ANIMAL SCIENCE

Effects of habitat perturbation on lizard assemblages in the center-west of the Arid Chaco region, Argentina

RODRIGO GÓMEZ ALÉS, JUAN CARLOS ACOSTA, GRACIELA BLANCO & ANA PAULA GALDEANO

Abstract: Several human disturbances contribute to the decrease of vertebrate species' richness and abundance, altering the processes of an ecosystem. We evaluate richness, diversity and relative abundance of species for lizard assemblages at sites with different degrees of perturbation in the center-west of the Arid Chaco region in Argentina. Between 2015 and 2018, six lizard assemblages were sampled monthly -using pitfall traps- in three areas of the Chaco, with a perturbed and an unperturbed (control) replica at each of the areas: (1) Chaco Mountain plain, (2) Chaco Mountain slope, and (3) Chaco Plains, and habitat characteristics of each study site were recorded. We captured 1446 lizards, belonging to 12 species. The perturbed area at the Chaco Mountain plain showed the greatest richness, diversity and abundance of species. In the perturbed Chaco Plains, species abundance decreased by about 50% with respect to the control site. *Liolaemus chacoensis* was the dominant species at all sites. Some species could be negatively affected by a total loss of arboreal strata, tree trunks and fallen leaves. Structural parameters of lizard assemblages were related to the habitat characteristics; therefore, these results provide information for the conservation and management of lands and lizard assemblages in the Arid Chaco.

Key words: diversity of species, habitat perturbation, logging and overgrazing, relative abundance, reptile assemblages, richness.

INTRODUCTION

Biodiversity loss as a consequence of human activity is an environmental problem of interest to scientists around the world (Prentice & Leemans 1990, Gardner et al. 2007, Pereira et al. 2010). Several human disturbances, such as habitat degradation and fragmentation, overexploitation of wildlife species, pollution, climate change or introduction of invasive species are factors that contribute to the decrease of vertebrate species' richness and abundance. Biodiversity loss alters the processes of an ecosystem, its resilience and the ecosystem services that the environment provides to society (Chapin et al. 2000, Mooney et al. 2009, Tellería 2013, Nori et al. 2016). An objective analysis of biodiversity and its changes over time requires accurate evaluation and monitoring. In this sense, long-term studies of the abundance and diversity of species of an assemblage are necessary in order to understand the dynamics of a community and the changes that occur due to habitat modification after a disturbance. These studies allow us to obtain the information necessary for making decisions that protect and conserve fauna (Martori et al. 2002).

The Arid Chaco of Argentina is located in the southwest sector of the Gran Chaco of South America and is the driest and least productive

area of the continent. The heterogeneity of its forests and its different vegetation structures are due to anthropic disturbances such as overgrazing and logging, with regeneration defined by the intensity of use, the degree of disturbance and the edaphic conditions (Márquez et al. 2008). As such, the arboreal strata is deteriorated, and shrubs, herbaceous annuals and arid plains predominate, transforming the landscape into scrubland of slow recovery (Bucher 1982, Karlin et al. 2013). The richness, abundance and distribution of fauna has varied in this region as a consequence of modifications to the wooded ecosystem, habitat loss occurring due to changes in land use, and as a result of humans' social and financial interactions (Reati et al. 2010, Karlin et al. 2013, Nori et al. 2016).

The habitat loss or degradation due to land use can have drastic consequences for lizards, particularly for those assemblages for which species diversity and abundance is related to microgeographic variation in habitat structure (Jones 1981, Gibbons et al. 2000, Menke 2003, Castellano & Valone 2006, Vitt et al. 2007). Logging and grazing are the main causes of desertification, especially in dry regions like the Arid Chaco (Boletta et al. 2006, Márquez et al. 2008). This can impact the structure of the assemblages, with uneven outcomes; on the one hand, it could create new spatial niches able to be colonized by species which are generalists in their use of spatial, temporal and trophic resources, while on the other hand, it could lead to a decrease in the abundance of specialist species (Vitt et al. 1998, Attum et al. 2006). That is to say, those changes in lizard species abundance following short-term or long-term perturbation will depend on the resulting heterogeneity of the vegetation structure and microclimate, on the availability of food sources and on the lizards' individual microhabitat preferences (Urbina-Cardona et al. 2006, Vitt

et al. 2007, Pelegrin et al. 2013). In this sense, the hypothesis of intermediate perturbation establishes that diversity and abundance may be greater with intermediate perturbation, as compared to sites with very high or very low levels of perturbation (Huston 1994, Mackey & Currie 2001, Attum et al. 2006, Azevedo-Ramos et al. 2006, Costa et al. 2013). For example, herpetofaunal species richness and abundance were higher in disturbed areas (fire and logging) as compared to undisturbed areas in the Bolivian humid tropical forest (Fredericksen & Fredericksen 2002), while Macip-Ríos et al. (2013) report an increase in the abundance of *Ameiva undulata* in environments with insolation and medium disturbance in mosaics of coffee plantations and native tropical forests.

In Neotropical environments, several authors have demonstrated how lizard assemblages respond to changes in habitat structure due to natural or anthropogenic disturbances (Vitt et al. 1998, Sartorius et al. 1999, Lima et al. 2001, Azevedo-Ramos et al. 2006, Urbina-Cardona et al. 2006, 2008, Carvajal-Cogollo & Urbina-Cardona 2008, 2015, Macip-Ríos & Muñoz-Alonso 2008, Mesquita et al. 2015, among others). However, only few studies have addressed the effects of anthropogenic habitat perturbation on lizard assemblages of the Argentine Chaco (Leynaud & Bucher 2005, Pelegrin et al. 2009, 2013, Cano & Leynaud 2010, Pelegrin & Bucher 2010, 2012), with results showing different patterns as responses to the transformation of the landscape by logging, grazing, fire and restoration activities, including changes in the use and selection of microhabitats, changes in the segregation of niches, a decrease in the abundance of specialist species or an increase in the abundance of generalist species and changes in species diversity. Due to the dissimilarity of species' responses when faced with perturbation, Leynaud & Bucher (2005)

and Cano & Leynaud (2010) have emphasized the importance of maintaining a certain degree of habitat heterogeneity in order to conserve reptile diversity as a criteria to be kept in mind for eventual ecological restauration plans.

For the center-west of the Arid Chaco, there are no studies on long-term monitoring of lizard assemblages which evaluate the changes caused by habitat degradation. Our objective was to evaluate changes in the structure of lizard assemblages at sites with varying degrees of perturbation. We hypothesize that, as a result of modifications to habitat structure, lizard assemblages inhabiting perturbed sites will exhibit differences in their structural parameters as compared to those inhabiting unperturbed

sites. At perturbed and unperturbed (control) sites, we evaluate the following: how habitat traits affect the structural traits of lizard assemblages in terms of species richness, diversity and relative abundance.

MATERIALS AND METHODS

Study area

We carried out our work in Valle Fértil, San Juan, Argentina (Figure 1) within the protected area of the Valle Fértil Natural Park. This site is located in the Arid Chaco region, which is made up of two areas: the Chaco Mountain and Chaco Plains (Márquez et al. 2017). It is part of the last Chaco foothills in western Argentina and is of great
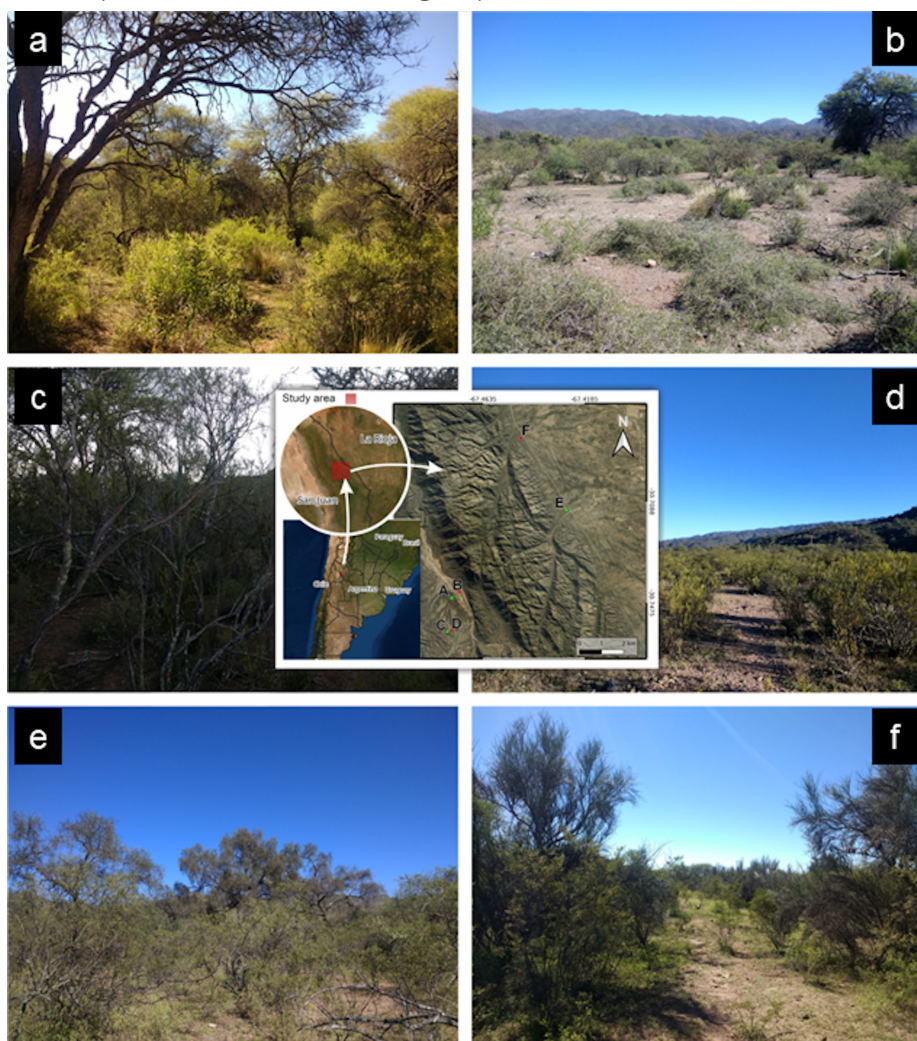

