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Habitat suitability models for the sand lizard *Liolaemus* wiegmannii based on landscape characteristics in temperate coastal dunes in Argentina

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Abstract The knowledge of environmental variables associated with the species occurrence allows the recognition of sites which fulfil ecological requirements eventually used for conservation of species. The coastal dunes of Argentina are inhabited by sand lizards. Anthropic activities have severely degraded this ecosystem, affecting the habitat structure at a large scale. In this context, the effects of landscape characteristics on the sand lizard's (Liolaemus wiegmannii, Liolaemidae) presence were analysed to build habitat suitability maps along the coastal dunes of Argentina. A thematic map of study area was obtained from supervised classification of satellite images to identify landscape characteristics. Surveys were conducted during the lizard activity season, and landscape variables were measured in two spatial units. All information collected was compiled into a Geographic Information System. The relationship between the presence of lizards and landscape variables was evaluated by Generalized Linear Models. The predictions of these models were transferred by using Geographic Information System to habitat suitability maps. Almost all individuals (80%) were observed in semi-fixed dunes. The analysis of landscape metrics in the two spatial extents showed complementary results. The habitat suitability models suggest that: (i) heterogeneous landscapes composed by disaggregated patches of semifixed dunes and low or null percentages of active dunes distant from the coastline are the preferred environments, and (ii) human modifications such as urbanizations and forestation of dunes, have a negative impact on species occurrence. Suitable habitats were almost absent in those sectors of coastal dunes with highest level of urbanization, whereas they were distributed almost continuously in those areas without human disturbances.

Key words: GIS, landscape metrics, Pampas coastal dunes, sand lizard, suitable habitats.

INTRODUCTION

In the last two decades, there has been a growing interest in modelling wildlife-habitat relationships, mainly because of the need of basic information applicable to conservation problems, and land management (Seoane & Bustamante 2001). Species distribution models (SDM; Zimmermann et al. 2010; Mateo et al. 2011) provide useful ecological insight, and strong predictive capability in those sites where direct observation is limited (Elith & Leathwick 2009). Predicting the probability of species occurrence based on environmental variables across complex landscapes allows us to infer potentially suitable habitats for a species (Guisan & Zimmermann 2000; Scott et al. 2002; Dayton & Fitzgerald 2006; Hirzel & Le Lay 2008). Habitat suitability maps constitute an important tool to help identify priority sites for conservation, at widely varying spatial scales (Gibson et al. 2004; Carter et al. 2006).

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Reptiles constitute a group of conservation concern, because they are ectotherms, have small ranges of distribution and are often associated with specific microhabitats, which makes them especially vulnerable to habitat disturbances (Gibbons et al. 2000; Gardner et al. 2007; Böhm et al. 2013). It has been observed that the presence and/or abundance of reptiles has been associated with certain landscape variables such as patch size (Hokit & Branch 2003a; Jellinek et al. 2004; Smolensky & Fitzgerald 2011; Cardozo et al. 2012), edges (Rubio & Simonetti 2011), patch connectivity (Smith et al. 1996; Attum et al. 2008; Ryberg et al. 2013) and the proportion of a habitat type (Atauri & de Lucio 2001; Fischer et al. 2005; Santos et al. 2008; Blevins & With 2011). Despite this, habitat suitability maps based on landscape metrics are lacking for reptiles, and they are based mainly on variables such as climate, vegetation type, topography and hydrology (Sá-Sousa 2000; Guisan & Hofer 2001; Raxworthy et al. 2003; Franklin et al. 2009).

In Argentina, the coastal dunes of Buenos Aires province are inhabited by an assemblage of lizards, specially adapted to live on sandy habitats (Vega 2001). This ecosystem has been historically subjected to different types of human activities (Isla 2013). Urban growth, forestation with exotic species and development of recreational activities have strongly affected sand dune landscapes by deterioration, fragmentation and loss of natural habitats (Dadon 2002; Faggi *et al.* 2010; Faggi & Dadon 2011). Lizards are highly vulnerable because there are reports of lower population abundances linked to habitat degradation caused by exotic forestations (Stellatelli *et al.* 2013a; 2014), up to declining populations as a result of the habitat loss produced by road constructions and vehicles' transit (Vega *et al.* 2000).

The Wiegmann's lizard (Liolaemus wiegmannii, Liolaemidae) is a small (snout-vent length: 42-64 mm) and diurnal species. It has specialized morphological features for living in sand as do the 10 remaining species of the monophyletic clade L. wiegmannii or 'arenicolous' (Etheridge 2000). This species is restricted to sandy soils of a vast region of Argentina and Uruguay (Scolaro 2006). In Buenos Aires province, this lizard inhabits exclusively the coastal dunes. Studies about the Wiegmann's lizard have been focused primarily on microhabitat use at local scale. Nevertheless, information about the habitat relationships of this species at landscape level is lacking. In some localities, this lizard uses the semi-fixed or secondary dunes usually far away from beaches (Vega 2001; Stellatelli et al. 2013a; 2014), and shows high affinity with shrubs and subshrubs as refuge and perch sites (Block et al. 2012; 2013). In order to examine if these local patterns can be generalized along coastal dune landscapes, we increased the scale and spatial extent of analysis. In this study, we assess the effects of landscape characteristics on the distribution of L. wiegmannii along the temperate coastal dunes of Argentina. Our specific aims were: (i) to evaluate the relationship between landscape characteristics and L. wiegmannii presence/absence; and (ii) to map potential distribution of L. wiegmannii from habitat suitability models using a GIS. This analysis will allow the identification of suitable habitats to establish critical areas and to detect natural corridors and dispersal barriers for this species taking into account anthropic modification of the coastal landscape of Buenos Aires province. The understanding of the ecological mechanisms driving L. wiegmannii distribution across coastal dune landscape broadens our conservation perspective of this ecosystem, based on the species with geographically restricted habitat requirements.

