

RESEARCH ARTICLE

Spatial segregation between the native Tropical mockingbird and the invader Chalk-browed mockingbird (Passeriformes: Mimidae) along a Neotropical natural-urban gradient

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ABSTRACT. Congeneric species have similarities in phenotypic and ecological traits. The sympatry of congeneric species constitutes an opportunity for studies on coexistence. Two bird species of Mimidae, the native Tropical mockingbird, *Mimus gilvus* Oberholser, 1919, and the restinga invader Chalk-browed mockingbird, *Mimus saturninus* (Lichtenstein, 1823), currently occur in sympatry across the sandy-coastal ecosystem (restinga) of Espírito Santo state, Southeastern Brazil. We studied the spatial distribution of Tropical mockingbird and Chalk-browed mockingbird to understand the degree of competition across a preserved and urban gradient. We sampled 1,451 sampling units across a preserved and urban landscape in a coastal area of southeastern Brazil. The best-fitting model for abundance (Punctual Abundance Index) included urbanization index, distance from the coast, and distance from the closest protected area, which explained 63% and 97% of the abundance of Tropical mockingbird and Chalk-browed mockingbird, respectively. The species exhibited a segregated spatial pattern at small scale, indicating that both species are avoiding one another. Chalk-browed mockingbird showed ecological plasticity in modified environments, whereas Tropical mockingbird was more sensitive to urbanization. We suggested that the coexistence of these species is associated with resource partitioning. Monitoring Tropical mockingbird populations may be a proxy for the assessment of habitat quality and restoration success in the highly threatened restinga ecosystem.

KEY WORDS. Interspecific competition, *Mimus gilvus*, *Mimus saturninus*, restinga, syntopy, urbanization.

INTRODUCTION

Invader species may establish populations in novel landscapes due to invasion or expansion of their original distribution (Lockwood et al. 2013, Chen et al. 2022). Invasion is generally related to human-induced alterations of the natural landscape (Grarock et al. 2014, Zorzal et al. 2021). Landscape alteration can promote native species to colonize

new habitats within their native range (Carey et al. 2012). The effects of habitat modification and invasive species are interrelated, and thus useful to investigate native species decline (Grarock et al. 2014). Invasion is context-dependent, and factors associated with invasion success are not uniform across time (Catford et al. 2019).

Congeneric species may have similar phenotypic and ecological attributes, which provides an opportunity to study

coexistence. The Tropical mockingbird, *Mimus gilvus antelius* Oberholser, 1919 and the Chalk-browed mockingbird, *Mimus saturninus* (Lichtenstein, 1823), currently occur in sympatry in the coast of Southeastern Brazil (Argel-de-Oliveira and Pacheco 1998), whereas co-occurrence records are lacking on historical publications (e.g., Bell et al. 1841, Hussey 1916, Arribáizaga 1920, Willis 1992). Regarding niche theory, competition through resource exploitation is the most important determinant of ecological segregation (Levins 1968). However, interference competition may also be decisive for characterizing species distribution and abundance (Case and Gilpin 1974). Species with high niche overlap are generally involved in territorial competition (Louarn et al. 2016), which may have a significant impact when native species have temporal niche overlap with an invasive species.

Mimus gilvus antelius is restricted to the Brazilian coast (Cody 2005), where it has close dietary relationship with plants of the restinga ecosystem (i.e., sandy-coastal plains) (Sick 1997). The Tropical mockingbird is a key species on dispersing restinga plants (Naranjo et al. 2003, Gomes et al. 2007), but it is Endangered in the states of Espírito Santo (Chaves et al. 2019) and Rio de Janeiro (Alves et al. 2000). Whereas, *M. saturninus* is common in semi-open natural areas, and also inhabits rural and urban areas from northern Bolivia to Midwest and Northeastern Brazil (Ridgely and Tudor 1989, Argel-de-Oliveira 1994). The Chalk-browed mockingbird is expanding its geographical distribution to deforested areas along the Atlantic coast (Ridgely and Tudor 1989), colonizing the restinga ecosystem of the southeastern region. At the coast of southeastern and northeastern Brazil, Tropical mockingbird is confined to patches of restinga, whereas Chalk-browed mockingbird was originally associated with inland xerophytic vegetation (Lamm 1948).