Figure 1. Study area location in the Arid Chaco, Valle Fértil, San Juan, Argentina. Sampling sites are indicated on the map and pictures of each are presented: Chaco Mountain plain (a) control, (b) perturbed; Chaco Mountain slope (c) control, (d) perturbed; Chaco Plains (e) control, (f) perturbed.

biogeographical interest due to its ecotonal nature, being a transition from the Monte desert to the Chaco region (Márquez et al. 2017). Vegetation is comprised of an open xerophilous forest made up of *Aspidosperma quebracho-blanco*, *Prosopis* spp., *Celtis ehrenbergiana*, and *Cercidium praecox*, among others. Characteristic species of the shrub strata include *Larrea divaricata*, *Mimozyganthus carinatus*, *Prosopis torquata* and some species of *Lycium*, in combination with diverse herbaceous and graminaceous species. The climate is dry with maximum seasonal rains in summer, with temperatures reaching 38°C in summer and -7°C in winter (Márquez et al. 2008, 2017).

Throughout the region, the economy is based on the raising of livestock (caprine and bovine), logging and farming/gardening for self-supply (Márquez et al. 2008). For this reason, the region is characterized by landscapes in severe states of degradation, with evidence of overgrazing and a low percentage of forest renewability. The different uses which the forests have been subject to historically have led to different types of recovery. In some areas, a process of dense shrub growth has been observed, represented by species of *Lycium*, *Bulnesia* and *Larrea*, while in other areas this process has been less intense with a great percentage of ground continuing to be exposed to the erosive effects of water and wind (Márquez et al. 2008, Karlin et al. 2013).

Fieldwork

Monthly samples were taken over the course of three periods (October 2015 – May 2016, October 2016 – May 2017, October 2017 – May 2018) in three different areas of the Arid Chaco, two at the Chaco Mountain (slope and plain) and one at the Chaco Plains. In each area, we selected two sites (control and perturbed; Figure 1), considering the state of the herbaceous, shrub and arboreal strata as evidence of land use (see details below). A total of 130 arbitrary pitfall traps were set up: 50 at the Chaco Mountain plain site (22 control, 28 perturbed), 40 at the Chaco Mountain slope site (20 control, 20 perturbed) and 40 at the Chaco Plains site (20 control, 20 perturbed). The distance between traps was 30 m and they were placed at transects separated by 50 m (De Pinho Werneck et al. 2009, Pelegrin & Bucher 2012). Each trap was made with two plastic tubs which were buried 3 m apart (without enclosure). Due to the different number of traps, captures were standardized in function of the sample effort (lizards/traps).

For each sample, traps were opened and checked twice during each campaign, with one site per day being checked every five days. For each lizard, we recorded species, sex and age-group before it was marked with a phalange cut (individual code) and released. We recorded habitat characteristics at each trap site in 5 x 5 m plots; ground coverage (%): herbaceous, shrub, logs and branches, leaf litter, cactus, canopy and bare ground. We also recorded the absolute number of trees, tree trunks and caves of each plot.

Site characteristics

Chaco Mountain plain

The control site is comprised of dense *Lycium chilense* brush, with the vegetation forming two strata. The upper, at a height of 4 m, is represented by *Prosopis chilensis* and *Celtis pallida* with approximately 5% coverage. Graminaceous species do not exceed 5% of coverage. The proportion of bare ground is less than 20%, while total vegetation coverage is 77% on average (Figure 1a). The perturbed site is comprised of open *L. chilense* brush and is located on the river's alluvial plain. Its soil is sandy with fine sediments, with a significant proportion of bare ground (40%) and an average

vegetation coverage of 60%, creating patterns of patches and interpatches. Arboreal strata is scarce due to logging, with a few isolated specimens of *P. chilensis*, *C. pallida* and *Parkinsonia praecox* (Figure 1b). Here there is a high degree of logging and caprine grazing.

Chaco Mountain slope

The control site is comprised of dense *Larrea cuneifolia* and *L. divaricata* brush, with vegetation coverage reaching 90%. Three strata are present, the highest exceeding 4 m with *P. chilensis*, *A. quebracho-blanco*, *C. pallida*, *Geoffroea decorticans* and *P. preacox* (Figure 1c). The perturbed site is comprised of open brush dominated by *L. cuneifolia*, with some isolated specimens of *P. chilensis* and *Vachellia caven* forming a poor arboreal strata. Among the shrub and herbaceous species, we find *Junelia crithmifolia*, *L. chilense*, and *Gomphrena tomentosa*, among others. The proportion of bare ground reaches approximately 30%. The predominant perturbations at the site are logging and trampling by bovines and caprines which cross the site (Figure 1d).

Chaco Plains

The control site is comprised of dense *L. divaricata* brush with numerous specimens of *A. quebracho-blanco* and *Prosopis* spp. which make up the arboreal strata with an approximate coverage of 80%. Characteristic shrub species include *Capsicum chacoense*, *P. preacox*, and *Lippia turbinata*, among others (Figure 1e). The perturbed site is comprised of brush dominated by *Bulnesia retama* (called "retamo") and *L. divaricata*. There is 60% coverage, with characteristic species being *L. cuneifolia*, *Parthenium hysterophorus*, *C. chacoense*, and *Opuntia sulphurea*, among others (Figure 1f). Due to logging, the arboreal strata is scarce and creosote bush, retamo and cacti predominate

as indicators of perturbation. There is a high percentage of bare ground because of intensive logging and the raising of livestock.

Data analysis

The sites were organized according to habitat characteristics, using Non-metric Multidimensional Scaling (NMDS) to obtain a representation based on similarities in values of vegetation coverage, bare ground, numbers of trees, caves and logs. A Gower distance matrix was utilized with the number of dimensions k = 3. We carried out an analysis of similarities (ANOSIM) using a Gower distance matrix (Clarke 1993).

We calculated the Shannon-Weiner index of diversity and Hill numbers for each of the sites: N_0 = richness of species; N_1 = number of species equally abundant (exponential H', where H' is the Shannon index); and N_2 = number of very abundant species ($1/\Sigma pi^2$, where Σpi^2 is the Simpson index). For comparisons between sites, we carried out permutations with the function "mcpHill" and rarefaction/extrapolation curves based on individuals for each order (q) with the function "iNEXT" (Hsieh et al. 2016). A rarefaction analysis was completed to compare the richness of species between sites, using the function "rarefy" (Oksanen 2009). We compared the observed richness (s) at each site with the estimated richness (se) using Chao1, Jack1 and Bootstrap non-parametric estimators, with 999 random permutations; the "specpool" function was utilized (Chiu et al. 2014).

We carried out grouping analysis using the Jaccard dissimilarity distance and the unweighted pair group method with arithmetic mean (UPGMA) to achieve comparisons of species composition between sites. The SIMPER method was utilized to evaluate dissimilarity between assemblages and allowed for identification of the taxon responsible for said dissimilarity and

the percentage of its contribution (Clarke 1993). The dissimilarities detected were corroborated with ANOSIM, utilizing a Bray-Curtis distance matrix.

Relative abundance (lizards/traps) was calculated for each site and for each species. These values were compared between sites using general linear models (GLM) with negative binomial distribution, since the residual data did not fit a normal distribution. These models were analyzed using the "glm.nb" function with the log link function. In order to obtain a representation of patterns of abundance and uniformity of species at each site, range-abundance curves were carried out (Feinsinger 2001) charting the logarithm of relative abundance for each species and species range from greatest to least abundance (Urbina-Cardona et al. 2006). The curves were adjusted to the models: geometric series, log series, log normal and broken stick. These models are known to be used in studies of diversity and abundance of species and are recommended for detecting signs of disturbance in an ecosystem (Hill & Hamer 1998, Aguirre-Calderón et al. 2008, Magurran & McGill 2011, Passos et al. 2016). The best models were selected with the lowest Akaike information criterion (AIC) and deviance information criterion (DIC) (Magurran & McGill 2011), utilizing the "radfit" function (Oksanen 2009).

The relationship between habitat characteristics and species abundance was evaluated using transformation-based redundancy analysis (tbRDA; Legendre et al. 2011). Independent variables consisted of a matrix of values of each coverage value. Prior to carrying out the analysis, an assessment of correlation between variables was completed in order to identify multicollinearity, eliminating variables correlated with a coefficient r ≥ 0.7. The dependent variables consisted of a matrix of the abundance (lizards/traps) of each species.

The species matrix was converted to Hellinger distances. The significance of the relationship between matrices was estimated using a Monte Carlo test with 999 permutations (Legendre et al. 2011). The significance of both the canonical centers and the explicative variables was also evaluated (Monte Carlo, 999 permutations).