The area included the Eastern Dune Barrier (EDB) of Buenos Aires province (Isla 1998) (Fig. 1), between La Caleta (37° 44'

METHODS

Study area

S, 57° 27' W) and Punta Rasa (36° 18' S, 56° 45' W). The area covered a surface of almost 50 000 ha along nearly 200 km of coast. Like any other temperate coastal dunes, this area shows different types of habitats inhabited by diverse plant communities: upper beach, active foredunes, active inland dunes, deflation plains, interdune depressions and semi-fixed dunes (Wiedemann & Pickart 2004). Landscape pattern is characterized by a progressive fragmentation of active dunes by the occurrence of vegetated dunes with increasing distance from the coastline (Monserrat et al. 2012). The vegetation consists of edaphic communities with particular physiognomic and floristic characters, and a gradual replacement of plant species from North to South (Cabrera 1941). Several areas of the coastal dune ecosystem have been structurally altered replacing native plants by forestation with exotic trees associated with human settlements (Zalba & Villamil 2002; Alberio & Comparatore 2014).

Satellite image processing and landscape variables

To identify landscape characteristics, we performed supervised classifications of satellite images Landsat 5 Thematic Mapper (spatial resolution: 30 m; date: February 2009, coordinate system: UTM, WGS-84 datum) using GPS field points to generate training sites (Campbell 2002). The urban areas were previously digitalized and masked for the classification procedures. We used an error matrix analysis and the Kappa index of agreement to assess classification accuracy (Jensen 1996; Campbell 2002). We obtained a thematic map of EDB with five habitat categories: active dunes (AD) with scarce or null coverage of natural grassland, sparse shrubs and clump herbs, which included upper beach, active foredunes, and active inland dunes, semi-fixed dunes (SD) with continuous natural grassland, clump herbs, sub shrubs and shrubs, interdune depressions (ID) with presence of vegetation associated with flooded environments, forested dunes (FD) with exotic trees and water bodies (WB).

Landscape metrics were obtained using software FRAGSTATS v4.0 (McGarigal et al. 2012) from the thematic map of EDB, using moving window mode. This means that a window of a particular shape and size passes through each pixel and the values of the selected metric are assigned to the central pixel. The scale at which animals perceive elements in landscape is often related to information available as they move through their environment (Lima & Zollner 1996). In general, models for species with small home ranges are fitted using predictors obtained from the near-neighbouring landscape (Elith & Leathwick 2009). Given that the pixel size $(30 \times 30 \text{ m})$ includes the home range estimated for L. wiegmannii ($\overline{X} = 37.80 \text{ m2}$, Stellatelli et al. 2016), the landscape metrics (Table 1) were measured in two circular windows (landscape units) with radius of 100 and 300 m (LU = 100 and LU = 300, respectively). The sizes of landscape units were chosen arbitrarily based on the lizard perception and the landscape variation. This served as a control to potential bias of not detecting landscape structures because of the selected scale. On the other hand, coastline, urban areas and roads were digitalized in a GIS to calculate



Fig. 1. Map of the study area showing the Eastern Dune Barrier of temperate coastal dunes of Buenos Aires province, Argentina.

straight line distance (m) to the coastline (d_coast), urban areas (d_urb) and roads (d_road), respectively.

Field surveys

Field surveys were conducted from November 2009 to April 2010 during the lizard activity season (Vega 2001) at 10 sites

distributed along the study area (Fig. 2). Stratified sampling method (Sutherland 2006) was performed using 182 square plots of 20×20 m. These plots were randomly located in AD and SD (95 and 87 plots, respectively), given the habitat preferences of the sand-dwelling lizards of Pampas coastal dunes (Vega 2001). Considering the home range estimated for *L. wiegmannii*, the distance between plots (at least

Table 1. Description of landscape metrics obtained from thematic map of the Eastern Dune Barrier of temperate coastal dunes of Buenos

 Aires province, Argentina

Variable	Description
area_SD	Mean (Ha) of the all patches area of semi-fixed dunes
area_cv_SD	Coefficient of variation (%) of the patches area of semi-fixed dunes
pladj_SD	Percentage of like adjacencies of semi-fixed dunes
te_SD	Sum of the lengths (m) of all edge segments of semi-fixed dunes
pd_SD	Patch density of semi-fixed dunes in 100 Ha
enn_SD	Distance (m) to the nearest neighbour patch of semi-fixed dunes
pland_AD	Percentage of landscape of all patches of active dunes
pland_SD	Percentage of landscape of all patches of semi-fixed dunes
pland_ID	Percentage of landscape of all patches of interdune depressions
pland_FD	Percentage of landscape of all patches of forested dunes

100 m) was large enough to consider them as independent samples. Surveys were conducted walking between 0900 and 1800 h corresponding to the daily activity period of this species (Vega 2001). Weather conditions were favourable for lizard activity during all surveys. In each plot, two people were systematically scanning the total area to detect lizards using visual encounters, and carefully searching under shrubs, subshrubs and clump herbs. Sampling effort was greater in vegetated dunes to avoid potential biases because of variation in the detectability. Thus, the possibility that individuals may have been present but not detected because of environmental variation among plots, or weather conditions, was assumed to be negligible in our study system. Nevertheless, in order to minimize the probability of false absences



Fig. 2. Habitat suitability maps for sand lizard *Liolaemus wiegmannii* constructed from habitat suitability models in the Eastern Dune Barrier of temperate coastal dunes, Argentina. LU: circular landscape unit (m). Values represent the probability of sand lizard presence in a 30-m pixel of semi-fixed dunes.

each plot was surveyed twice. The geographical coordinates of each plot were recorded using a handheld Global Positioning System (GPS) unit (Coordinate system: UTM, Datum: WGS84). Presence/absence data were converted to point shape files in a GIS.

