The Role of Landscape in Contact Zones of Sister Species of Lizards

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1. Introduction

Elucidating the factors regulating the spatial distribution of ecologically similar species is a key pursuit (Dammhahn and Kappeler, 2008; Peres-Neto, 2006). Many biotic and abiotic variables might influence species distribution and determine allopatry or simpatry (Di Cola & Chiaraviglio, 2010). Moreover, species patterns are strongly associated with habitat variables at different spatial scales (Hatten & Paradzick, 2003). However, the role of landscapes in contact zones is not completely understood.

Contact zones have long been recognized as natural laboratories of evolution (Bridle et al., 2001). The geographic structure of contact zones determines dynamic evolutionary processes; however, since landscape structure influences population processes (Cardozo et al, 2007; Cardozo & Chiaraviglio, 2008) the maintenance of contact zones is likely to depend on landscape patterns.

Morphologically similar species are more likely to interact than morphologically dissimilar ones simply because a major portion of the behavioral and ecological activities of animals is associated with morphology (Losos, 1990; Pianka, 1986). Morphological similarity among coexisting animal species induces potential interactions that may lead to niche segregation (Huey, 1974; Huey & Pianka 1977). It is widely accepted that niche differentiation is often the basis for the coexistence of competitors (MacArthur & Levins, 1967; Roughgarden, 1979); however, how the coexisting species use landscape-scale resources is not clear. Interspecific competition might favour niche differentiation between competitors because it may optimise their behaviour in different ways (Law et al., 1997; Maynard Smith & Parker, 1976). Thus, niche differentiation in ecologically similar species might induce divergence of landscape-scale habitat use.

In this work, we focused on two closely related lizard species: *Tupinambis merianae* and *Tupinambis rufescens*; they are particularly interesting because they occupy the southernmost area of *Tupinambis* group distribution in South America (Peters & Donoso-Barros, 1986). *T. rufescens* would be restricted to the dry Chaco whereas *T. merianae* would occur in diverse regions (Cei, 1993; Colli et al., 1998; Lopes & Abe, 1999) from southern Amazonia to

northern Patagonia (Carvalho et al., 2006). The contact zone of the two lizards coincides principally with the arid South American Gran Chaco.

The species have similar body size and external morphological traits, as well as overlapping macro-habitat use and general foraging mode (Castro & Galetti, 2004; Williams et al., 1993). Therefore, a potentially extensive interspecific interaction would represent a significant pressure in sympatric areas. The combination of morphological similarity, typically terrestrial habits and territoriality renders *Tupinambis* lizards ideal models for examining differential use of resources in sympatric areas based on landscape structure.

Considering that habitat loss is a serious environmental problem in many ecosystems (Ishwar et al., 2003; Luiselli & Capizzi, 1997; Mac Nally & Brown, 2001), the conservation status of landscapes in key wildlife habitats, such as contact zones, becomes strikingly relevant for species conservation. Numerous research works indicate that several species are globally threatened by habitat loss, and how changes in spatial patterns influence ecological processes has received great attention. For instance, Cardozo & Chiaraviglio (2008) found that landscape influences life history parameters and spatial distribution of reproductive individuals in snakes, leading to geographical variations in mating systems and therefore variations in reproductive potential. Furthermore, Cardozo et al. (2007) showed that landscape fragmentation affects dispersal patterns, reducing gene flow.

Investigations on landscape-scale Squamata habitats may provide essential knowledge to understand interspecific interactions and to implement measures for the conservation of herpetological communities (Filippi & Luiselli, 2006). Nevertheless, not only does habitat loss pose a threat to individual species but also landscape modifications could affect species interactions. Thus, the understanding of the associations between landscape conservation status and the distribution of sister species in contact zones could be useful to design conservation plans not only for individual species but also for ecological systems.

We examined landscape-scale habitat use in contact and allopatric zones between the two teiid lizards (*T. merianae* and *T. rufescens*) that occur in the Chaco region of central Argentina. Habitat heterogeneity is expected to increase the probability of coexistence among sister species (Tews et al., 2004). Therefore, we hypothesized divergence in landscape use in contact zones by both species, which would exploit high quality resources and take advantage of habitat heterogeneity. Within a regional context, animals that need either to maximize the availability of resources or to minimize interspecific interactions may select areas dominated by patches of a particular vegetation type (Jonshon et al., 2004).