In order to carry out the aforementioned analyses, we utilized R version 3.6 (R Development Core Team 2019), with the following statistical packages: *vegan* (Oksanen 2009), *simboot* (Scherer & Schaarschmidt 2013), *BiodiversityR* (Kindt & Coe 2005), *MASS* (Venables & Ripley 2002), *iNEXT* (Hsieh et al. 2016) and *cluster* (Maechler 2019).

RESULTS AND DISCUSSION

Habitat characteristics between sites

Results for habitat characteristics by site are shown in Table I. The Chaco Mountain slope perturbed site presented the greatest percentage of bare ground (66.75%), while shrub coverage was greatest at the Chaco Mountain plain control site (55.17%). With NMDS, no clear differentiation was observed between sites with regard to habitat variables (Stress = 0.125, R^2 = 0.32; Figure 2). Nevertheless, the perturbed sites were significantly different from each other and from the control sites (ANOSIM: R = 0.302, P = 0.001), while no significant differences were observed between the control sites (ANOSIM: R = 0.09; P > 0.05).

Species composition, richness and diversity

A total of 1446 individuals were recorded, representing 12 species from five families (Table II). In general, richness was similar to that reported for lizard assemblages in the Semi-arid and Arid Chaco region of Argentina (Table IV). However, the richness of species typically from the Chaco was low compared with other natural

Table I. Habitat Characteristics. ChMP-C: Chaco Mountain plain control (n = 28), ChMP-P: Chaco Mountain plain perturbed (n = 58), ChMS-C: Chaco Mountain slope control (n = 40), ChMS-P: Chaco Mountain slope perturbed (n = 40), ChP-C: Chaco Plains control (n = 40), ChP-P: Chaco Plains perturbed (n = 40). Average values are presented ± standard error.

| Variable	ChMP-C	ChMP-P	ChMS-C	ChMS-P	ChP-C	ChP-P
Cover (%)						
Shrubs	55.18 ± 3.66	43.62 ± 1.62	44.00 ± 1.59	39.5 ± 1.28	44.37 ± 1.11	33.62 ± 1.67
Cactus	-	0.05 ± 0.03	0.03 ± 0.02	0.35 ± 0.13	2.46 ± 0.68	17.95 ± 2.42
Canopy	13.42 ± 3.06	6.53 ± 1.19	18.47 ± 3.12	0.00	7.86 ± 1.23	2.00 ± 1.23
Herbs	5.60 ± 1.45	2.75 ± 0.90	7.57 ± 1.65	2.08 ± 0.64	2.67 ± 0.46	-
Leaf litter	4.17 ± 1.53	4.32 ± 0.98	1.75 ± 0.59	1.20 ± 0.28	7.13 ± 1.07	19.2 ± 2.62
Branches	21.60 ± 2.09	8.25 ± 0.93	17.15 ± 1.93	2.55 ± 0.38	10.79 ± 0.8	9.47 ± 1.65
Rocks	-	0.56 ± 0.18	-	5.77 ± 1.12	1.55 ± 0.38	-
Bare ground	24.92 ± 4.04	53.10 ± 2.32	37.12 ± 2.97	66.75 ± 1.69	48.07 ± 1.83	41.25 ± 3.92
Others (n°/ha)						
Trees	0.78 ± 0.14	0.86 ± 0.19	1.17 ± 0.11	-	0.39 ± 0.07	0.12 ± 0.05
Caves	-	-	-	0.08 ± 0.04	0.59 ± 0.07	-
Fallen logs	0.89 ± 0.16	0.67 ± 0.12	0.77 ± 0.16	0.03 ± 0.02	0.03 ± 0.01	0.03 ± 0.02
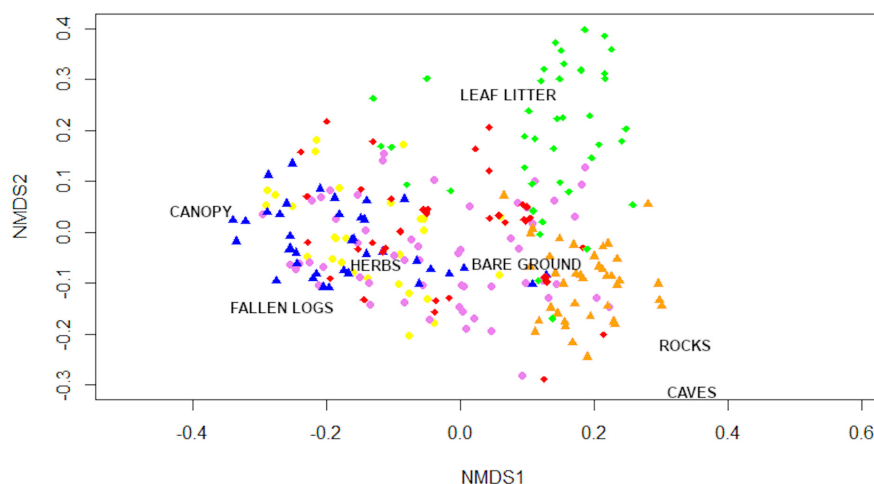
Figure 2. Non-metric Multidimensional Scaling (NMDS) showing ordering of sites based on habitat characteristics. Chaco Mountain plain control (yellow circle) and perturbed (violet circle); Chaco Mountain slope control (blue triangle) and perturbed (orange triangle); Chaco Plains control (red square) and perturbed (green square).

and degraded environments, and the absence of *Tropidurus etheridgei*, *T. spinulosus* and *Vanzosaura rubricauda* is noteworthy (Fitzgerald et al. 1999, Leynaud & Bucher 2005, Pelegrin et al. 2006). The absence of these species may be due to the greater similarities between the center-west Arid Chaco region and the Monte region (R. Gómez Alés, unpublished data), and to historic biogeographical factors that limit their distribution, creating turnover and decline in the richness of typical Chaco species in the ecotone between the Monte region and extreme southwest Chaco (lower latitude). At the Chaco Mountain plains control site and Chaco Mountain slope control and perturbed sites, the rarefaction/extrapolation curves are not stable, suggesting the presence of rare species that may have led to biased curves or that new species may have been detected in the assemblages (Figure 3). Therefore, the use

Table II. Relative species abundance (lizards/traps). ChMP-C: Chaco Mountain plain control, ChMP-P: Chaco Mountain plain perturbed, ChMS-C: Chaco Mountain slope control, ChMS-P: Chaco Mountain slope perturbed, ChP-C: Chaco Plains control, ChP-P: Chaco Plains perturbed. Average values are presented ± standard error. The P value obtained for Negative Binomial GLM (P < 0.05) is indicated.

Family	Species	ChMP-C N= 22	ChMP-P N= 28	ChMS-C N= 20	ChMS-P N= 20	ChP-C N= 20	ChP-P N= 20	z	P
LIOLAEMIDAE	*Liolaemus chacoensis*	0.29 ±0.06[AB]	0.32 ±0.03[A]	0.22 ±0.02[B]	0.29 ±0.04[AB]	0.49 ±0.05[A]	0.19 ±0.02[B]	17.18	<0.001
	Liolaemus darwinii	-	0.07 ±0.01	-	-	-	-	-	-
	Liolaemus gracilis	0.03 ±0.00[B]	0.01 ±0.00[B]	0.08 ±0.01[A]	0.005 ±0.00[B]	-	-	2.87	0.004
TEIIDAE	*Teius teyou*	0.05 ±0.01	0.08 ±0.01	0.05 ±0.01	0.09 ±0.02	0.06 ±0.01	0.07 ±0.01	0.95	0.338
	Aurivela longicauda	0.006 ±0.00[C]	0.19 ±0.02[A]	-	0.05 ±0.01[B]	0.007 ±0.00[C]	-	-3.16	0.001
	Ameivula abalosi	-	-	-	-	0.01 ±0.00	-	-	-
	Salvator rufescens	0.02	-	0.02	-	-	0.005	-	-
TROPIDURIDAE	*Stenocercus doellojuradoi*	0.008 ±0.00[B]	0.03 ±0.00[A]	0.01 ±0.00[B]	0.002	0.002	0.01 ±0.00[B]	-3.21	0.001
PHYLLODACTYLIDAE	*Homonota horrida*	0.002	0.003 ±0.00	0.002	-	-	0.002	-	-
	Homonota borelli	-	0.001	-	-	-	-	-	-
	Homonota underwoodi	-	-	-	-	0.005 ±0.00	-	-	-
LEIOSAURIDAE	*Leiosaurus paronae*	-	0.003 ±0.00	0.002	0.002	-	-	-	-
ALL SPECIES		0.39 ±0.07[BC]	0.73 ±0.04[A]	0.38 ±0.03[BC]	0.44 ±0.05[BC]	0.59 ±0.07[B]	0.28 ±0.03[C]	21.47	<0.001
	Total individuals*	189	576	152	178	237	114	-	-
	Adults*	158	403	107	97	177	72	-	-
	Juveniles*	31	173	45	81	60	42	-	-

Note: N indicates the number of traps at each site. *Number of lizards without differentiating species. Different letters indicate significant differences between sites.

of techniques not included in this study, such as fence-bucket traps and active searches at different times, would allow more species to be detected at all sites.