Statistical analysis

In order to evaluate relationship between lizard presence/ absence and landscape variables, we used generalized linear models (GLM) with the binomial error structure and log-link function (Crawley 2007). We evaluated support for models with all possible combinations of landscape variables (predictor variables), and model selection was based on Akaike's information criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002). We used two additional measures to model selection: the difference in AICc between the best approximating model and all the other models (ΔAIC_c , values between 0 and 2 indicate substantial support for the models); and model weights (w_i) , which indicate the probability that the model is the best among the whole set of candidate models (Burnham & Anderson 2002). Parameter estimates were calculated by the technique of model averaging (multimodel inference) from w_i for all candidate models (Burnham & Anderson 2002). We also assessed the degree to which 95% confidence intervals of parameter estimates overlapped zero. All statistical analyses were carried out using R software, version 2.15.0 (R Development Core Team 2012).

Multicollinearity was analysed previously to model analysis and we considered two predictors to be collinear when the Spearman rank correlation coefficient (R) was > 0.6. Among strongly correlated variables we retained those with the clearest ecological meaning for the species (Austin 2007).

Habitat suitability models

Habitat suitability models were built with those landscape predictors with a significant effect on the presence/absence of *L. wiegmannii*. As the number of presences was low compared to the absences, we used a re-sampling scheme to obtain a balanced sample (McPherson *et al.* 2004; Liu *et al.* 2005) randomly selecting equal number of absences than presences. We reserved a random sample of 30% of presences and 30% of absences for model cross-validation and used the remaining 70% for model fitting. This procedure was repeated 100 times.

Assessing the predictive performance of a model is an essential step for allowing its proper use in ecological applications. The area-under-the-curve (AUC) of the receiver operating characteristic (ROC) plot was computed for each of the 100 models with each set of validation data, to estimate its predictive power through cross-validation (Murtaugh 1996). The AUC ranges from 0.5 (when model discrimination is not better than random) to 1 (perfect discriminatory ability, Pearce & Ferrier 2000). Predictive models are considered usable if AUC \geq 0.7 (Harrell 2001).

Predictive habitat suitability maps

We used the habitat suitability models to build predictive distribution maps of *L. wiegmannii* in coastal dunes of Buenos Aires province, Argentina. We employed the option in IDRISI Kilimanjaro (Eastman 2009) to export predictors as a data matrix to S-Plus and applied the predict.glm procedure to make predictions on the new data matrix. Then, we exported the predicted values at the scale of the response from S-Plus back to IDRISI to produce a probability map. The estimated probability of occurrence of *L. wiegmannii* was categorized into four classes of habitat suitability: low (<0.25), medium (0.25–0.499), high (0.5–0.75) and very high (>0.75).

RESULTS

From the total area of EDB, AD covered 27.47%, SD 21.20%, ID 17.47%, FD 10.30%, WB 0.35% and urban areas 23.26%.

Landscape variables and lizard occurrence

L. wiegmannii was observed at 7 out of 10 sites surveyed (Fig. 2). Lizard presence was detected in 25 plots located in SD and in six plots located in AD. In most plots (29 of 31) individuals were observed once. More frequent abundance was 1–3 individuals/plot and one exceptional case of six individuals/plot.

Considering landscape variables obtained in the circular unit of 100 m, GLMs indicated that the presence of *L. wiegmannii* was positively associated with the distance to the coastline, whereas it was negatively associated with patch density of SD and the percentage of active and FD (Tables 2 and 3). Distance to urban areas together with the percentage of like adjacencies of SD were included in the models but these variables presented confidence intervals that included zero (Table 3). Probability of lizard occurrence increased in SD moving inland and decreased with the rising percentage of AD and FD.

Considering the landscape variables obtained in the circular unit of 300 m, GLMs indicated that presence of *L. wiegmannii* was positively associated with distance to the coastline and urban areas, while it was negatively associated with the percentage of like adjacencies of SD, and the percentage of AD and FD (Tables 2 and 3). Percentage of ID was included in the models, but this variable presented confidence intervals that included zero (Table 3). Probability of lizard occurrence increased in disaggregated patches of inland SD distant from urban areas, and decreased with rising percentage of AD and FD.

