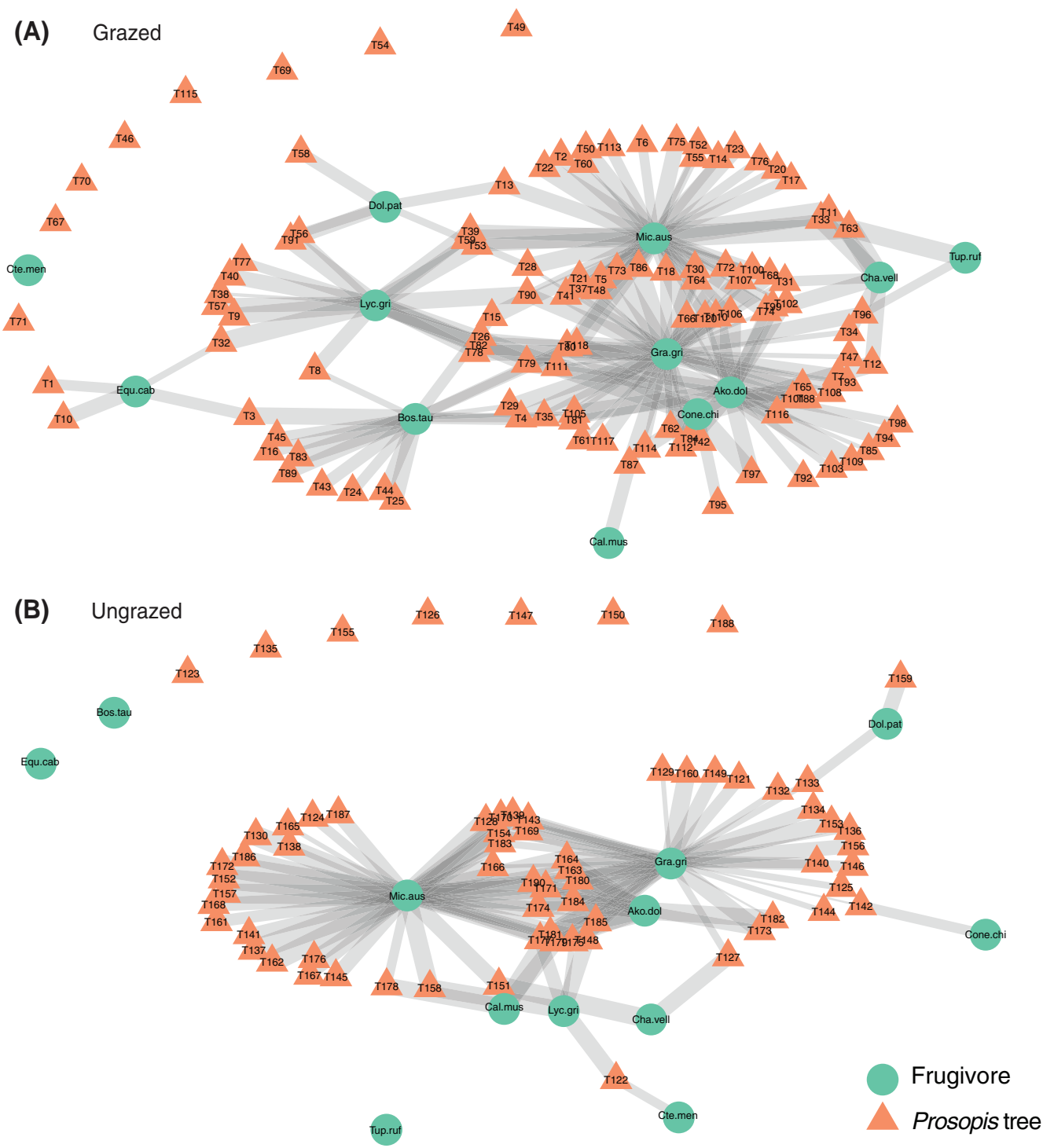
Figure 2. Energy-minimization graphs illustrating weighted bipartite networks between individual *Prosopis* trees (orange nodes) and frugivore species (green nodes) in sites under different anthropogenic land managements, (A) grazed and (B) ungrazed land uses. Lines (edges) represent a frugivory interaction. The width of the edges represents the scaled interaction strength (total effect) between frugivore species and individual trees. Codes for frugivore species represent: Gra.gri = *Graomys griseoflavus*; Ako.dol = *Akodon dolores*; Cal.mus = *Calomys musculinus*; Mic.aus = *Microcavia australis*; Dol.pat = *Dolichotis patagonum*; Cte.men = *Ctenomys mendocinus*; Bos.tau = *Bos taurus*; Equ.cab = *Equus caballus*; Lyc.gri = *Lycalopex griseus*; Cone.chi = *Conepatus chinga*; Cha.vell = *Chaetophractus vellerosus*; Tup ruf = *Tupinambis rufescens*.