Pelegrin & Bucher (2010, 2012) reported greater richness and diversity of lizards in areas of non-degraded and moderately degraded primary forest of the Arid Chaco. However, Cano & Leynaud (2010) suggest that the heterogeneity created by perturbations in a sector of the Humid Chaco favors greater species diversity. This last pattern was observed at the Chaco Mountain plains perturbed site with greater heterogeneity of habitats, where richness and diversity were also greater (Table III, Figure 3), and could be attributed to greater equitability and to the presence of *Liolaemus darwinii* and *Homonota borelli*, only registered at this site. The structure resulting from logging and grazing at the Chaco Mountain perturbed site has, as a result, open brushland made up of patterns of patches and interpatches of arboreal and shrub vegetation and grasslands. This heterogeneity would allow for maintaining the presence and abundance
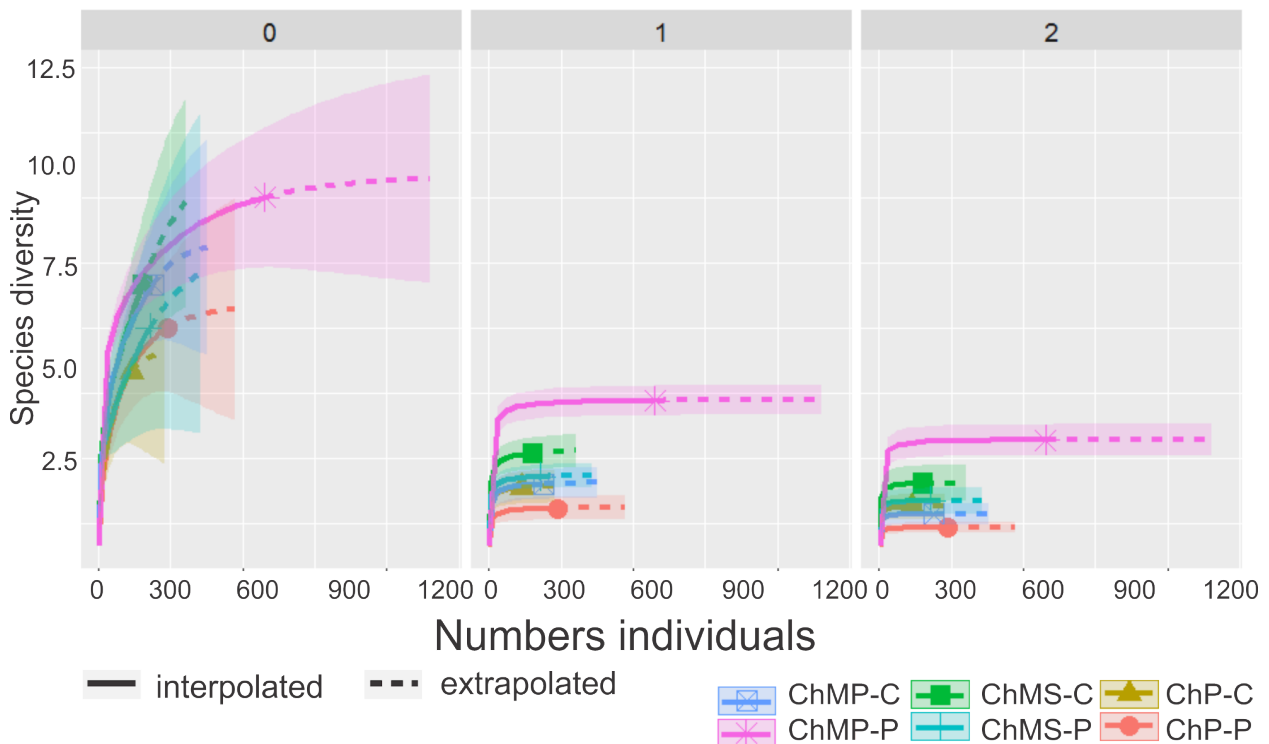
Figure 3. Rarefaction/extrapolation curve based on sample size of lizard diversity for Hill numbers at each site. ChMP: Chaco Mountain plain (C: control, P: perturbed); ChMS: Chaco Mountain slope (C: control, P: perturbed); ChP: Chaco Plains (C: control, P: perturbed).

of specialist species such as *Stenocercus doellojuradoi*, while at the same time benefitting generalist and heliothermic species such as *Liolaemus chacoensis*, *Aurivela longicauda* and *Teius teyou* due to greater availability of open sites for thermoregulation and food finding (see next section; Vitt & Carvalho 1995, Vitt et al. 1998, Astudillo et al. 2019, Ortega et al. 2019). The least diversity and richness was observed at the Chaco Plains control and perturbed sites, respectively (Table III). These sites are characterized by being relatively homogenous in terms of vegetation structure, either because of the conservation of arboreal and shrub strata or as a result of an extreme perturbation, transformed to homogenous creosote bush and retamo bush.

Accordingly, it can be inferred that richness and diversity may not change or be benefitted by conditions of intermediate perturbation (Huston 1994, Mackey & Currie 2001, Smart et al. 2005, Macip-Ríos et al. 2013), while in the north of the Semi-arid Chaco, Leynaud & Bucher (2005) suggest that maintaining a certain heterogeneity of habitat resulting from perturbations could help to maintain reptile diversity. However, it is important to clarify that though reptiles may be favored by environmental perturbation, this does not mean that it has a positive effect on the environment. The importance of these results is that they demonstrate that lizards can be bioindicator species that experience changes due to human or climatic alteration and must be analyzed together with other species in the ecosystem. For example, an increase in the diversity or abundance of lizards in the region could be due to the fact that populations of other predatory vertebrates (snakes, birds of prey, carnivorous mammals) have been affected by the same human causes, and that is somewhat negative for wildlife conservation (Read 2002,

Table III. Shannon Diversity (H'), Hill numbers (N_0, N_1, N_2), rarefied richness and estimated richness (se). ChMP-C: Chaco Mountain plain control, ChMP-P: Chaco Mountain plain perturbed, ChMS-C: Chaco Mountain slope control, ChMS-P: Chaco Mountain slope perturbed, ChP-C: Chaco Plains control, ChP-P: Chaco Plains perturbed. The P value obtained for permutations carried out to Hill numbers is indicated.

	ChMP-C N= 22	ChMP-P N= 28	ChMS-C N= 20	ChMS-P N= 20	ChP-C N= 20	ChP-P N= 20	P
H'	0.86	1.46	1.13	0.95	0.62	0.84	-
N_0 (richness)	7 [B]	9 [A]	7 [B]	6 [B]	6 [B]	5 [B]	< 0.001
N_1	2.415[BC]	4.333[A]	3.115[B]	2.586[BC]	1.860[C]	2.331[BC]	< 0.001
N_2	1.723[BC]	3.427[A]	2.426[B]	2.028[BC]	1.407[C]	1.897[BC]	< 0.001
Rarefied richness	6.12	6.9	6.24	5.15	5.06	5	-
Chao1 (se)	8.9	9.48	9.85	7.9	6.23	5.47	-
Jack1 (se)	8.9	9.96	9.85	7.9	6.95	5.95	-
Bootstrap (se)	7.88	9.52	8.07	6.83	6.60	5.49	-

Note: N indicates the number of traps at each site. Different letters indicate significant differences between sites.

Table IV. Richness of species and Shannon Diversity (H') in the Chaco region of Argentina.

Locations	Type	Coordinates	Richness	H'	References
Mburucuyá National Park	Humid	27° 58′ S; 57° 59′ W	6	1.13	Cano & Leynaud 2010
El Bagual Reserve		26° 10′ S; 58° 56′ W	12	-	Scrocchi & Giraudo 2005
Pirané		25° 44′ S; 59° 06′ W	6	-	Pesci et al. 2018
Joaquín V. González	Semi-Arid	25° 05′ S; 64° 09′ W	17	1.92	Cruz et al. 1992, Fitzgerald et al. 1999
Los Colorados Biological Station		24° 41′ S; 63° 18′ W	11	1.69	Leynaud & Bucher 2005
Campo Grande		24° 43′ S, 63° 17′ W	8	1.56	
Chancaní	Arid	30° 22′ S, 65° 26′ W	13	1.23	Pelegrin et al. 2006, Pelegrin & Bucher 2012
Valle Fértil		30° 45′ S; 67° 28′ W	12	1.3	This paper

Ficetola et al. 2007, Pelegrin & Bucher 2012, Hoare et al. 2012, Monks et al. 2014, Caruso et al. 2016, French et al. 2018, Nordberg & Schwarzkopf 2019). We propose a comprehensive study of the ecosystem in the future to corroborate these hypotheses.

According to the Jaccard dissimilarity index, the Chaco Mountain plain and slope control sites present the greatest similarity in species composition (dissimilarity 25%). The Chaco Plains control site, which has the characteristics of a primary forest, presents a dissimilarity of 60% with the rest of the sites. Table V shows the percentages of ensemble dissimilarity between sites and the species which contribute to these differences.

Species abundance and its relationship to habitat characteristics

For assemblages with low richness of species or which are under some type of stress, the species range-abundance curves tend to fit models of less equitability like the log series and geometric series (Aguirre-Calderón et al. 2008, Magurran & McGill 2011), both useful as indicators of perturbed environments. In this sense, the range-abundance curves fit the geometric series model at the Chaco Mountain plain perturbed site, Chaco Mountain slope control and perturbed sites and Chaco Plains perturbed site, while at the Chaco Mountain plain control site and Chaco Plains control site, they fit the log series model (Table VI). In all cases, low numbers of abundant species and high numbers of rare

Table IV. Richness of species and Shannon Diversity (H') in the Chaco region of Argentina.