We generated useful knowledge to guide conservation efforts including landscape-level process-oriented considerations, to contribute to avoid disruption of the evolutionary process and to ensure healthy biodiversity at all levels.

2. Methods

2.1 Study area

The study area was located in the province of Córdoba, central Argentina, which is an ideal natural scenario for the study of landscape-scale niche differentiation of *T. merianae* and *T. rufescens* because this area includes the southernmost contact zone between the species

distributions. The province of Córdoba has a central-western mountain area with a maximum elevation of 2790 m a.s.l. surrounded by vast plains of 600-900 m a.s.l. The study area lies largely within the Gran Chaco, which is the largest dry forest in South America; vegetation in the region comprises a mosaic of xerophytic forests and scrubs (Zak & Cabido, 2002). The Gran Chaco is a highly threatened wooded region, strongly affected by extensive livestock raising, extractive forestry and poorly planned agricultural expansion (Zak et al., 2004, 2008). To the east, the study area also includes the Pampas region, which was originally composed of natural grasslands but which is currently severely degraded mainly due to the advance of crop farming (Cozzani et al., 2004).

2.2 Species data

We used a database that includes approximately 700 records of the presence of *T. rufescens* and *T. merianae* in central Argentina, which were gathered during field work conducted in the framework of a major project on lizard ecology developed by our research group at the Universidad Nacional de Córdoba, Argentina. Presence records were classified according to their locality of origin (69 localities of presence of *T. merianae* and 32 localities of presence of T. *rufescens*) (Fig. 1).
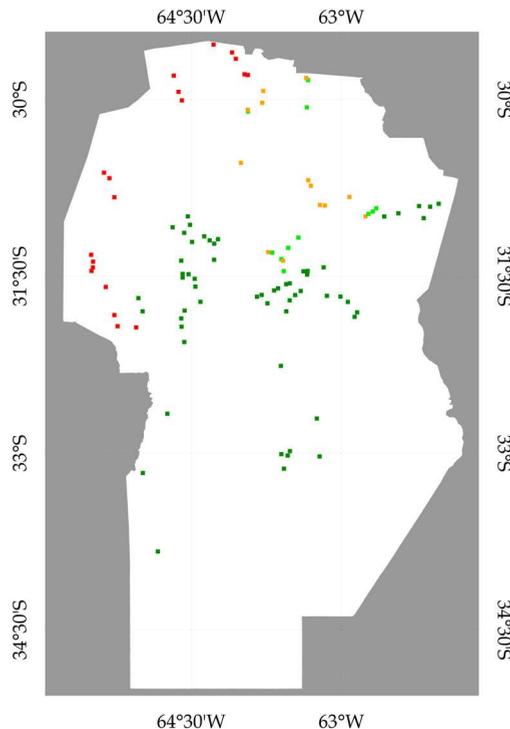

Fig. 1. Localities of presence of *T. merianae* (dark green: allopatry, light green: sympatry) and *T. rufescesns* (dark red: allopatry, light red: sympatry) in the province of Córdoba, central Argentina.

External polygons, considering presence of each species and the geographical characteristics of the study area were drawn. Localities were categorized as sympatric or allopatric depending on whether or not they were included within the intersection of the polygons or next to any heterospecific record of presence within a radius of 10 km (58 allopatric and 11 sympatric localities of presence of *T. merianae*, and 19 allopatric and 13 sympatric localities of presence of *T. rufescens*).

We defined the sample unit as a buffer area around the exact geographical coordinates of the locality of presence (Westphal et al., 2003). Sample units were circular plots of 2-km radius, which is equivalent to twice the area that contains the ecological range reported for other *Tupinambis* spp. (Mendoza & Noss, 2003; Winck, 2007). We intersected those areas with landscape cover features, i.e., we selected "mini-landscapes", for further characterization with landscape metrics (Westphal et al., 2003). To determine landscape availability we selected mini-landscapes at random within the distribution area delimited by the external polygon of the localities of presence for each species. We also quantified landscape availability in the contact zone considering the external polygon of the localities classified as sympatric.