vertices interactions by a factor of exp $(0.004764) = 1.005$. Attributes that significantly decreased the odds of tree interactions with frugivore species were: tree height, number of intraspecific neighbors, vegetation mean cover beneath the tree canopy, variation in litter cover and the mean cover of the low vegetation stratum at the habitat scale (Table 3).

Table 2. Coefficients for the original sets of variables on the first canonical variable, testing the overall correlation between frugivore visitation and plant traits at grazed and ungrazed land uses. Only the first canonical variables had λ > 1. SD = standard deviation.

Original variable	Grazed land uses Canonical variable I λ = 1.88 (46.3%) R = 0.808***	Ungrazed land uses Canonical variable I λ = 1.45 (43.2%) R = 0.769[NS]
Frugivore variables		
G. griseoflavus	–0.024	0.001
A. dolores	0.047	0.018
C. musculinus	–0.072	–0.303
M. australis	–0.004	0.019
D. patagonum	0.016	–0.200
L. griseus	0.010	–0.121
C. chinga	**0.393**	2.438
C. vellerosus	**–0.514**	–0.110
T. rufescens	**1.361**	–0.054
B. taurus	0.033	–
E. caballus	0.115	–
C. mendocinus	–	0.322
Plant variables		
height	–0.002	–0.001
crown fruits	0.008	0.002
ground fruits	0.001	0.002
no. inters. neighbours	–0.045	–0.112
no. intras. neighbours	–0.027	0.022
vegetative cover SD	**0.279**	0.113
bare ground cover	**–0.324**	–1.749
bare ground SD	**–0.569**	–
low height cover	–	–3.182
low height cover SD	**1.101**	–2.559
medium height cover	**–0.241**	–
medium height cover SD	**–1.079**	0.555
high height cover	**–0.379**	–0.273
H' Shannon–Wiener	**–1.345**	–
litter cover (habitat)	**0.671**	1.522
low height cover (habitat)	**0.497**	2.029
medium height cover (habitat)	–	0.661
high height cover (habitat)	**0.917**	–

***: F= 1.62; df = 176,761; p< < 0.0001. NS, non-significant.

On the other hand, attributes that significantly increased the odds of interactions were: the number of fruits on tree crown, number of interspecific neighbors, the cover variation of the high-height vegetation stratum and the litter cover at the habitat scale (Table 3).

For ungrazed-lands, the graph model containing variables of tree size, fecundity, neighborhood and microhabitat was the one with the lowest BIC value (994). The selected model showed that, contrary to the grazed-lands graph, the number of fruits on the crown decreases the odds of plant–frugivore interactions by a factor of exp (–0.007903) = –1.008. Moreover, tree height increases the odds of interactions by 1.01. In the ungrazed-lands graph, attributes that significantly decreased the odds of plant–frugivore interactions

were: number of fruits on crown, and mean and variation of vegetation cover beneath tree canopy (Table 3). Conversely, attributes that increased the odds of interactions were: tree height, the number of fruits on ground and the mean cover of bare ground beneath tree canopy. For the ungrazed-lands graph, neither the neighborhood nor habitat variables were significant in explaining the odds of tree–frugivore interactions (Table 3).