Locations	Type	Coordinates	Richness	H'	References
Mburucuyá National Park		27° 58' S; 57° 59' W	6	1.13	Cano & Leynaud 2010
El Bagual Reserve	Humid	26° 10' S; 58° 56' W	12	-	Scrocchi & Giraudo 2005
Pirané		25° 44' S; 59° 06' W	6	-	Pesci et al. 2018
Joaquín V. González		25° 05' S; 64° 09' W	17	1.92	Cruz et al. 1992, Fitzgerald et al. 1999
Los Colorados Biological Station	Semi-Arid	24° 41' S; 63° 18' W	11	1.69	Leynaud & Bucher 2005
Campo Grande		24° 43' S; 63° 17' W	8	1.56	
Chancaní	Arid	30° 22' S; 65° 26' W	13	1.23	Pelegrin et al. 2006, Pelegrin & Bucher 2012
Valle Fértil		30° 45' S; 67° 28' W	12	1.3	This paper

species are observed (Figure 4). This pattern implies that one or few factors determine an assemblage's species abundance, which could be associated with less heterogeneity in habitat characteristics or fewer resources available with respect to totally unaltered areas of the Chaco region. At the Chaco Mountain plain perturbed site, *L. chacoensis* and *A. longicauda* were observed as dominant species, representing 70% of total captures (Figure 4; Table II). At the Chaco Mountain plain control site, Chaco Mountain slope perturbed site and Chaco Plains sites, the most abundant species found (about 90% of total captures) were *L. chacoensis* and *T. teyou* (Figure 4; Table II). *Liolaemus chacoensis* and *Liolaemus gracilis* were the most abundant species at the Chaco Mountain slope control site, making up 80% of total captures (Figure 4; Table II).

Relative abundance of lizards in the Chaco Mountain varied between control and perturbed sites and was higher for the perturbed areas (Table II). Similar results were reported by Cano & Leynaud (2010), Jellinek et al. (2004) and Fredericksen & Fredericksen (2002), who suggest that loss of forest coverage and other changes brought about by logging and forest fires do not necessarily imply loss of abundance of some wild species from open areas. However, this is not common for forest species (e.g. Neilly et al. 2018). On the contrary, the Chaco Plains control site had a significantly greater abundance of

lizards than the perturbed site (Table II). The control site maintained characteristics of a primary forest made up of *A. quebracho-blanco* and carob, similar to that described by Pelegrin & Bucher (2012) for areas of moderately degraded forests in the central Arid Chaco, where relative abundance of lizards was greater with respect to primary forests and areas degraded by grazing and fire. This reinforces the intermediate perturbation hypothesis.

Nevertheless, changes in species abundance, either after or during perturbation, depend on the individual vegetation structure preferences of each species, the availability of food and specific microhabitats (Molina et al. 1999, Vitt et al. 2007, Kacoliris et al. 2009). The tbRDA revealed that variation in lizard abundance was only explained by habitat characteristics at low percentages (14%, $F_{11, 116} = 1.87$, $P = 0.001$; Figure 5). As regards the two central axis, the first explained 7.48% and the second 4.14%, with the explained variation only statistically significant for the first axis ($F_{11, 116} = 9.72$, $P = 0.001$). The habitat variable which most contributed to variation was bare ground for axis one ($R = -0.70$, $F_{11, 116} = 5.14$, $P = 0.002$), while axis two was negatively associated with herbaceous species ($R = -0.45$, $F_{11, 116} = 2.63$, $P = 0.027$) and positively associated with shrub ($R = 0.17$, $F_{11, 116} = 2.66$, $P = 0.026$). Relationships are observed between species and habitat variables: *A. longicauda* and *L. darwinii* with bare ground, *L. gracilis* and *S. doellojuradoi*

Table V. Dissimilarity between assemblages. Below the diagonal line, the percentage of dissimilarity between sites and statistical significance are presented (ANOSIM); above the white diagonal, species responsible for the dissimilarity and the accumulated percentage contributing to the difference are shown.

Sites	Chaco Mountain plain control	Chaco Mountain plain perturbed	Chaco Mountain slope control	Chaco Mountain slope perturbed	Chaco Plains control	Chaco Plains perturbed
Chaco Mountain plain control		*L. chacoensis* *A. longicauda* *L. darwinii* 76.30 %	*L. chacoensis* *A. gracilis* *T. teyou* 90.26 %	*L. chacoensis* *T. teyou* *A. longicauda* 90.13 %	*L. chacoensis* *T. teyou* *L. gracilis* 92.41 %	*L. chacoensis* *T. teyou* *L. gracilis* 90.75 %
Chaco Mountain plain perturbed	60.7 % / R= 0.45 P< 0.001		*A. longicauda* *L. chacoensis* *L. gracilis* 68.72 %	*A. longicauda* *L. chacoensis* *T. teyou* 77.04 %	*L. chacoensis* *A. longicauda* *T. teyou* 77.77 %	*A. longicauda* *L. chacoensis* *L. darwinii* 77.09 %
Chaco Mountain slope control	53.06 % / R= 0.06 P= 0.56	59.96 % / R= 0.51 P< 0.001		*L. chacoensis* *T. teyou* *L. gracilis* 83.54 %	*L. chacoensis* *L. gracilis* *T. teyou* 90.96 %	*L. chacoensis* *L. gracilis* *T. teyou* 89.55 %
Chaco Mountain slope perturbed	55.31 % / R= 0.05 P= 0.58	52.83 % / R= 0.23 P< 0.01	55.61 % / R= 0.15 P< 0.01		*L. chacoensis* *T. teyou* *A. longicauda* 93.09 %	*L. chacoensis* *T. teyou* *A. longicauda* 92.34 %
Chaco Plains control	50.66 % / R= 0.14 P= 0.04	51.84 % / R= 0.43 P< 0.001	52.27 % / R= 0.31 P< 0.001	46.04 % / R= 0.08 P= 0.27		*L. chacoensis* *T. teyou* *A. abalosi* 93.62 %
Chaco Plains perturbed	50.95 % / R= 0.03 P= 0.12	57.37 % / R= 0.50 P< 0.001	52.18 % / R= 0.17 P< 0.005	51.79 % / R= 0.09 P= 0.10	49.19 % / R= 0.25 P< 0.01	

with herbaceous and caves, *L. chacoensis* with canopy and branches and *T. teyou* with cactus and leaf litter (Figure 5).

Liolaemus chacoensis was abundant at all sites and does not vary for different habitat conditions between Chaco Mountain sites (Table II). However, its abundance was greater at the Chaco Plains control site, as compared to the perturbed site (Table II) where it was primarily associated with canopy and logs, habitats not as represented at the perturbed site. These results are consistent with the species' plasticity in the use of microhabitats, even under different perturbation conditions in different regions of the Chaco (Pelegrin et al. 2009, Pelegrin & Bucher 2010, T. Martínez, unpublished data). *Liolaemus gracilis* was only found in the Chaco Mountain, primarily associated with rocky slope environments and bare ground. This differs from what has been reported by other authors, who find *L. gracilis* associated with sandy areas with open vegetation in the Monte region (Videla & Puig 1994), and with sandy habitats with closed vegetation on coastal dunes (Vega et al. 2000).

Table VI. Distribution models for species abundance. ChMP-C: Chaco Mountain plain control, ChMP-P: Chaco Mountain plain perturbed, ChMS-C: Chaco Mountain slope control, ChMS-P: Chaco Mountain slope perturbed, ChP-C: Chaco Plains control, ChP-P: Chaco Plains perturbed. Bold values indicate the selected model, with least deviance (DIC) and AIC.

Models		Sites					
		ChMP- C	ChMP- P	ChMS- C	ChMS- P	ChP- C	ChP- P
Geometric series	DIC	10.99	**12.96**	**5.12**	**5.49**	14.20	**3.37**
	AIC	38.59	**58.00**	**33.21**	**30.98**	39.93	**24.68**
Log series	DIC	**3.77**	90.60	16.88	15.67	**0.09**	11.09
	AIC	**33.38**	137.64	46.97	43.16	**27.83**	34.40
Log normal	DIC	4.59	36.77	8.58	7.77	5.20	6.30
	AIC	34.19	83.81	38.66	35.26	32.94	29.61
Broken stick	DIC	128.15	133.53	52.25	70.99	193.05	40.23
	AIC	153.76	176.57	78.34	94.48	216.78	59.53

The abundance of this species was greater at the Chaco Mountain slope control site (Table II), probably due to its location in the foothills, with many rocks and open sites. The heterogeneous nature of *L. gracilis'* microhabitat use throughout its wide range of distribution (Videla & Puig 1994, Vega et al. 2000, Acosta et al. 2018) could allow it to soften the effects of intermediate perturbation conditions.

Aurivela longicauda predominates in sandbanks and carob forests in the Monte region, associated with low shrubs and bare ground, moving between sites in search of prey (Videla & Puig 1994, J.C. Acosta, unpublished data). In the Chaco Mountains, the abundance of *A. longicauda* was greater at the perturbed sites and was associated primarily with bare ground (Figure 5; Table II). *Teius teyou* is considered a generalist species and a pioneer associated with bare ground and perturbed patches (Varela & Bucher 2002). Pelegrin et al. (2009) report changes in the use of microhabitats between sites, where *T. teyou* uses less bare ground and more shrubs in degraded forests as compared to primary or restored forests. In this sense, *T. teyou* was observed at the Chaco Mountain and Chaco Plains control sites associated with tree canopy, while at the perturbed sites was found

to be associated with herbaceous species, leaf litter and shrubs. These changes in habitat use could explain the similarity in abundance of this species between sites (Table II; Leynaud & Bucher 2005, Pelegrin & Bucher 2012, T. Martínez, unpublished data). These results coincide with hypotheses on the condition of pioneering species at degraded sites and the greater abundance of heliothermic lizards in open environments, as for example *Ameivula ocellifera* in the Cerrado region of Brazil, *Cnemidophorus lemniscatus* in farmlands of Colombia and *Ameiva ameiva* greatly abundant at grazing sites of the Semi-arid Chaco in Argentina (Sartorius et al. 1999, Leynaud & Bucher 2005, Mesquita & Colli 2003, Melo & Pino 2008, Pelegrin et al. 2009, Ortega et al. 2019). The endemic Chaco lizard, *Ameivula abalosi*, was only recorded at the Chaco Plains control site, where arboreal and shrub structure predominates, associated with an herbaceous microhabitat. Considering the low number of captures and its absence from degraded areas, we infer that this species could be negatively affected by habitat perturbations.