2.3 Landscape analysis

The vegetation land-cover map of the province of Córdoba was created by the Multidisciplinary Institute of Plant Biology (IMBIV) of the National University of Córdoba and CONICET, Argentina (Zak, 2008). This map was obtained from the classification of Landsat 5 TM images together with phytosociological data. The researchers originally identified, described and mapped 19 land-cover types (Zak & Cabido, 2002). The classification of the Landsat imagery was based on the application of a maximum likelihood classifier using the sixth bands of the TM images and their Normalized Difference Vegetation Index (NDVI). Training sites were determined after analysis and field recognition of clusters defined by previous unsupervised classifications and the multivariate analysis of Braun-Blanquet (1950) phytosociological releves.

We grouped the original vegetation land-cover map according to the ecological function of the land-cover types for the bioecology of the study species. Among the environmental factors that might influence behaviors in Squamata, vegetation structure would be of great importance (Blouin-Demers & Weatherhead, 2001; Chiaraviglio & Bertona, 2007; Row & Blouin-Demers, 2006) because it provides alternative thermal environments for thermoregulation (Chiaraviglio, 2006) and might affect reproductive processes and life history traits (Cardozo & Chiaraviglio, 2008; Cardozo & Chiaraviglio, 2011). Therefore, according to the complexity of the vertical structure of the land covers, we determined three major vegetation classes: forest, shrublands and low vertical structures (LVS). Forest includes lowland forests and highland forests; shrublands includes lowland scrubs and highland scrubs; and LVS vegetation includes natural grasslands, halophytes, cordgrass, palustrine vegetation, cultural vegetation, saline zones, waterlogged soils, highland grasslands and bare soils.

To obtain consistent fragmentation metrics, we refined image classification by applying a moving window using the majority analysis (Baldi et al., 2006; Cardozo et al., 2007). We assessed the configuration of the three major vegetation classes in each mini-landscape by

calculating the following fragmentation metrics: a. Class Metrics: proportional abundance in the landscape (PLAND) ; mean patch area (hectare) (AREA_MN); number of patches (NP); landscape shape index (LSI), which is a measure of the total edge of each class and increases as the patch type becomes more disaggregated; shape complexity (PARA_MN), which is calculated as mean perimeter area ratio; heterogeneity (IJI), which increases when the corresponding patch type becomes equally adjacent to all other patch types (i.e., maximally interspersed and juxtaposed to other patch types); proximity (PROX_MN), which increases as the neighborhood (defined as 2830 m to include the entire the area of the mini-landscape) is increasingly occupied by patches of the same type and as those patches become closer and more contiguous (or less fragmented) in distribution. b. Land Metrics: the total edge length in the landscape (LSI); contagion (CONTAG), which increases when all patch types are maximally aggregated and minimally interspersed (equal proportions of all pair-wise adjacencies); diversity (SHDI), which increases as the number of different patch types (i.e., patch richness, PR) increases and/or the proportional distribution of area among patch types becomes more equitable; contrast-weighted edge density (CWED) (metres per hectare), which increases as the amount of edge in the landscape increases and/or as the contrast in edges increases. We introduced the following edge contrast weights: forest-shrubs=0.25, forest-LVS=0.99, shrubs-LVS=0.75. All metrics were calculated using FragStats 3.3 (Cardozo & Chiaraviglio, 2008; McGarigal & Marks, 1995; Rutledge, 2003).

2.4 Analyses

We compared the landscape-scale habitat availability in the allopatric and sympatric localities areas of *T. merianae* and *T. rufescens* with Kruskall-Wallis test of landscape features of the random mini-landscapes. Then we compared the landscape-scale habitat use and selection between species by applying Wilcoxon test. Niche differentiation analysis was based on the comparison of landscape features of the sympatric localities between the two species. Intraspecific variations in habitat use were determined by comparing landscape features between allopatric and sympatric localities for each species by applying Wilcoxon test. We also analyzed the results in an information theoretical framework, which allowed us to examine various models including interactions among variables. We fit the generalized linear models (GLM) and employed the Akaike Information Criterion (AIC) to select the models (Westphal et al., 2003) that best identify the landscape features determining species distribution. The model with the lowest AIC was selected as the 'best' model (Mazerolle, 2006). These analyses were performed with R: A Language and Environment for Statistical Computing (2011).