Discussion

According to our hypothesis, individual plant–frugivore networks for grazed and ungrazed lands were structured by individual ecological traits and affected by anthropogenic modifications of habitat. Yet the number of interaction links did not differ between networks, and the frugivore species-specific ranks in interaction intensity remained significantly consistent among the ungrazed and grazed landscapes. However, both networks were significantly modular, with the grazed network showing a higher number of modules than the ungrazed network. For grazed lands, variables describing individual tree traits, the neighborhood surrounding each tree, the microhabitat and the habitat at the mesoscale were the ones that best explained correlation between frugivore visitation and plant traits. Nonetheless, no significant correlation of these variables was found for ungrazed plant–frugivore interactions. Finally, we clearly identified ecological traits that explained individual network structures. Variation of individual traits and microhabitat variables was significant in explaining the structure of the bipartite networks. The sign and significance of the ecological parameters included in models differed between grazed and ungrazed-lands graphs. These results demonstrate that anthropogenic land uses together with individual traits heterogeneity influence the structure of mutualistic networks.

Individual plant–frugivore networks at different anthropogenic land uses

Assessing the impacts of drivers of global ecosystem changes on ecological interactions is crucial to better predict their consequences for communities and biodiversity maintenance and also for the supply of ecosystem services to human well-beings (Tylianakis et al. 2008, Eckert et al. 2009, Kiers et al. 2010). Thus, by examining the topology of interaction networks one can assess their susceptibility to be influenced by anthropogenic drivers (Tylianakis et al. 2010, Spiesman and Inouye 2013, Vanbergen et al. 2017). Taking into account this theoretical and practical approach, we found that the frugivore species that constitute the core of interactions did not differ between networks at grazed and ungrazed land uses, except of domestic species (cows and horses) that were present only at grazed lands. The species involved include a relatively limited assemblage of small- and medium-sized native mammals inhabiting the *Prosopis flexuosa* ecosystem.

Table 3. Results of selected exponential random graph models (ERGMs) evaluating the effects of node (tree) characteristics underlying the interaction network graph structure (response variable) for the grazed and ungrazed land uses. The edges effect evaluates the influence of just the interaction patterns among individual *Prosopis* trees and frugivore species; then, additional effects of node-specific covariates are included. Significant effects suggest factors increasing or decreasing the probability of a tree to interact with the set of frugivore species. SE = standard error; NS = non-significant; SD = standard deviation.

Selected models	Predictor variables	Estimates	SE	p-value
Grazed-lands graph ~	edges	21.05	2.55	<0.0001
	tree height	−0.02	0.002	<0.0001
	fruits on crown	0.005	0.001	0.0007
	interspecific neighbours	0.16	0.06	0.01
	intraspecific neighbours	−0.39	0.08	<0.0001
	mean vegetation cover	−4.72	0.62	<0.0001
	bare ground SD	1.56	1.34	NS
	litter SD	−5.21	1.59	0.001
	low height stratum SD	2.15	1.14	0.06
	medium height stratum SD	0.74	1.11	NS
	high height stratum SD	4.33	1.09	<0.0001
	litter mean cover (habitat)	4.66	0.59	<0.0001
	low height stratum (habitat)	−1.58	0.44	0.0004
Ungrazed-lands graph ~	edges	−5.37	1.47	0.0003
	tree height	0.01	0.001	<0.0001
	crown fruits	−0.008	0.002	<0.0001
	ground fruits	0.008	0.002	0.0001
	interspecific neighbours	0.04	0.03	NS
	mean vegetation cover	−2.72	0.39	<0.0001
	variation in vegetation cover	−1.14	0.39	0.004
	bare ground cover	2.38	0.53	<0.0001
	low height stratum SD	0.86	0.56	NS
	medium height stratum	−0.24	0.44	NS

Moreover, the ranking of interaction importance of frugivore species remained consistent when comparing both land uses. Thus, the composition of the frugivore assemblage was not significantly affected by the land use evaluated. Nonetheless, the way frugivore interactions were structured and the ecological covariates that predict the observed network structures differed between land-use regimes. Previous research has documented significant effects of anthropogenic drivers on seed dispersal mutualisms (Markl et al. 2012), frequently associated to loss of species or drastic changes in mutualistic assemblages. Our results indicate that more subtle changes related to less severe disturbance regimes (e.g. grazing) may also trigger changes in interaction modes for individual trees giving rise to structural changes in the interaction networks. Despite not being addressed in this study, such changes in the interaction patterns between grazed and ungrazed areas likely affected the dispersal effectiveness in the two landscapes, as *Prosopis* recruitment has been documented to subtly depend on moderate levels of grazing (Brown and Archer 1989, Aschero and García 2012).