The first published record of the Chalk-browed mockingbird in the Cerrado Biome was in 1926 (Rogers 2016), 715 km distant from our study site. In 1930, the Chalk-browed mockingbird was recorded in the Atlantic Forest biome (Cicero 2017) at 238 km from our study site. In 1941, it was recorded in an urbanized area 70 km from our study site (GBIF 2022). Currently, Chalk-browed mockingbird occurs in sympatry with Tropical mockingbird. Contrarily, Tropical mockingbird is endemic to restinga ecosystem (Gonzaga et al. 2000), whereas Chalk-browed mockingbird is a habitat generalist using open and mountainous regions, but absent from forested regions of southeastern Brazil (Ridgely and Tudor 1989). Thus, Chalk-browed mockingbird is an invader of restinga, leading to the current sympatry of these two congeneric species.

The presence of Chalk-browed mockingbird in the restinga is likely detrimental to the Tropical mockingbird due to its novel competitive effect (Argel-de-Oliveira 1994). Chalk-browed mockingbird has been observed expelling a pair of Tropical mockingbird from a constructed nest for egg laying (R. Morais, pers. com.) and we have also recorded other agonistic interactions between these species (C. Duca pers. obs.). Tropical mockingbird is not highly sensitive to habitat disturbance (Parker III et al. 1996), but Chalk-browed mockingbird inhabits coastal urban environments where Tropical mockingbird is absent or uncommon. However, the interaction between these two congeneric species may expose the Tropical mockingbird to further selection pressure in its native habitat.

Considering that the concept of ecological tolerance includes the acclimatization to physical conditions and the behavioral indifference of one species towards another (Begon et al. 2007), our goal was to compare the abundance and spatial distribution of the Tropical mockingbird and the Chalk-browed mockingbird to understand their recent coexistence. We studied a gradient from preserved to urban sites of Southeastern Brazil to determine: the landscape features related to the presence and abundance of the two species; the patterns of association between the species; and the role of space and environment in explaining these patterns.

MATERIAL AND METHODS

Study site

The study site is located in the municipalities of Vila Velha and Guarapari, state of Espírito Santo, southeastern Brazil (Fig. 1). It is in the Atlantic Forest biome, and it was originally covered by restinga vegetation (Pereira 2003), which has rocky outcrop, open herbaceous vegetation, flood-meadow, and forest (Fabris and Cesar 1996). The study site comprises a gradient from preserved to urban areas. In the south of the sampled site, data were collected in the Setiba Environmental Protection Area (APA-Setiba, 12,960 ha) (Lausche 2011), which includes the Paulo César Vinha State Park (PEPCV, 1,500 ha) located inside the APA-Setiba. In the north of the sampled site, there are urban areas in the municipality of Vila Velha, which is a highly urbanized city with 210 km². This region has an Am tropical monsoon climate (Köppen) (Alvares et al. 2013).

Sampling design

Data were collected from November 2015 to April 2017. The sampling design had 30 transects perpendicular to the