LU	Models	ΔAIC_{c}	w_i
100	d_ciu + d_cost + pd_SD + pladj_SD + pland_FD + pland_AD	0.00	0.27
	d_cost + pd_SD + pladj_SD + pland_FD + pland_AD	0.40	0.22
	d_cost + pd_SD + pland_FD + pland_AD	1.13	0.15
	d_ciu + d_cost + pd_SD + pland_FD + pland_AD	1.19	0.15
	d_ciu + d_cost + pd_SD + pladj_SD + pland_ID + pland_FD + pland_AD	1.79	0.11
	d_cost + pd_SD + pladj_SD + pland_ID + pland_FD + pland_AD	1.93	0.10
300	d_ciu + d_cost + pladj_SD + pland_ID + pland_FD + pland_AD	0.00	0.58
	d_ciu + d_cost + pladj_SD + pland_FD + pland_AD	0.67	0.42

Table 2. Generalized linear models influencing *Liolaemus wiegmannii* occurrence in the Eastern Dune Barrier of Buenos Aires province, Argentina. LU: circular landscape unit (m). w_i : model weight. Only models with strong support (i.e. $\Delta AIC_c < 2$) are shown

Table 3. Coefficient estimates (\pm SE) from generalized linear models influencing *Liolaemus wiegmannii* occurrence in the Eastern Dune Barrier of Buenos Aires province, Argentina. LU: circular landscape unit (m). CI: confidence interval (95%). Parameters likelihoods are w_i summed across all models that contained that parameter and are indicative of the importance of the variable. Explanatory variables with CI excluding zero are in bold

LU	Variable	Coefficient ± SE	CI	Parameter likelihood
100	Intercept	1.19 ± 1.67	-2.1; 4.47	_
	d_ciu	0.000047 ± 0.000059	-0.000069; 0.00016	0.52
	d_cost	0.00054 ± 0.00022	0.0001; 0.00098	1.00
	pd_SD	-0.0231 ± 0.00971	-0.0423; -0.00392	1.00
	pladj SD	-0.0202 ± 0.0192	-0.0581; 0.0176	0.70
	pland_ID	-0.0039 ± 0.00936	-0.0223; 0.0145	0.21
	pland FD	-0.0764 ± 0.0356	-0.146; -0.00627	1.00
	pland AD	-0.0305 ± 0.0154	-0.061; -0.00021	1.00
300	Intercept	3.1 ± 1.86	-0.562; 6.77	_
	d-ciu	0.0002 ± 0.00007	0.000057; 0.00032	1.00
	d cost	0.0009 ± 0.00026	0.00036; 0.0014	1.00
	pladi SD	-0.072 ± 0.0245	-0.12; -0.024	1.00
	pland ID	-0.0248 ± 0.0286	-0.0811; 0.0314	0.58
	pland FD	-0.0805 ± 0.0327	-0.145; -0.016	1.00
	pland_AD	-0.0449 ± 0.0214	-0.0871; -0.0028	1.00

Habitat suitability models and predictive distribution maps

For the two landscape units, the models built had a better predictive ability than random, because in both cases the mean AUC value was greater than 0.70 (Table 4). Because lizards were detected mainly in SD, the probability of lizard occurrence was only predicted in this habitat category. The habitat suitability model constructed with variables obtained from landscape unit of 100 m, indicated that habitats with high probability of lizard occurrence (0.50 to 0.75) occupied 14.24% of SD. The availability of these habitats was relatively low, with a high degree of fragmentation among the biggest towns, such as Mar de Ajó, Pinamar and Villa Gesell, and they were definitively absent from the extreme north to Mar de Ajó. Suitable habitats were distributed almost continuously at the south of the small towns, such as Mar Azul. Most suitable habitats

(probability of lizard occurrence > 0.75) were not observed at this scale. The moderately suitable habitats for *L. wiegmannii* (probability of occurrence between 0.25 and 0.499) comprised 40.56% of SD, while those habitats with low suitability (probability 0.25) occupied 45.20% (Fig. 2).

The habitat suitability model constructed with those variables obtained from landscape unit of 300 m showed that the most suitable habitats for this species encompassed 13.27% of SD, while suitable habitats occupied 18.41%. In both cases, the habitats were distributed as isolated pixels among the biggest towns such as San Clemente, Las Toninas, Santa Teresita and Mar de Ajó, but they were best represented between Mar de Ajó and Pinamar. Both habitat types were distributed almost continuously in the south of small towns such as Mar Azul (Fig. 2). The moderately suitable habitats comprised 22.75% of SD, while those habitats with low suitability occupied 45.57% of SD.

LU	Models	AUC ± SE
100	d_cost + pd_SD + pland_FD + pland_AD	0.767 ± 0.011
300	$d_ciu + d_cost + pladj_SD + pland_FD + pland_AD$	0.784 ± 0.010

Table 4. Habitat suitability models for *Liolaemus wiegmannii* in the Eastern Dune Barrier of temperate coastal dunes of Buenos Aires province, Argentina. LU: circular landscape unit (m)

AUC, mean area-under-the-curve; SE, standard error.

DISCUSSION

The results obtained in this study allowed the recognition of key factors in the composition and structure of the landscape that regulate the distribution of the most widely spread sand lizard L. wiegmannii in coastal dunes of Argentina. Main landscape predictors explaining the current distribution of L. wiegmannii coincide in both sampled units. SD are the main habitat for this species because almost all of the observed individuals (80%) were found in this habitat throughout the study area, and this result is consistent with local patterns observed in previous studies. The distribution of L. wiegmannii in SD distant from the coastline is opposite to the distribution of the sympatric lizard L. multimaculatus, which is mainly located in active foredunes near to the coastline (Block 2014). This spatial segregation has also been observed in sand lizard assemblages from other localities in the coastal dunes of the Buenos Aires province (Vega 2001).

An increase in the spatial extent of the landscape unit (from 100 to 300 m) resulted in an increase in the number of variables explaining the presence of *L. wiegmannii*. Landscapes are spatially heterogeneous areas, and their structure, function and changes are scale-dependent. Thus, landscape metrics also depend on the scale at which they are measured (Turner 1989). In addition, an increase in the extent of the landscape unit increases variability and, therefore it also increases the probability of including different strata or environments within the sample (Lopez de Casenave *et al.* 2007). Opposite to this, patch density tends to decrease in larger spatial extensions because of the fact that the number of patches is higher near the edges than far away from them (Saura & Martínez-Millán 2001).