Stenocercus doellojuradoi is considered endemic to the Chaco region and is associated with closed vegetation, leaf litter and primary forests without perturbations (Leynaud & Bucher
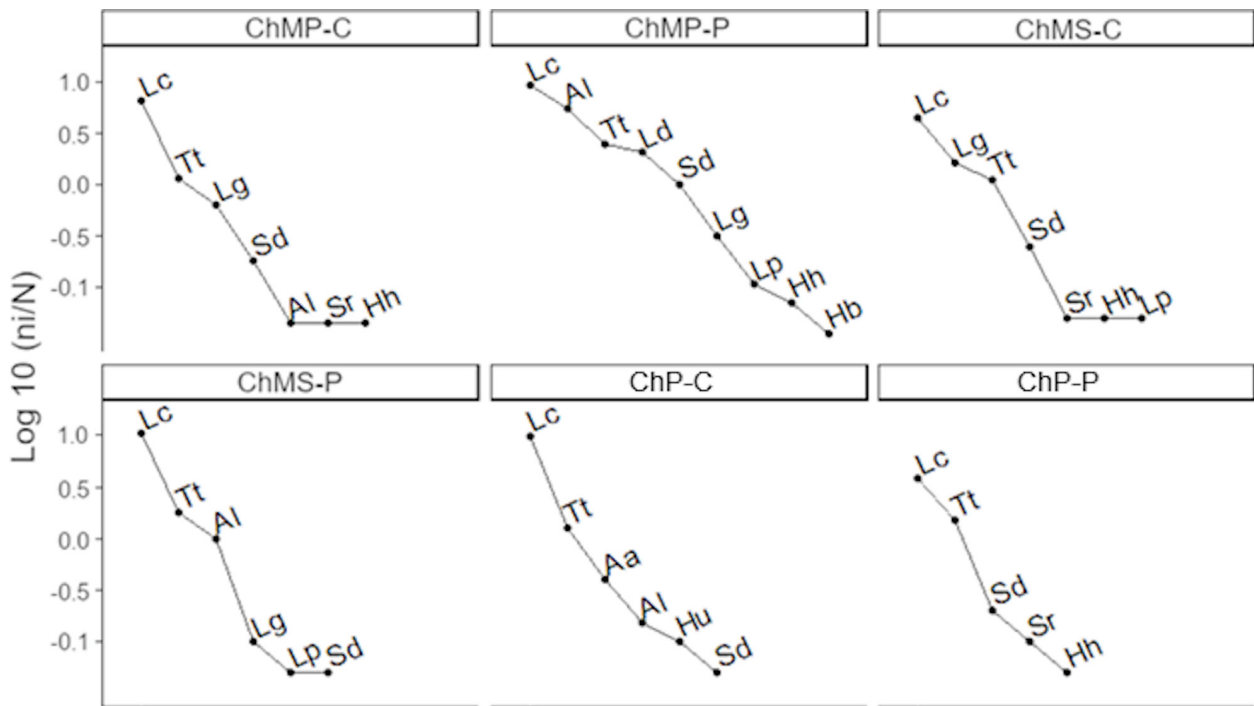
Figure 4. Range – Abundance curves for lizard assemblages in Valle Fértil, San Juan, Argentina. ChMP: Chaco Mountain plain (C: control, P: perturbed); ChMS: Chaco Mountain slope (C: control, P: perturbed); ChP: Chaco Plains (C: control, P: perturbed). For each site, relative abundance of each species was depicted (ni/N) in logarithmic scale against the range of species ordered from most to least abundant. Lc: *Liolaemus chacoensis*, Tt: *Teius teyou*, Al: *Aurivela longicauda*, Ld: *Liolaemus darwinii*; Sd: *Stenocercus doellojuradoi*; Lg: *Liolaemus gracilis*, Aa: *Ameivula abalosi*, Sr: *Salvator rufescens*, Lp: *Leiosaurus paronae*, Hh: *Homonota horrida*, Hb: *Homonota borelli*, Hu: *Homonota underwoodi.*

2005, Pelegrin et al. 2009, Pelegrin & Bucher 2012). However, a greater abundance of this species was found at the Chaco Mountain perturbed sites (Table II) and was generally associated with herbaceous species and caves (Figure 5). On the other hand, *Leiosaurus paronae* was found in low densities in the Chaco Mountain control and perturbed sites, while Pelegrin & Bucher (2012) associate this species with highland forest areas of the Chaco region. Therefore, considering the progressive advance of perturbations in the natural forest habitat, the population densities of *L. paronae* could be diminished. In this sense, species least abundant were those of the genus *Homonota*, associated with logs, leaf litter and caves, similar to observations made by other authors, which means it could be considered a specialist in habitat use (Cruz 1994, Pelegrin &

Bucher 2010, 2012). Taking into account the low capture numbers of *Homonota* spp., it is difficult to make predictions about these species' response to perturbations. Nevertheless, Tonini et al. (2016) suggest that some species (e.g. geckos) with strong phylogenetic influence are more vulnerable to risks of extinction from anthropogenic perturbations and therefore must be priorities for conservation efforts.

The use of land and native forests over the decades in the Arid Chaco of Argentina, together with modern activities carried out by rural inhabitants, including logging and livestock raising, have resulted in diverse landscapes in terms of vertical and horizontal stratification of vegetation. Consequently, the various lizard assemblages present in the center-west of the Arid Chaco in San Juan, both in the Mountain and
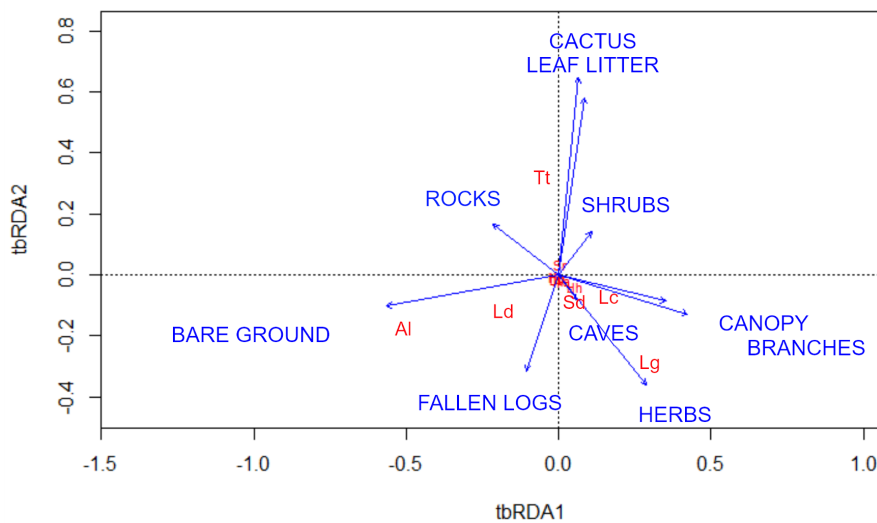
Figure 5. Redundancy Analysis based on transformations (tbRDA). Vector longitude and angle indicate greater or lesser correlation with tbRDA1 and tbRDA2 axes. The distance between a species and a vector indicates the strength of the species – habitat association. Species codes are shown in Figure 4.

Plains sectors, experience changes in structural parameters as regards the modification of habitat characteristics, supporting the hypothesis of this work. Considering the complexity of these arid and semi-arid ecosystems, characterized by a Chaco-Monte ecotone, it is likely that various landscape factors, such as types of perturbation and historic biogeography, interact with environmental and phylogenetic characteristics to create the dynamic and structure of the lizard community.

In conclusion, these and future results have implications for conservation biology in general and for the conservation and management of lizard assemblages in the Arid Chaco in particular, as many species depend on specific vegetation or structural aspects of the habitats in which they live. Some species, such as *S. doellojuradoi*, *L. paronae*, *A. abalosi* and *Homonota* spp. could be negatively affected by the total loss of arboreal strata, logs and leaf litter, which are necessary for thermoregulation, foraging and protection against predators. In the Chaco Plains, logging and cattle grazing have created a homogeneous environment with creosote bush, retamo and cacti, with a consequent decrease (about 50%) in the abundance of lizard species. It is therefore necessary to maintain the arboreal (e.g. *Aspidosperma quebracho-blanco*), shrub and herb stratum in order to conserve habitat heterogeneity and the abundance and diversity of species. Moreover, in sectors where it is impossible to protect large areas due to the fact that local populations depend on them, considered Multiple Use Reserves, the protection of smaller sectors and bridges that connect them, where richness, diversity and abundance is great, could represent a compromise between the needs of environmental managers and the needs of local communities (Attum et al. 2006). Therefore, taking into account the results obtained for abundance and richness of species in relation to habitat characteristics, it is necessary to work together with locals regarding the importance of carrying out correct land management in order to preserve reptile assemblages and the multiple ecosystem services they provide (food and medicinal resources, raw materials, cultural services, disease control, seed dispersion and frugivory, trophic web and nutrient cycling; see Valencia-Aguilar et al. 2013). The linking of scientific research with outreach activities is fundamental for biodiversity conservation and ecosystem functions.