When downscaling plant–frugivore interactions from species to individuals, we found networks were organized in modules of individual plants highly connected by frugivore species and modularity increased at sites under a grazing productive system, when compared to ungrazed lands. The effect of modularity in mutualistic networks has been referred to less cohesive networks, in which the probability of

network fragmentation increases when connector species are removed (Melián and Bascompte 2004, Jordano et al. 2006). On the other hand, it has been proposed that disturbances are expected to highly affect and rapidly propagate through a non-modular than a modular network (Olesen et al. 2007, Gilarranz et al. 2017). Here, the grazed lands interaction network was more modular than the ungrazed lands, probably as an effect of the domestic species introduced and the changes in habitat. A characteristic two-phase mosaic of vegetation encroachment dominates the grazed lands (Aguiar and Sala 1999), while a more homogeneous scrubland is characteristic of the ungrazed areas (Tabeni et al. 2007). Furthermore, the majority of modules in the grazed areas were organized by only one frugivore species. This web organization may imply a more fragile interaction network in which any effect on only one frugivore species might affect the structure of the entire network.

Studies at the community level found mutualistic networks to be less modular than antagonistic networks (Thébault and Fontaine 2010). Moreover, when focused on individuals, modularity was a topological pattern characterizing plant-pollination (Dupont et al. 2014, Tur et al. 2014) and plant–frugivore networks when evaluated interactions between plants and multiple groups of seed-disperser animals (Donatti et al. 2011). However, studies including only a single group of seed-dispersers found networks to be highly nested and less modular (e.g. bats; Fortuna et al. 2010). Nonetheless,

by focusing in one group of frugivore animals, mammals, we found modularity as a significant topological pattern of these individual-based plant–frugivore networks. Although we did not include ecological information of frugivore species in our analysis, modularity may be explained by the fact that the *Prosopis* frugivore assemblage is comprised by a taxonomically diverse group of mammals, from small rodents (<100 g, e.g. *Graomys griseoflavus*) to carnivorous species (*Lycalopex griseus*). Moreover, the modular pattern reflects variability of traits among conspecific trees and how these individual tree traits relate to the particular habitat requirements by the frugivores (Tabeni and Ojeda 2003). Thus, differences among trees in the extent and heterogeneity of the shrub cover in the neighborhood, as well as tree size and fruit crop size differences set limits to the specific mammal species visiting the trees, with small-mammal species favoring high vegetation cover locations.

The frugivore species that interacted with a high number of *Prosopis* trees and formed single-species modules at both land uses were two rodent species, *Microcavia australis* and *Akodon dolores*. The other frugivore species reorganized their interactions according to their occurrence patterns at grazed or ungrazed land, thus, conforming species-specific modules or sharing modules with other frugivore species. For example, *Microcavia australis* is proposed as a mutualistic partner of *P. flexuosa* (legitimate disperser; Campos et al. 2017), instead of *A. dolores,* which is considered to maintain antagonistic frugivore interactions with *Prosopis* (largely a seed predator; Giannoni et al. 2013). Consistent with previous studies in the area (Miguel et al. 2017, Tabeni et al. 2017), we found that the rodent species *G. griseoflavus* is also a frequent frugivore visitor of *Prosopis* trees. This antagonistic partner (Giannoni et al. 2013) was included in modules with other frugivore species at both land use networks. Thus, interaction patterns of *Prosopis* trees appear to be driven by the habitat and microhabitat differences in preference patterns of mammal species, with a prominent influence of the grazing disturbances determining vegetation cover heterogeneity (Okin et al. 2015) that modulates these preferences.