3. Results

3.1 Landscape-scale habitat availability

The configuration of the available landscape presented a gradient from the distribution area of *T. merianae* to that of *T.rufescens* (SE-NW) (Table 1) of decreasing proportion (PLAND) and mean area (AREA_MN) of LVS patches, and increasing values of these metrics for the forest and shrubland areas. Along this gradient, toward the NW, LVS vegetation exhibited greater edge length because of increasing disaggregation (LSI), and increased patch shape complexity (PARA_MN). Shrublands became more interspersed (IJI), with more irregular edges (PARA_MN), than to the SE.

		Landscape availability *T. merianae*	Landscape availability contact zone	Landscape availability *T. rufescens*	P value
		N=87	N=21	N=32	
Class Metrics					
PLAND	LVS	93.23	74.33	64.11	<0.0001
	Forest	4.26	25.64	26.09	0.0002
	Shrublands	2.51	0.03	9.80	>0.9999
AREA_MN	LVS	1347.24	849.46	684.06	<0.0001
	Forest	27.01	127.40	147.10	0.0002
	Shrublands	5.01	0.20	38.67	>0.9999
NP	LVS	1.47	3.19	4.28	>0.9999
	Forest	1.23	4.00	3.69	0.0042
	Shrublands	1.34	0.86	3.00	>0.9999
LSI	LVS	1.27	1.96	2.21	0.0004
	Forest	2.48	2.49	2.84	>0.9999
	Shrublands	3.02	1.30	2.58	>0.9999
PARA_MN	LVS	40.35	107.40	145.21	0.0005
	Forest	236.77	186.41	181.42	>0.9999
	Shrublands	262.30	635.03	382.32	0.0013
PROX_MN	LVS	21.99	28.67	54.19	>0.9999
	Forest	9.63	26.59	26.84	>0.9999
	Shrublands	16.64	0.01	21.28	>0.9999
IJI	LVS	77.77	10.71	48.06	>0.9999
	Forest	72.86	11.33	45.34	>0.9999
	Shrublands	69.73	97.25	86.62	0.0040
Land Metrics					
LSI		1.29	1.80	2.18	<0.0001
CWED		2.19	7.99	9.20	<0.0001
CONTAG		92.73	74.81	69.63	<0.0001
IJI		74.77	13.58	49.86	0.0005
SHDI		0.11	0.35	0.46	<0.0001

Table 1. Landscape availability in the distribution areas of *T. merianae* and *T. rufescens* in central Argentina.

The proximity (PROX_MN) among patches of the landscape cover types did not vary. Regarding mean landscape metrics, diversity (SHDI), landscape shape index (LSI) and contrast-weighted edge density (CWED) increased in the contact zone and in the distribution area of *T. rufescens*. By contrast, connectivity (CONTAG) decreased, showing more heterogeneous landscapes.

3.2 Landscape-scale habitat use and selection

Although occurring in landscapes with prevailing LVS vegetation distributed in few large patches, *T. merianae* selected landscapes with a greater proportion of forest and shrublands – about 20%- than the available average -7%- (forest :W=6542.00, P<0.0001; shrubland: W=6166.00, P=0.0008). *Tupinambis merianae* required forest patches of an average of 50 ha and shrub patches of 30 ha (Fig. 2 a).