The percentage of adjacent cells is a way to measure of the degree of patch aggregation (McGarigal 2002). The observed negative relationship between lizard occurrence and this metric indicates that *L. wiegmannii* uses landscape areas composed of disaggregated patches of SD. A similar pattern of space use was observed in *Sceloporus arenicolous*, an endemic and specialized lizard inhabiting open sand-dune depressions or blowouts in a matrix of shinnery-oak in a sand ecosystem of southeastern New Mexico (Smolensky & Fitzgerald 2011). In spite of the fact that species of small size and low vagility may be affected by the lack of connectivity between patches (D'Eon *et al.* 2002), there are cases in which some environments act as temporary suboptimal habitats (Arellano et al. 2008). Considering that L. wiegmannii avoids landscapes with a high percentage of AD and FD, the ID with relatively low and medium vegetation cover could act as corridors facilitating the movement of individuals between patches of SD. Adult individuals of L. wiegmannii have shown short distance movement, and we have not observed displacement among patches of SD (Stellatelli et al. 2016). Nevertheless, the migration across these suboptimal habitats could be performed by juveniles during the search and acquisition of territories as it occurs with other lizard species (Clobert et al. 1994; Rocha 1999). L. wiegmannii is considered to be the least specialized species of the monophyletic clade of arenicolous lizards (Etheridge 2000). This attribute could allow this lizard to persist in naturally fragmented environments as has been observed in other species with low space requirements (Smith et al. 1996; Jellinek et al. 2004).

The proximity to urban areas and dunes with exotic trees negatively affected the presence of L. wiegmannii by decreasing the habitat suitability. The advance of exotic forestations upon native vegetation communities impacts negatively on the structure and functioning of coastal ecosystems around the world (Kutiel et al. 2004; Yelenik et al. 2004) and specifically generates disadvantages for native lizards (Hawlena et al. 2010; Bateman & Ostoja 2012; Hacking et al. 2014). At local scale, the presence of exotic trees negatively affects L. wiegmannii by diminishing its thermoregulatory efficiency (Stellatelli et al. 2013b), by increasing the proportion of individuals exposed to full shade (Block et al. 2013), and by causing an increase of predation pressures (Stellatelli et al. 2015). Stellatelli et al. (2013a, 2014) studied the relative abundance of L. wiegmannii in six sites along coastal dunes of Argentina, and they demonstrated that the forested sites had the lowest abundances of lizards. In agreement with these findings, our habitat suitability models were able to classify as low suitable habitats those areas with low abundances of lizards, and as high suitable habitats those places with a high abundance of lizards. Consequently, the long-term proliferation of trees on dunes with native grassland vegetation will adversely affect the presence of L. wiegmannii in the study area.

The maps obtained from both models showed that SD with the highest probability of *L. wiegmannii*

presence (very high suitable areas) were always far away from areas with high degree of urbanization and forestation. More suitable habitats were almost absent in the northern sector of coastal dunes, which exhibited the highest level of urbanization, while they were scattered and isolated in those sectors that showed a medium level of urbanization. These results are concordant with the spatial distribution pattern estimated for the species L. multimaculatus in the study area (Block 2014). Unfortunately, more than 30% of the natural habitats in the EDB have been replaced by urban areas and forestation, and close to 50% of the SD show low suitability for L. wiegmannii. The landscapes that have been modified by human action can alter the abilities of individuals to move through them and also increase the mortality rates when the individuals are dispersed across unsuitable habitats (Fahrig 2007). Patch occupancy depends on dispersal abilities and space requirements of individuals (Harrison & Fahrig 1995; Attum et al. 2008). However, the spatial context or surrounding matrix can facilitate or impede the movement of individuals among patches of suitable habitat (D'Eon et al. 2002; Zajitschek et al. 2012). In lizards with low dispersal ability such as Sceloporus woodi, patch occupancy was negatively affected by patch isolation because the landscape matrix and an increase in the distance between suitable patches, inhibited lizard dispersion (Hokit et al. 1999). Taking into account our results, the progressive increase of urbanization and forestation in coastal dunes could raise the risk of isolating and decreasing population sizes of L. wiegmannii by interfering with the individual migration and gene flow (Chan et al. 2009; Ryberg et al. 2013). Small populations with limited access to suitable habitats and reduced migration rates are highly vulnerable to stochastic processes, which could lead to local extinctions (Hokit & Branch 2003b; Fahrig 2007).

More than 40% of the world's population resides near the coastal area, which accounts for just 4% of the land surface (UNEP 2006). This presents a series of conflicts between sustainability of economic activities and the conservation of natural resources (Schlacher et al. 2008). In Argentina, the advance of urbanization and forestation of coastal areas without planning has increased the fragmentation of the natural landscape (Dadon 2002; Barragán et al. 2003). Continuous alteration of the coastal landscape by human activities tends to result in loss and fragmentation of suitable habitats for L. wiegmannii. This context has negative effects on dispersal of individuals, increasing the risk of isolating lizard populations. To ensure the persistence of this species, and other components of the native biodiversity in sand dune ecosystem, conservation efforts should focus on the reduction of habitat modification and the avoidance of lizard population isolation. Conservation planning requires the identification of priority areas with a high probability of persistence of species. Thus,

suitability models and predictive distribution maps obtained for *L. wiegmannii* constitute useful tools to promote the protection of those specific areas with the highest probability of occurrence of this species. Using habitat models based on landscape variables for small species implies a poorly explored methodological challenge. For species with reduced mobility and small size, microhabitat features are usually the most important cues for habitat selection. Identifying landscape variables that transcend the small scale, and finding out how they are modified by anthropic disturbance, implies a significant contribution to species conservation.