Context dependency of frugivore visitation to trees

Mutualistic interactions are dynamic over time and space (Chamberlain et al. 2014), and, specifically, the plant–frugivore interaction is highly influenced by the biotic and abiotic context in which it takes place (Carlo 2005, Rodríguez-Rodríguez et al. 2017). Here we found that traits related with tree size and fecundity, neighborhood, microhabitat physiognomy immediately surrounding individual trees and larger-scale habitat variables strongly correlated with frugivore visitation to trees at grazed lands. Nonetheless, this pattern of plant–frugivore traits correlation was not found at ungrazed land uses. In spite of previous studies did not find an effect of grazing on the spatial organization of vegetation mosaics (Cipriotti and Aguiar 2005), we detected, in grazed land, two distinct patterns of microhabitat surroundings at *Prosopis* trees that accounted for the pattern of fru-

givore visitation. On one hand, microhabitats characterized by a high cover of bare ground and of the medium and high height vegetation stratum beneath tree canopies were negatively correlated with frugivore visitation. On the other hand, the variation of vegetation cover and the low-height vegetation stratum beneath tree canopies, besides to the cover of the low and medium height vegetation stratum at the habitat near trees were positively correlated with frugivore visitation. These results indicate that trees growing in a more complex microhabitat received less visits by frugivores compared with that growing in more open spaces. The resulting patterns reflect a heterogeneous landscape, with different tree physiognomies and surroundings that influence frugivore visitation to trees. However, at adjacent ungrazed lands other different ecological and/or abiotic variables, not evaluated here, may influence and explain visits by frugivores. Long-term grazing exclusion not only favors more homogenous shrub cover, but also influences *Prosopis* recruitment (Brown and Archer 1989, Aschero and García 2012) and thus modifies conditions for interactions with specific frugivores.

Similar to previous studies (Carlo 2005, Dupont et al. 2014) we found that intraspecific trait variation among trees significantly explained correlations between plant and frugivore variables sets when considering grazed lands. Moreover, the neighborhood surrounding each *Prosopis* tree together with variables describing the microhabitat and the habitat characterizing grazed fields were also influential on the canonical variables describing the multivariate habitat physiognomy. The influence of microhabitat and habitat on frugivore visitation only at grazed lands is an interesting result that may respond to the fact that the grazing activity by large herbivores modifies the structure of vegetation at different spatial scales, altering the habitat required by other animal species (Tabeni and Ojeda 2003, Tabeni et al. 2007), which in turn could affect frugivore visitation to plants (Campos et al. 2016). This influence of vegetation physiognomy of the trees growing place and its immediate surroundings, driving frugivore visitation patterns, is especially evident in heterogeneous landscapes with prominent forest edges and two-phase mosaics of open grassland (Jordano and Schupp 2000, Carlo et al. 2007, Morales et al. 2012).

Ecological correlates underlying plant–frugivore networks

Results of ERG models showed that different sets of ecological variables explained the probability of node interactions (individual trees–frugivore species) at grazed and ungrazed land uses. This modeling approach was a useful tool to explain and recognize ecological traits that have molded the structures of individual plant–frugivore networks at different context of land uses. Traditionally, network analysis has been focused on detecting and describing structural patterns of interaction webs such as nestedness, modularity and connectance within a highly descriptive framework (Bascompte and Jordano 2014) and on recognizing the most likely ecological and evolutionary traits in predicting such patterns (Vázquez et al.

2009). To the best of our knowledge, this is the first attempt to apply this predictive, modeling framework to the analysis of complex networks of ecological interactions (Kolaczyk and Csárdi 2014).

Variation in individual traits among conspecifics is recognized as an important force in structuring interaction networks (Olesen et al. 2010, Donatti et al. 2011, Dupont et al. 2014). Particularly, crop yield is an intrinsic plant trait that influences disperser activity (Jordano and Schupp 2000, Blendinger and Villegas 2011). In accordance with this, our results showed that fecundity (number of fruits produced) was a significant individual trait that increased the strength of plant–frugivore interactions at both ungrazed and grazed lands networks. However, other individual variables included in analysis, such as tree height, had a contrary effect in both network graphs. Thus, while at grazed-lands network taller plants decreased the odds of *Prosopis*–frugivore interactions, at ungrazed-lands network taller plants increased the odds of interaction. One possible interpretation of this result may be that older and taller trees are found in the ungrazed site, supported by previous studies that described a higher density of adult *Prosopis* plants at ungrazed lands compared with grazed woodlands (Aschero and Vázquez 2009).