Tupinambis rufescens also selected landscapes that are different from those available, with low proportion of LVS vegetation disaggregated in patches, and a high proportion of forest and shrubs, reaching 56%, which is slightly higher than landscape availability - 36%- (LVS: W=1210.00, P<0.0223; forest: W=931.00, P=0.1240; shrublands: W=951.00, P=0.2235). Landscapes selected by *T. rufescens* presented more forest patches than landscapes selected by *T. merianae*. *Tupinambis rufescens* required forest patches of approximately 224 ha and shrub patches of 188 ha (Fig. 2 b).
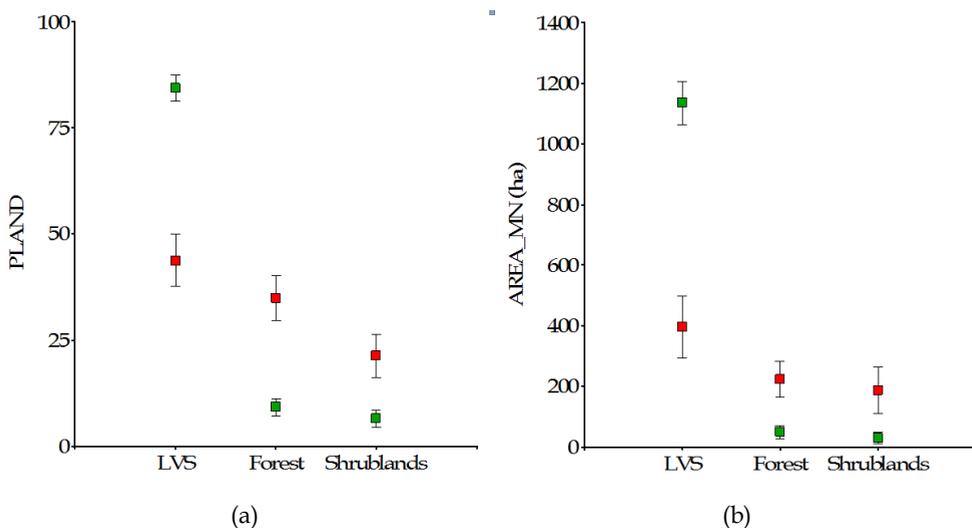

Fig. 2. Landscape use of *T. merianae* (green) and *T. rufescens* (red): (a) Percentage of landscape (PLAND); (b) Mean patch area (AREA_MN).

Species differed in the landscape-scale habitat use in terms of proportion of land cover types and mean area of the patches (LVS: PLAND, W=946.00, P<0.0001, AREA_MN, W=955.00, P<0.0001; forest, PLAND, W=2238.5, P<0.0001, AREA_MN, W=2212.5, P<0.0001; shrublands, PLAND, W=1995.00, p=0.0047, AREA_MN, W=2010.00, P=0.0032). Moreover, landscapes used by *T. rufescens* presented patches of LVS vegetation with more complex shape (PARA_MN) and more compact forest patches than landscapes used by *T.merianae. Tupinambis rufescens* used landscapes where LVS patches and forest patches exhibit greater proximity than landscapes used by *T. merianae.* The amount and contrast of edges (LSI and CWED) and diversity (SHDI) differed between landscapes used by both species (Table 2).

		T. merianae N=69	*T. rufescens* N=32	P value
Class Metrics				
NP	LVS	2.52	5.16	0.0001
	Forest	3.45	4.31	0.0389
	Shrublands	3.09	3.56	0.1161
LSI	LVS	1.72	2.50	0.0001
	Forest	2.68	2.68	0.6500
	Shrublands	2.96	2.73	0.6385
PARA_MN	LVS	76.87	201.44	<0.0001
	Forest	244.85	183.95	0.0132
	Shrublands	369.32	289.04	0.1980
PROX_MN	LVS	21.24	38.74	0.0003
	Forest	8.35	30.09	0.0021
	Shrublands	22.75	14.55	0.6023
IJI	LVS	58.22	56.44	0.6224
	Forest	53.35	47.75	0.6815
	Shrublands	72.92	73.85	>0.9999
Land Metrics				
LSI		1.77	2.31	0.0013
CWED		5.75	9.57	0.0033
CONTAG		82.60	62.56	0.0001
IJI		58.02	57.42	0.8055
SHDI		0.27	0.57	0.0002

Table 2. Landscape use of *T. merianae* and *T. rufescens* in central Argentina.