Acknowledgments

REFERENCES

ACOSTA JC, BLANCO GM, GÓMEZ ALÉS R, ACOSTA R, PIAGGIO KOKOT L, VICTORICA AE, VILLAVICENCIO HJ & FAVA GA. 2018. Los Reptiles de San Juan. Córdoba: Editorial Brujas, 132 p.

AGUIRRE-CALDERÓN OA, CORRAL RIVAS J, VARGAS LARRETA B & JIMÉNEZ PÉREZ J. 2008. Evaluación de modelos de diversidad-abundancia del estrato arbóreo en un bosque de niebla. Rev. Fitotec Mex 31: 281-289.

ASTUDILLO G, CÓRDOBA M, GÓMEZ ALÉS R, ACOSTA JC & VILLAVICENCIO HJ. 2019. Termorregulación de la lagartija *Liolaemus chacoensis* (Squamata: Liolaemidae) durante su ciclo reproductivo, en el Chaco occidental, Argentina. Rev Biol Trop 67(6): 1505-1019.

ATTUM O, EASON P, COBBS G & EL DIN SMB. 2006. Response of a desert lizard community to habitat degradation: do ideas about habitat specialists/generalists hold? Biol Conserv 133(1): 52-62.

AZEVEDO-RAMOS C, DE CARVALHO JR O & DO AMARAL BD. 2006. Short-term effects of reduced-impact logging on eastern Amazon fauna. For Ecol Manag 232: 26-35.

BOLETTA PE, RAVELO AC, PLANCHUELO AM & GRILLI M. 2006. Assessing deforestation in the Argentine Chaco. For Ecol Manag 228: 108-114.

BUCHER EH. 1982. Chaco and Caatinga- South American Arid Savannas, Woodlands and Thickets. Ecol Stud 42: 48-79.

CANO PD & LEYNAUD GC. 2010. Effects of fire and cattle grazing on amphibians and lizards in northeastern Argentina (Humid Chaco). Eur J Wild Res 56(3): 411-420.

CARUSO N, LUCHERINI M, FORTIN D & CASANAVE EB. 2016. Species-specific responses of carnivores to human-induced landscape changes in central Argentina. PLoS ONE 11(3): e0150488.

CARVAJAL-COGOLLO JE & URBINA-CARDONA JN. 2008. Patrones de diversidad y composición de reptiles en fragmentos de bosque seco tropical en Córdoba, Colombia. Trop Conserv Sci 1: 397-416.

CARVAJAL-COGOLLO JE & URBINA-CARDONA N. 2015. Ecological grouping and edge effects in tropical dry forest: reptile-microenvironment relationships. Biodivers Conserv 24(5): 1109-1130.

CASTELLANO MJ & VALONE TJ. 2006. Effects of livestock removal and perennial grass recovery on the lizards of a desertified arid grassland. J Arid Environ 66(1): 87-95.

CHAPIN III FS ET AL. 2000. Consequences of changing biodiversity. Nature 405(6783): 234-242.

CHIU CH, WANG YT, WALTHER BA & CHAO A. 2014. Improved nonparametric lower bound of species richness via a modified Good-Turing frequency formula. Biometrics 70: 671-682.

CLARKE KR. 1993. Non-parametric multivariate analyses of changes in community structure. Australian J Ecol 18: 117-143.

COSTA BM, PANTOJA DL, VIANNA MCM & COLLI GR. 2013. Direct and short-term effects of fire on lizard assemblages from a Neotropical Savanna hotspot. J Herpetol 47(3): 502-510.

CRUZ FB. 1994. Actividad reproductiva en *Homonota horrida* (Sauria: Gekkonidae) del Chaco Occidental en Argentina. Cuad Herpetol 8: 119-125.

CRUZ FB, PEROTTI MG & FITZGERALD LA. 1992. Lista de anfibios y reptiles colectados en una localidad del chaco salteño. Acta Zool Lilloana 42: 101-107.

DE PINHO WERNECK F, COLLI GR & VITT LJ. 2009. Determinants of assemblage structure in Neotropical dry forest lizards. Austral Ecol 34(1): 97-115.

FEINSINGER P. 2001. Designing Field Studies for Biodiversity Conservation. Washington DC: Island Press, 212 p.

FICETOLA GF, SACCHI R, SCALI S, GENTILLI A, DE BERNARDI F & GALEOTTI P. 2007. Vertebrates respond differently to human disturbance: implications for the use of a focal species approach. Acta Oecol 31(1): 109-118.

FITZGERALD LA, CRUZ FB & PEROTTI GM. 1999. Phenology of a lizard assemblage in the dry Chaco of Argentina. J Herpetol 33: 526-535.

FREDERICKSEN NJ & FREDERICKSEN TS. 2002. Terrestrial wildlife responses to logging and fire in a Bolivian tropical humid forest. Biodivers Conserv 11(1): 27-38.

FRENCH SS, WEBB AC, HUDSON SB & VIRGIN EE. 2018. Town and country reptiles: a review of reptilian responses to urbanization. Integr Comp Biol 58(5): 948-966.

GARDNER TA, BARLOW J & PERES CA. 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol Conserv 138: 166-179.

GIBBONS JW, SCOTT DE, RYAN TJ, TUBERVILLE TD, METTS BS, GREENE JL, MILLS T, LEIDEN Y, POPPY S & WINNE C. 2000. The global decline of reptiles, déjà vu amphibians. Bioscience 50: 653-666.

HILL JK & HAMER KC. 1998. Using species abundance models as indicators of habitat disturbance in tropical forests. J Appl Ecol 35: 458-460.

HOARE JM, MONKS A & O'DONNELL CF. 2012. Can correlated population trends among forest bird species be predicted by similarity in traits? Wildl Res 39(6): 469-477.

HSIEH TC, MA KH & CHAO A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7: 1451-1456.

HUSTON MA. 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge: Cambridge University Press, 681 p.

JELLINEK S, DRISCOLL DA & KIRKPATRICK JB. 2004. Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. Austral Ecol 29: 294-304.

JONES KB. 1981. Effects of grazing on lizard abundance and diversity in western Arizona. Southwes Nat 26(2): 107-115.

KACOLIRIS FP, BERKUNSKY I & WILLIAMS JD. 2009. Methods for assessing population size in sand dune lizards (*Liolaemus multimaculatus*). Herpetologica 65: 219-226.

KARLIN MS, KARLIN UO, COIRINI RO, REATI GJ & ZAPATA RM. 2013. El Chaco Árido. Córdoba: Universidad Nacional de Córdoba, 422 p.

KINDT R & COE R. 2005. Tree diversity analysis: A manual and software for common statistical methods for ecological and biodiversity studies. Nairobi: World Agroforestry Centre (ICRAF), 196 p.

LEGENDRE P, OKSANEN J & TERBRAAK CJF. 2011. Testing the significance of canonical axes in redundancy analysis. Methods Ecol Evol 2: 269-277.

LEYNAUD GC & BUCHER EH. 2005. Restoration of degraded Chaco woodlands: effects on reptile assemblages. For Ecol Manag 213(1-3): 384-390.

LIMA AP, SUÁREZ FIO & HIGUCHI N. 2001. The effects of selective logging on the lizards *Kentropyx calcarata*, *Ameiva ameiva*, and *Mabuya nigropunctata*. Amphibia-Reptilia 22: 209-216.

MACIP-RÍOS R, LÓPEZ-ALCAIDE S & MUÑOZ-ALONSO A. 2013. Abundancia, uso de hábitat, microhábitat y hora de actividad de *Ameiva undulata* (Squamata: Teidae) en un paisaje fragmentado del Soconusco chiapaneco. Rev Mex Biodivers 84(2): 622-629.

MACIP-RÍOS R & MUÑOZ-ALONSO A. 2008. Diversidad de lagartijas en cafetales y bosque primario en el Soconusco chiapaneco. Rev Mex Biodivers 79(1): 185-195.

MACKEY RL & CURRIE DJ. 2001. The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82: 3479-3492.

MAECHLER M. 2019. Finding Groups in Data'': Cluster Analysis Extended Rousseeuw et. R Package version 2.0, 6. Available at https://cran.r-project.org/web/packages/cluster/.

MAGURRAN AE & MCGILL BJ. 2011. Biological Diversity: frontiers in measurement and assessment. Oxford: Oxford University Press, 345 p.

MÁRQUEZ J, CARRETERO EM & DALMASSO A. 2017. Provincias Fitogeográficas de la Provincia de San Juan. In: Martínez-Carretero E & García A (Eds), San Juan Ambiental. San Juan: Universidad Nacional de San Juan, p. 187-197.

MÁRQUEZ J, PASTRÁN G, ORTIZ G, VARELA S & SÁNCHEZ V. 2008. Procesos de Deterioro Ambiental en el Chaco Árido sanjuanino. In: Geomorfología y Cambio Climático. Tucumán: Universidad Nacional de Tucumán, p. 119-136.

MARTORI R, JUÁREZ R & AÚN L. 2002. La taxacenosis de lagartos de Achiras, Córdoba, Argentina: parámetros biológicos y estado de conservación. Rev Esp Herpetol 16: 73-91.