Composition and neighborhood density are also influencing and previously-studied aspects of frugivore interaction with plants (Carlo 2005, Morales et al. 2012). Our results showed that for *Prosopis* trees at grazed lands, being in an interspecific neighborhood has a positive effect on their interaction with frugivores compared to growing sites with an intraspecific neighborhood. Moreover, intraspecific neighborhoods (i.e. more conspecific plants) significantly decreased the odds of plant–frugivore interactions, supporting previous findings of a negative effect of conspecific neighborhoods on disperser activity (Carlo et al. 2007). Nonetheless, and similar to other studies (Blendinger and Villegas 2011), the neighborhood density surrounding each focal tree at the ungrazed network was not a significant predictor variable in models. Interaction networks at ungrazed lands may respond more to individual local traits (i.e. fecundity, tree height and microhabitat physiognomy) whose effect disappears when considering wider neighborhoods and habitat scales. According to variables describing the microhabitat in which individual trees was growing, we found that the likelihood of grazed-network *Prosopis*–frugivore interaction increased with variation in plant cover at the high stratum (1.1 to 1.4 m) and decreased with high vegetation cover beneath the tree canopy. On the other hand, at the ungrazed network, the odds of frugivore interaction with trees increased with high bare ground cover beneath tree canopy and decreased with the vegetation cover beneath tree crown. Only at grazed-lands the habitat variables were significant predictors in the network models; while the cover of litter increased the odds of nodes interaction, the cover of the low height stratum decreased the interactions.

Our results indicate that at grazed lands, smaller trees producing high quantity of fruits, with low vegetation cover beneath its canopy, surrounded by interspecific neighbors and with less cover of the low height stratum in the near landscape, significantly increased their probability of interaction with frugivores. However, taller trees with high density of fruits on ground, and high bare ground cover beneath tree crowns were the *Prosopis* tree traits that increased the odds of interaction with frugivores at ungrazed lands. An interesting future issue will be to assess how robust in time interaction networks are (i.e. the temporal component of interspecific interactions; Valverde et al. 2016), considering variation in local animal population abundances and fruit crops through years. In addition, the comparison of plant–frugivore interactions across habitat chronosequences or gradients of grazing intensity may help to understand critical transitions and shifts in interactions with specific frugivores after a given level of encroachment. Our results with *Prosopis* indicate that small to large mammals would vary their interaction strength along this type of gradient.

Conclusions

Anthropogenic land uses influence not only the topological patterns of plant–frugivore mutualistic networks but also the frugivore visitation to *Prosopis* trees through modification of vegetation structure and habitat complexity and the effect of tree traits. Furthermore, individual conspecific variation in traits significantly affected the structure of interaction networks, specifically in grazed lands. By using exponential random graph models (ERGMs) we move forward in identifying specific ecological traits at different scales (individual, microhabitat and habitat) that explain the observed plant–frugivore networks. Future applications of this modeling framework may help to describe and predict individual trees that concentrate a large number of interactions with frugivore species. The approach might be especially useful in the context of anthropogenic land management and for spotting key trees for conservation within forest management actions. Our individual-plant based approach suggests that effects of anthropogenic land uses at the individual tree level may scale-up to distinct modes of interaction reshaping higher levels of biological organization (Bolnick et al. 2011). Further research considering plant–frugivore mutualistic networks at the community scale are necessary to elucidate whether topological patterns found here are also observed or maintained at the species level. Along this line, explicit modeling approaches like ERGMs and its variants are promissory, moving forward from more descriptive analyses of ecological networks.

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Supplementary material (Appendix oik-04978 at <www.oikosjournal.org/appendix/oik-04978>). Appendix 1.