3.3 Landscape-scale habitat use and selection: Sympatry and allopatry

Tupinambis merianae both in allopatry and sympatry used similar landscapes in terms of proportions of land-cover types (LVS: W=307.50, P=0.1943; forest: W=451.00, P=0.2690; shrubs: W=360, P=0.6507). By contrast, *T. rufescens* in allopatry and sympatry used the landscape differentially. In sympatry, this species used landscapes with lower proportion of forest and shrubs, and higher proportion of LVS vegetation than in allopatry (LVS: W=289.00, P=0.0042; forest: W=161.00, P=0.0399; shrubs: W=151.50, P=0.0136). Landscape use did not differ between *T. rufescens* and *T. merianae* in sympatry, according to proportion of land cover types (LVS: W=145.50, P=0.6423; forest: W=134.00, P=0.8386; shrubs: W=136.50, P=0.9483) (Fig. 3a). Landscape-scale habitat use did not differ from landscape availability in either species (PLAND: LSV: H=55, P=0.7601; forest: H=1.67, P=0.4315; shrubs: H=0.10, P=0.9401).

Landscape-scale habitat use did not differ between *T. rufescens* and *T. merianae* in sympatry in terms of mean patch area (LVS: W=149.50, P=0.4859; forest: W=134.00, P=0.8386; shrubs: W=136.50, P=0.9483) or number of patches. *Tupinambis rufescens* in sympatry used landscapes with fewer patches of forest and shrubs than those used in allopatry (Table 3). In addition, shrubland patches were smaller and LVS vegetation patches were larger than in allopatry (LVS: W=284.00, P=0.0076; forest: W=177.00, P=0.1498; shrubs: W=155.00, P=0.0197) (Fig. 3b).
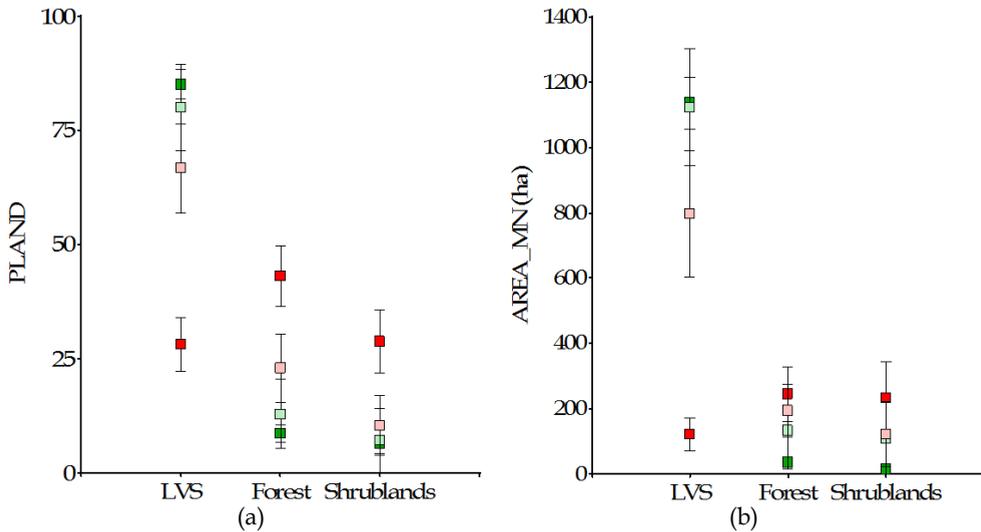
Fig. 3. Landscape use of *T. merianae* (green) and *T. rufescens* (red) in allopatry (dark) and sympatry (light). (a) Percentage of landscape (PLAND); (b) Mean patch area (AREA_MN).

Shape complexity (PARA_MN) of land cover types did not vary within or between species in sympatry (Table 3). *Tupinambis rufescens* in sympatry used landscapes with more dispersed forest patches (PROX_MN) than those used in allopatry. Landscapes used by *T.rufescens* in sympatry presented lower amount of edge (LSI) than those used in allopatry. *Tupinambis merianae* in sympatry used landscapes with shrubland patches more dispersed and with lower amount of edge than those used in allopatry.