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REFERENCES

- Alberio C. & Comparatore V. (2014) Patterns of woody plant invasion in an Argentinean coastal grassland. *Acta Oecol.* 54, 65–71.
- Arellano L., León-Cortés J. L. & Ovaskainen O. (2008) Patterns of abundance and movement in relation to landscape structure: a study of a common scarab (*Canthon cyanellus cyanellus*) in Southern Mexico. *Landsc. Ecol.* 23, 69–78.
- Atauri J. A. & de Lucio J. V. (2001) The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landsc. Ecol.* 16, 147–59.
- Attum O., Lee Y. M., Roe J. H. & Kingsbury B. A. (2008) Wetland complexes and upland–wetland linkages: landscape effects on the distribution of rare and common wetland reptiles. *J. Zool.* 275, 245–51.
- Austin M. (2007) Species distribution models & ecological theory: a critical assessment and some possible new approaches. *Ecol. Model.* 200, 1–19.
- Barragán J. M., Dadon J. R., Matteucci S. D., Baxendale C., Rodríguez A. & Morello J. (2003) Bases preliminares para un Programa de Gestión Integrada de Zonas Costeras en Argentina. In: La Gestión de Áreas Litorales en España y Latinoamérica (ed J. M. Barragán) pp. 72–101. Universidad de Cádiz, Cádiz.
- Bateman H. L. & Ostoja S. M. (2012) Invasive woody plants affect the composition of native lizard and small mammal communities in riparian woodlands. *Anim. Conserv.* 15, 294–304.
- Blevins E. & With K. A. (2011) Landscape context matters: local habitat and landscape effects on the abundance and patch occupancy of collared lizards in managed grasslands. *Landsc. Ecol.* 26, 837–50.

- Block C. (2014) Selección de hábitat a escala de paisaje y microhábitat en lagartijas arenícolas. Herramientas para el manejo sustentable del ecosistema dunícola costero de la provincia de Buenos Aires. PhD. Thesis. Universidad Nacional de Mar del Plata, Argentina.
- Block C., Vega L. E. & Stellatelli O. A. (2012) Vegetation refuges of a sand lizard assemblage in temperate coastal sand dunes. *J. Herpetol.* 46, 608–13.
- Block C., Stellatelli O. A., García G. O., Vega L. & Isacch J. P. (2013) Factors affecting the thermal behavior of the sand lizard *Liolaemus wiegmannii* in natural and modified grassland of temperate coastal dunes from Argentina. *J. Therm. Biol.* 38, 560–69.
- Böhm M. et al. (2013) The conservation status of the world's reptiles. Biol. Consev. 157, 372–85.
- Burnham K. P. & Anderson D. R. (2002) Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach, 2nd edn. Springer-Verlag, New York.
- Cabrera A. L. (1941) Las comunidades vegetales de las dunas costeras de la provincia de Buenos Aires. *DAGI* 1, 1–44.
- Campbell J. B. (2002) Introduction to Remote Sensing, 3rd edn. The Guildford Press, New York.
- Cardozo G., Naretto S., Zak M. & Chiaraviglio M. (2012) The role of landscape in contact zones of sister species of lizards. In: Perspectives on Nature Conservation – Patterns, Pressures and Prospects (ed J. Tiefenbacher) pp. 161–176. InTech, Rijeka.
- Carter G. M., Stolen E. D. & Breininger D. R. (2006) A rapid approach to modeling species–habitat relationships. *Biol. Conserv.* 127, 237–44.
- Chan L. M., Fitgerald L. A. & Zamudio K. R. (2009) The scale of genetic differentiation in the dunes sagebrush-lizard (*Sceloporus* arenicolus), an endemic habitat specialist. *Conserv. Genet.* 10, 131–42.
- Clobert J., Massot M., Lecomte J., Sorci G., de Fraipont M. & Barbault R. (1994) Determinants of dispersal behavior: the common lizard as a case study. In: *Lizard Ecology: Historical* and Experimental Perspectives (eds L. J. Vit & E. R. Pianka) pp. 183–206. Princeton University Press, New Jersey.
- Crawley M. J. (2007) *The R Book.* John Wiley and Sons Inc., New York.
- Dadon J. R. (2002) El impacto del turismo sobre los recursos naturales en la costa pampeana. In: Zona Costera de la Pampa Argentina: Recursos Naturales, Sustentabilidad, Turismo, Gestión y Derecho Ambiental (eds J. R. Dadon & S. D. Matteucci) pp. 101–121. Lugar Editorial, Buenos Aires.
- Dayton G. H. & Fitzgerald L. A. (2006) Habitat suitability models for desert amphibians. *Biol. Conserv.* 132, 40–9.
- D'Eon R. G., Glann S. M., Parfitt I. & Fortin M. (2002) Landscape connectivity as a function of scale and organism vagility in a real forested landscape. *Conserv. Ecol.* **6**, 10.
- Eastman J. R. (2009) IDRISI Taiga. Clark University, Worcester.
- Elith J. & Leathwick J. R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677–97.
- Etheridge R. (2000) A review of the *Liolaemus wiegmannii* group (Squamata, Iguania, Tropiduridae), and a history of morphological change in the sand dwelling species. *Herpetol. Monogr.* 14, 293–352.
- Faggi A. & Dadon J. R. (2011) Temporal and spatial change in plant dune diversity in urban resorts. J. Coast. Conserv. 15, 585–94.
- Faggi A., Perepelzin P. & Dadon J. R. (2010) South Atlantic Tourist resorts: predictors for changes induced by afforestation. In: Urban Biodiversity and Design (eds N. Müller, P. Werner & J. G. KelceyChapter 19). Wiley-Blackwell, Oxford.