MELO AI & PINO EP. 2008. Estructura y abundancia poblacional de *Ameiva Ameiva* y *Cnemidophorus Lemniscatus* (Sauria: Teiidae) en el sector Nororiental del embalse el Guájaro, la peña, departamento del Atlántico, Colombia. Herpetotropicos 4(1): 31-37.

MENKE SB. 2003. Lizard community structure across a grassland–creosote bush ecotone in the Chihuahuan Desert. Can J Zool 81(11): 1829-1838.

MESQUITA DO & COLLI GR. 2003. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). Copeia 2003(2): 285-298.

MESQUITA DO, COLLI GR, PANTOJA DL, SHEPARD DB, VIEIRA GH & VITT LJ. 2015. Juxtaposition and disturbance: Disentangling the determinants of lizard community structure. Biotropica 47(5): 595-605.

MOLINA SI, VALLADARES GR, GARDNER S & CABIDO MR. 1999. The effects of logging and grazing on the insect community associated with a semi-arid Chaco forest in central Argentina. J Arid Environ 42(1): 29-42.

MONKS JM, MONKS A & TOWNS DR. 2014. Correlated recovery of five lizard populations following eradication of invasive mammals. Biol Invasions 16(1): 167-175.

MOONEY H, LARIGAUDERIE A, CESARIO M, ELMQUIST T, HOEGH-GULDBERG O, LAVOREL S, MACE GM, PALMER M, SCHOLES R & YAHARA T. 2009. Biodiversity, climate change, and ecosystem services. Curr Opin Env Sust 1(1): 46-54.

NEILLY H, NORDBERG EJ, VANDERWAL J & SCHWARZKOPF L. 2018. Arboreality increases reptile community resistance to disturbance from livestock grazing. J Appl Ecol 55(2): 786-799.

NORDBERG EJ & SCHWARZKOPF L. 2019. Predation risk is a function of alternative prey availability rather than predator abundance in a tropical savanna woodland ecosystem. Sci Rep 9(1): 1-11.

NORI J, TORRES R, LESCANO JN, CORDIER JM, PERIAGO ME & BALDO D. 2016. Protected areas and spatial conservation priorities for endemic vertebrates of the Gran Chaco, one of the most threatened ecoregions of the world. Divers Distrib 22(12): 1212-1219.

OKSANEN J. 2009. Vegan: Community Ecology Package, R package version 1.15-4.

ORTEGA Z, MENCÍA A, MARTINS K, SOARES P, FERREIRA VL & OLIVEIRA-SANTOS LG. 2019. Disentangling the role of heat sources on microhabitat selection of two Neotropical lizard species. J Trop Ecol 35(4): 149-156.

PASSOS DC, MESQUITA PCMD & BORGES-NOJOSA DM. 2016. Diversity and seasonal dynamic of a lizard assemblage in a Neotropical semiarid habitat. Stud Neotrop Fauna E 51(1): 19-28.

PELEGRIN N & BUCHER EH. 2010. Long-term effects of a wildfire on a lizard assemblage in the Arid Chaco forest. J Arid Environ 74(3): 368-372.

PELEGRIN N & BUCHER EH. 2012. Effects of habitat degradation on the lizard assemblage in the Arid Chaco, central Argentina. J Arid Environ 79: 13-19.

PELEGRIN N, CHANI JM, ECHEVARRIA AL & BUCHER EH. 2009. Effects of forest degradation on abundance and microhabitat selection by ground dwelling Chaco lizards. Amphibia-Reptilia 30: 265-271.

PELEGRIN N, CHANI JM, ECHEVARRIA AL & BUCHER EH. 2013. Habitat degradation may affect niche segregation patterns in lizards. Acta Oecol 51: 82-87.

PELEGRIN N, LEYNAUD GC & BUCHER EH. 2006. Reptile fauna of the Chancaní Reserve (Arid Chaco, Argentina): species list and conservation status. Herpetozoa 19: 85-86.

PEREIRA HM, LEADLEY PW, PROENÇA V, ALKEMADE R, SCHARLEMANN JP, FERNANDEZ MANJARRÉS JF & CHINI L. 2010. Scenarios for global biodiversity in the 21st century. Science 330: 1496-1501.

PESCI GP, SÁNCHEZ JM, MUNIZ LEÃO S & PELEGRIN N. 2018. Reptiles y anfibios de una localidad del Chaco Húmedo en Formosa, Argentina. Cuad Herpetol 32(1): 47-54.

PRENTICE IC & LEEMANS R. 1990. Pattern and process and the dynamics of forest structure: a simulation approach. J Ecol: 340.

R DEVELOPMENT CORE TEAM. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

READ JL. 2002. Experimental trial of Australian arid zone reptiles as early warning indicators of overgrazing by cattle. Austral Ecol 27(1): 55-66.

REATI GJ, ALLIER S, AVALOS C, MONGUILLOT J & GOIRÁN S. 2010. Fauna Silvestre. En: Coirini RO, Karlin MS & Reati GJ (Eds), Manejo sustentable del ecosistema Salinas Grandes, Chaco Árido. Córdoba: Encuentro Grupo Editor, p. 129-169.

SARTORIUS SS, VITT LJ & COLLI GR. 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. Biol Conserv 90(2): 91-101.

SCHERER R & SCHAARSCHMIDT F. 2013. Simultaneous confidence intervals for comparing biodiversity indices estimated from over dispersed count data. Biometrical J 55: 246-263.

SCROCCHI GJ & GIRAUDO AR. 2005. Reptiles de la reserva El Bagual. Historia natural y paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina. Inventario de la fauna de vertebrados y de la flora vascular de un área protegida del Chaco Húmedo. Temas de Naturaleza y Conservación 4: 155-198.

SMART R, WHITING MJ & TWINE W. 2005. Lizards and landscapes: integrating field surveys and interviews to assess the impact of human disturbance on lizard

assemblages and selected reptiles in a savanna in South Africa. Biol Conserv 122(1): 23-31.

TELLERÍA JL. 2013. Pérdida de biodiversidad. Causas y consecuencias de la desaparición de las especies. Mem Real Soc Esp Hist Nat 10: 13-25.

TONINI JFR, BEARD KH, FERREIRA RB, JETZ W & PYRON RA. 2016. Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. Biol Conserv 204: 23-31.

URBINA-CARDONA JN, LONDOÑO-MURCIA MC & GARCÍA-ÁVILA DG. 2008. Dinámica espacio-temporal en la diversidad de serpientes en cuatro hábitats con diferente grado de alteración antropogénica en el Parque Nacional Natural Isla Gorgona, Pacífico Colombiano. Caldasia: 479-493.

URBINA-CARDONA JN, OLIVARES PÉREZ M & REYNOSO VH. 2006. Herpetofauna diversity and microenvironment correlates across a pasture–edge–interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. Biol Conserv 132: 61-75.

VALENCIA-AGUILAR A, CORTÉS-GÓMEZ AM & RUIZ-AGUDELO CA. 2013. Ecosystem services provided by amphibians and reptiles in Neotropical ecosystems. Int J Biodivers Sci Ecosyst Serv Manag 9(3): 257-272.

VARELA RO & BUCHER EH. 2002. The lizard *Teius teyou* (Squamata: Teiidae) as a legitimate seed disperser in the dry Chaco forest of Argentina. Stud Neotrop Fauna Environ 37(2): 115-117.

VEGA LE, BELLAGAMBA PJ & FITZGERALD LA. 2000. Long term effects of anthropogenic habitat disturbance on a lizard assemblage inhabiting coastal dunes in Argentina. Can J Zool 78: 1653-1660.

VENABLES WN & RIPLEY BD. 2002. Modern applied statistics with S. Fourth. Springer, New York, NY.

VIDELA F & PUIG S. 1994. Estructura de una comunidad de lagartos del Monte. Patrones de uso espacial y temporal. Multequina 3: 99-112.

VITT LJ, AVILA-PIRES TC, CALDWELL JP & OLIVEIRA VR. 1998. The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. Conserv Biol 12(3): 654-664.

VITT LJ, COLLI G, CALDWELL JP, MESQUITA D, GARDA AA & FRANÇA FG. 2007. Detecting variation in microhabitat use in low-diversity lizard assemblages across small-scale habitat gradients. J Herpetol 41: 654-663.

VITT LJ & DE CARVALHO CM. 1995. Niche partitioning in a tropical wet season: lizards in the lavrado area of northern Brazil. Copeia (2): 305-329.

RODRIGO GÓMEZ ALÉS[1,2]
https://orcid.org/0000-0002-4150-9255

JUAN CARLOS ACOSTA[1]
https://orcid.org/0000-0003-2524-3474

GRACIELA BLANCO[1]
https://orcid.org/0000-0003-2592-0420

ANA PAULA GALDEANO[1,2]
https://orcid.org/0000-0002-2052-5352

[1]DIBIOVA (Gabinete Diversidad y Biología de Vertebrados del Árido), Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Av. Ignacio de la Roza 590 (O), Rivadavia, San Juan, Argentina

[2]CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Av. Ignacio de la Roza 590 (O), Rivadavia, San Juan, Argentina

Correspondence to: **Rodrigo Gómez Alés**
E-mail: rodri.gomezales@gmail.com

Author contributions

Rodrigo Gómez Alés carried out fieldwork, performed the analysis and wrote the manuscript. Juan Carlos Acosta carried out fieldwork and contributed to the final version of the manuscript. Graciela Blanco contributed to the final version of the manuscript. Ana Paula Galdeano carried out fieldwork.