		T. merianae allopatry N=58	*T. merianae* sympatry N=11	P value	*T. rufescens* allopatry N=19	*T. rufescens* sympatry N=13	P value	P value Interspecific sympatry
Class Metrics								
NP	LVS	2.59	2.18	0.8619	5.32	4.92	0.2704	0.1541
	Forest	3.40	3.73	0.2711	5.68	2.31	0.0020	0.3034
	Shrublands	3.55	0.64	0.4358	5.00	1.46	0.0084	0.9739
LSI	LVS	1.70	1.85	0.2344	2.76	2.14	0.0654	0.6843
	Forest	2.78	2.32	0.4050	2.78	2.45	0.3893	0.7440
	Shrublands	3.24	1.52	0.0190	2.93	2.09	0.1265	0.2809
PARA_MN	LVS	80.35	58.51	0.4166	229.22	162.98	0.0926	0.3529
	Forest	248.15	233.32	0.2870	202.17	145.50	0.1761	0.1777
	Shrublands	335.32	539.34	0.0613	287.42	294.24	0.8359	0.1473
PROX_MN	LVS	20.67	24.24	0.8061	48.75	24.87	0.0988	0.2314
	Forest	10.28	1.57	0.1304	40.33	8.49	0.0581	0.0972
	Shrublands	27.30	0.0016	0.0033	17.88	3.90	0.4035	0.1258

		T. merianae allopatry N=58	T. merianae sympatry N=11	P value	T. rufescens allopatry N=19	T. rufescens sympatry N=13	P value	P value Interspecific sympatry
IJI	LVS	66.51	16.77	0.0105	55.44	60.19	0.8415	0.2207
	Forest	57.40	33.08	0.3301	45.35	56.77	0.6892	0.8065
	Shrublands	71.81	78.52	0.1722	74.83	70.19	0.6886	0.5221
Land Metrics								
LSI		1.79	1.66	0.4460	2.64	1.83	0.0015	0.8845
CWED		5.65	6.27	0.3355	11.07	7.39	0.1028	0.9537
CONTAG		82.59	82.70	0.3614	57.21	70.39	0.1112	0.3236
IJI		65.71	19.58	0.0059	56.06	62.53	0.4839	0.2207
SHDI		0.28	0.23	0.4612	0.68	0.40	0.0148	0.2958

Table 3. Comparison of landscape use in allopatry and sympatry of *T. merianae* and *T. rufescens* in central Argentina.

The amount of edge of the land-cover types in the landscapes did not vary between species in sympatry. *Tupinambis rufescens* in sympatry used less diverse landscapes (SHDI) than in allopatry. *Tupinambis merianae* in sympatry used less interspersed landscapes (IJI) than in allopatry because the LVS vegetation was less juxtaposed than in allopatry. Land metrics and proximity of land-cover types did not differ between species in sympatry.

3.4 Model selection

According to the lowest AIC, the presence of *T. merianae* at landscape scale is determined by the proportion and the area of the patches of the shrublands, and the number of patches of forest (residual deviance: 80.55, AIC: 86.55), and the presence of *T. rufescens* by the mean area of the patches of shrublands and the proportion of forest in the landscape (residual deviance: 81.63, AIC: 87.63).

4. Discussion

The role of the landscape for reptiles has been largely discussed (Blouin-Demers & Weatherhead, 2001; Cardozo et al., 2007; Driscoll, 2004; Luiselli & Capizzi, 1997; Mac Nally & Brown, 2001; Marchand & Litvaitis, 2004; Stow & Sunnucks, 2004). However, the novelty of our approach lies in the importance of landscape conservation to the maintenance of ecological interactions between lizard sister species. Since landscape ecology analysis is useful to gain a better understanding of environmental suitability (Fouquet et al., 2010), the present work provides useful knowledge for the conservation of these species.

Identifying the habitat characteristics that regulate the ecological processes of reptiles is imperative to determine threats to the species (Urbina-Cardona et al., 2006). Our results showed that the configuration of the available landscape presented a gradient from the distribution area of *T. merianae* to that of *T.rufescens* (SE-NW) of decreasing proportion of mean area of LVS patches and increasing proportion of forest and shrublands area. Along

this gradient, the landscape became more heterogeneous. These results show that landscape configuration is a main factor regulating the spatial distribution of ecologically similar species and has a central role in contact zones. Therefore, changes in distribution-related factors at landscape scale, such us habitat loss, might pose a threat for herpetofauna (Filippi & Luiselli, 2000).