- Fahrig L. (2007) Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* **21**, 1003–15.
- Fischer J., Lindenmayer D. B., Barry S. & Flowers E. (2005) Lizard distribution patterns in the Tumut fragmentation "Natural Experiment" in south-eastern Australia. *Biol. Conserv.* 123, 301–15.
- Franklin J., Wejnert K. E., Hathaway S. A., Rochester C. J. & Fisher R. N. (2009) Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. *Divers. Distrib.* 15, 167–77.
- Gardner T. A., Barlow J. & Peres C. A. (2007) Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biol. Conserv.* 138, 166–79.
- Gibbons J. W., Scott D. E., Ryan T. J., et al. (2000) The global decline of Reptiles, déjà vu Amphibians. Bio Science 50, 653–66.
- Gibson L. A., Wilson B. A., Cahill D. M. & Hill J. (2004) Modelling habitat suitability of the swamp antechinus (Antechinus minimus maritimus) in the coastal heathlands of southern Victoria. Australia. Biol. Cons. 117, 143–50.
- Guisan A. & Hofer U. (2001) Predicting reptile distributions at the mesoscale: relation to climate and topography. *J. Biogeog.* 30, 1233–43.
- Guisan A. & Zimmermann N. E. (2000) Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–86.
- Hacking J., Abom R. & Schwarzkopf L. (2014) Why do lizards avoid weeds? *Biol. Invasions* 16, 935–47.
- Harrell F. E. (2001) *Regression Modelling Strategies*. Springer, New York.
- Harrison S. & Fahrig L. (1995) Landscape pattern and population conservation. In: *Mosaic Landscapes and Ecological Processes* (eds L. Hansson, L. Fahrig & G. Merriam) pp. 203–308. Chapman & Hall, London.
- Hawlena D., Saltz D., Abramsky Z. & Bouskila A. (2010) Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. *Conserv. Biol.* 24, 803–9.
- Hirzel A. H. & Le Lay G. (2008) Habitat suitability modelling and niche theory. *J. Appl. Ecol.* **45**, 1372–81.
- Hokit G. D. & Branch L. C. (2003a) Habitat patch size affects demographics of the Florida scrub lizard (*Sceloporus woodi*). *J. Herpetol.* 37, 257–65.
- Hokit G. D. & Branch L. C. (2003b) Association between patch area and vital rates: consequences for local and regional populations. *Ecol. Appl.* 13, 1060–8.
- Hokit G. D., Stith B. M. & Branch L. C. (1999) Effects of landscape structure in Florida scrub: a population perspective. *Ecol. Appl.* 9, 124–34.
- Isla F. I. (1998) Holocene coastal evolution of Buenos Aires. *Quaternary South Am, A. A. Balkrena* 11, 297–321.
- Isla F. I. (2013) From touristic villages to coastal cities: the costs of the big step in Buenos Aires. Ocean Coast. Manag. 77, 59–65.
- Jellinek S., Driscoll D. A. & Kirkpatrick (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.
- Jensen J. R. (1996) Introductory Digital Image Processing: A Remote Sensing Perspective. Prentice-Hall, New Jersey.
- Kutiel P., Cohen O., Shoshany M. & Shub M. (2004) Vegetation establishment on the southern Israeli coastal sand dunes between the years 1965 and 1999. *Landsc. Urban Plan.* 67, 141–56.
- Lima S. L. & Zollner P. A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* 11 (3), 131–5.
- Liu C., Berry P. M., Dawson T. P. & Pearson R. G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28, 385–93.

- Lopez de Casenave J., Marone L., Camus P. A. & Jaksic M. (2007) Escalas. In: *Ecología de Comunidades* (eds F. Jaksic & L. Marone) pp. 193–213. Ediciones Universidad Católica de Chile, Santiago.
- Mateo R. G., Felicísimo A. M. & Munoz J. (2011) Modelos de distribución de especies: una revisión sintética. *Rev. Chil. Hist. Nat.* 84, 217–40.
- McGarigal K. (2002) Landscape pattern metrics. Volume 2. In: Encyclopedia of Environmetrics (eds A. H. El-Shaarawi & W. W. Piegorsch) pp. 1135–1142. John Wiley & Sons, Sussex.
- McGarigal K., Cushman S. A. & Ene E. (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps, Computer software program produced by the authors at the University of Massachusetts, Amherst. [Cited on 4 September 2014] Available from URL: http://www. umass.edu/landeco/research/fragstats/fragstats.html.
- McPherson J. M., Jetz W. & Rogers D. J. (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *J. Appl. Ecol.* 41, 811–23.
- Monserrat A. L., Celsi C. E. & Fontana S. L. (2012) Coastal dune vegetation of the southern pampas (Buenos Aires, Argentina) and its value for conservation. *J. Coast. Res.* 28, 23–35.
- Murtaugh P. A. (1996) The statistical evaluation of ecological indicators. J. Appl. Ecol 6, 132–9.
- Pearce J. & Ferrier S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* 133, 225–45.
- R Development Core Team. (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria [Cited on 9 October 2014]. Available from URL: http://www.R-project.org
- Raxworthy C. J., Martinez-Meyer E., Horning N., et al. (2003) Predicting distribution of know and know reptile species in Madagascar. Nature 426, 837–41.
- Rocha C. F. D. (1999) Home range of the Tropidurid lizard Liolaemus lutzae: sexual and body size differences. Rev. Bras. Biol. 59, 125–30.
- Rubio A. V. & Simonetti J. A. (2011) Lizard assemblages in a fragmented landscape of central Chile. *Eur. J. Wildl. Res.* 57, 195–9.
- Ryberg W. A., Hill M. T., Painter C. W. & Fitzgerald L. A. (2013) Landscape pattern determines neighborhood size and structure within a lizard population. *PLoS One* 8, 1–7.
- Santos T., Díaz J. A., Pérez-Tris J., Carbonell R. & Tellería J. L. (2008) Habitat quality predicts the distribution of a lizard in fragmented woodlands better than habitat fragmentation. *Anim. Conserv.* 11, 46–56.
- Sá-Sousa P. (2000) A predictive distribution model for the Iberian wall lizard (*Podarcis hispanicus*). *Herpetol. J.* **10**, 1–11.
- Saura S. & Martínez-Millán J. (2001) Sensitivity of landscape pattern metrics to map spatial extent. *Photogramm. Eng. Remote. Sens.* 67, 1027–36.
- Scott J. M., Heglund P. J., Samson F., et al. (2002) Predicting Species Occurrences: Issues of Accuracy and Scale. Island Press, Covelo.
- Seoane J. & Bustamante J. (2001) Modelos predictivos de la distribución de especies: una revisión de sus limitaciones. *Ecología* 15, 9–21.
- Schlacher T. A., Schoeman D. S., Dugan J., et al. (2008) Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. Mari. Ecol. 29, 70–90.
- Scolaro A. (2006) Reptiles Patagónicos Norte: Una Guía de Campo. Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia.

- Smith G. T., Arnold G. W., Sarre S., Abensperg-Traun M. & Steven D. E. (1996) The effect of habitat fragmentation and livestock grazing on animal communities in remnants of gimlet *Eucalyptus salubris* woodland in the Western Australian wheatbelt. II. Lizards. J. Appl. Ecol. 33, 1302–10.
- Smolensky N. L. & Fitzgerald L. A. (2011) Population variation in dune-dwelling lizards in response to patch size, patch quality, and oil and gas development. *Southwest. Nat.* 56, 315–24.
- Stellatelli O. A., Vega L. E., Block C. & Cruz F. B. (2013a) Effect of the tree invasion on the habitat use of sand lizard. *Herpetologica* 69, 455–65.
- Stellatelli O. A., Vega L. E., Block C. & Cruz F. B. (2013b) Effects on the thermoregulatory efficiency of two native lizards as a consequence of the habitat modification by the introduction of the exotic tree *Acacia longifolia*. J. Therm. Biol. 38, 135–42.
- Stellatelli O. A., Block C., Vega L. E. & Cruz F. B. (2014) Responses of two sympatric sand lizards to exotic forestations in the coastal dunes of Argentina: some implications for conservation. *Wildl. Res.* 41, 480–9.
- Stellatelli O. A., Block C., Vega L. E. & Cruz F. B. (2015) Nonnative vegetation induces changes in predation pressure and escape behavior of two sand lizards (Liolaemidae: Liolaemus). *Herpetologica* 71, 136–42.
- Stellatelli O. A., Block C., Vega L. E., Isacch J. P. & Cruz F. B. (2016) Factors affecting the spatial ecology of the lizard *Liolaemus wiegmannii* in the pampasic coastal dunes of Argentina. *J. Herpetol.* 26, 11–9.
- Sutherland W. J. (2006) Planning a research programme. In: *Ecological Census Techniques. A Handbook* (ed W. J. Sutherland) pp. 1–10. Cambridge University Press, New York.
- Turner M. G. (1989) Landscape ecology: the effect of pattern and processes. Annu. Rev. Ecol. Syst. 20, 171–97.
- UNEP (2006) Marine and Coastal Ecosystems and Human Wellbeing: A Synthesis Report Based on the Findings of the Millennium Ecosystem Assessment. UNEP, Nairobi.
- Vega L. (2001) Herpetofauna: diversidad, ecología e historia natural. In: Reserva de Biosfera Mar Chiquita: Características Físicas, Biológicas y Ecológicas (ed O. Iribarne) pp. 213–226. Editorial Martín, Mar del Plata.
- Vega L., Bellagamba P. & Fitzgerald L. (2000) Long-term effects of anthropogenic habitat disturbance on a lizard assemblage inhabiting coastal dunes of Argentina. *Can. J. Zool.* 78, 1–8.
- Wiedemann A. M. & Pickart A. J. (2004) Temperate zone coastal dunes. In: *Coastal Dunes. Ecology and Conservation* (eds M. L. Martínez & N. P. Psuty) pp. 53–65. Ecological Studies, Vol 171. Springer-Verlag, Berlin Heidelberg.
- Yelenik S., Stock W. & Richardson D. (2004) Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restor. Ecol.* 12, 44–51.
- Zajitschek S. R. K., Zajitschek F. & Clobert J. (2012) The importance of habitat resistance for movement decisions in the common lizard, *Lacerta vivipara*. BMC Ecol. 12, 13.
- Zalba S. M. & Villamil C. B. (2002) Woody plant invasion in relictual grasslands. *Biol. Invasions* 4, 55–72.
- Zimmermann N. E., Edwards T. C., Graham C. H., Pearman P. B. & Svenning J. C. (2010) New trends in species distribution modeling. *Ecography* 33, 985–9.