Moreover, besides understanding how landscape patterns provide resource heterogeneity in the species distribution areas, it is vitally important to elucidate how these species use that heterogeneity i.e. , species might reveal diverse responses to the spatial variations in habitat resources (Cagle, 2008; Urbina-Cardona et al., 2006). We observed that species are selective on landscape patterns; for example, although occurring in landscapes with prevailing LVS vegetation distributed in few large patches, *T. merianae* selected landscapes with a greater proportion of forest and shrubs. *Tupinambis rufescens* also selected landscapes that are different from those available, with low proportion of LVS vegetation disaggregated in patches, and a high proportion of forest and shrubs. Considering the relevance of forest and shrublands to both species, the present results might guide conservation efforts including landscape-level process-oriented considerations.

Although morphological similarity among species induces niche similarity because behavioral and ecological activities of animals are associated with morphology (Losos, 1990; Pianka, 1986) we observed that these sister species differ in several features of the landscape-scale habitat use (e.g., shape complexity, patch proximity, length of edges and diversity). Taking into account the diversity of responses of the species, conservation strategies should be species-specific (Keogh et al., 2001). Our results indicate that *T. rufescens* and *T. merianae* have complex habitat requirements. Specialized habitat requirements make species more vulnerable to extinction (CITES, 2010; Santos et al., 2009; Webb et al., 2002). Since *T. rufescens* and *T. merianae* showed differences in landscape-scale habitat requirements, planning of conservation strategies should consider such interspecific heterogeneity.

Although the results obtained showed that species differed in the landscape-scale habitat use in their distribution areas, in the contact zone where species are in sympatry, and therefore have the same landscape-scale habitat availability, interespecific interactions would represent a significant pressure on the use of the resources. When we analyzed niche differentiation in terms of landscape-scale resources, we observed that species did not differ in the use of landscape resources in contact zones. Both species used landscapes with similar proportions of land-cover types, mean patch area and number of patches; further research is need to elucidate if the coexistence of these species could be explained by niche divergence at local scale. Furthermore, the results obtained enable us to get a better understanding of the strategies of the species in sympatric zones in terms of landscape-scale habitat use and selection. *Tupinambis merianae* both in allopatry and sympatry used similar landscapes. By contrast, *T. rufescens* in allopatry and sympatry used the landscape differentially, showing niche modification. In sympatry this species used landscapes with lower proportion of forest and shrubs, and higher proportion of LVS vegetation than in allopatry. Therefore, despite their ecological and morphological similarity, the species respond differently to spatial changes in landscape structure. Moreover, we remark the importance of landscape heterogeneity for the maintenance of species interactions in the contact zone.

5. Conclusion

Understanding the associations between landscape conservation status and distribution of sister species in contact zones might be useful to design conservation plans not only for individual species but also for ecological systems. Among the weaknesses of the regional conservation plans, poor information regarding behavioural ecology is one of the fundamental issues (The Nature Conservancy et al., 2005). To know whether species might be threatened by habitat change it is necessary to determine the relation between ecological processes and environmental patterns (Cardozo & Chiaraviglio, 2008). Our study provides useful knowledge about the important role of native forest and shrublands in allopatric and sympatric distribution areas of the lizard species. Furthermore, similar allopatry-simpatry systems might be occurring in this contact zone, which –as we mentioned above– coincides principally with the arid South American Gran Chaco. Considering that only 9% of the South American Gran Chaco is protected (The Nature Conservancy et al., 2005), we underline the need for efficient control of deforestation, protection of forest remnants and establishment of corridors. According to Beaudry et al. (2010) regional-scale conservation planning has to answer specific questions, such as the type of habitat that is needed and where it should be protected. The present work provides information that may be useful to guide conservation plans. Efforts to prevent habitat loss should involve preserving not only allopatric areas but also these critical heterogeneous sympatric areas where biological interactions might modify ecological processes of species (Brito et al., 2009; Santos et al., 2009).

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7. References

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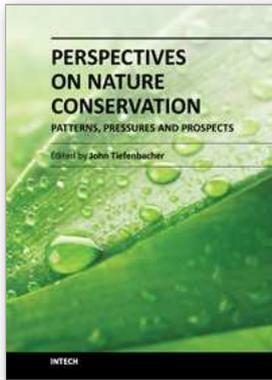
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