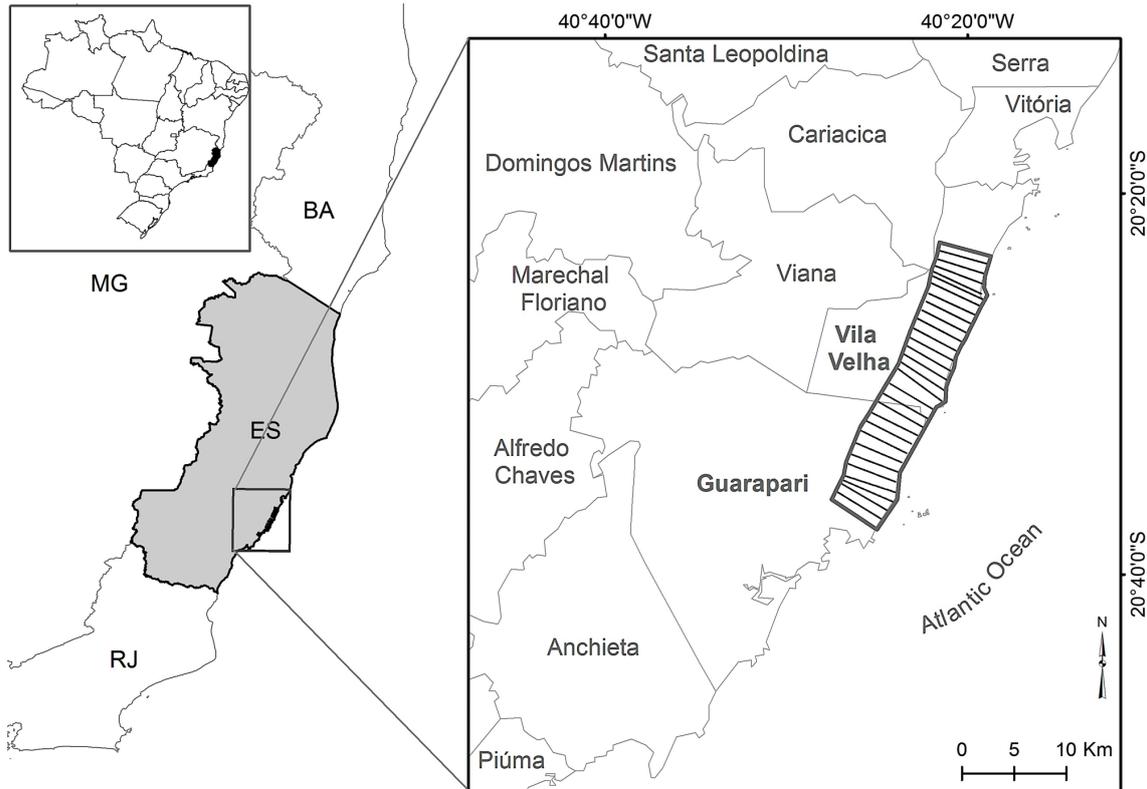


Figure 1. Sampling design (transects) in the municipalities of Vila Velha and Guarapari, state of Espírito Santo, southeastern Brazil.

coast, each 5,000 m long and placed 1,000 m apart from each other (Fig. 1). Each transect had up to 50 sampling units, which was a circle of 50 m radius (area 7,854 m²). A pilot study showed that both species were reliably identified and counted up to 50 m without recounting by the observer using Tasco 10 × 50 binoculars. The total sampling area is about 1,140 ha. Each sampling unit was surveyed twice for five minutes using the point count method (Bibby et al. 2000) between dawn and 10:00 in the morning, which is the highest activity period of both species and consequently has a higher probability of detection (Anjos et al. 2010). A pilot study using plastic color bands showed an individual was not counted twice due to the distance between our sampling units and the time reserved for detection (see Morais et al. 2019).

Predictive variables

The predictive variables were the distance from each site to the coast (hereafter ‘coast distance’) and to the protected area (hereafter ‘protected area distance’) and the Normalized Difference Built-up Index (hereafter ‘NDBI’; see description below). Coast distance and protected area

distance were calculated based on aerial imagery from the Integrated System of Geospatial Bases of the State of Espírito Santo (GEOBASES) using the QGIS program (QGIS 2016) and validated by in situ observation. The NDBI was developed mainly for Landsat TM satellite data by analyzing the spectral response of built-up areas in different image bands, indicating the degree of urbanization (Zha et al. 2010). Landsat-8 OLI images were used in this predictive variable, following four main steps: pre-processing and satellite data analysis; image enhancement by resolution fusion; development of the built-up area extraction method; and precision evaluation (Zha et al. 2010). The file format and data type of the Landsat-8 OLI images were the ESRI ASCII (American Standard Code), a raster file format for digital imaging. In order to resize the NDBI to values between zero and one, each element of the set was logarithm transformed, and the maximum value of the set was used as the base of the logarithm. The resized NDBI value (hereafter ‘urbanization index’) resulted in values close to zero indicating areas of higher vegetation coverage and values close to one indicating higher amount of construction.

Response variables

The response variables were frequency of occurrence and abundance. The frequency of occurrence (FO) and total abundance of Tropical mockingbird and Chalk-browed mockingbird were based on the presence and absence and number of individuals recorded at each site. The FO was the ratio between the number of sampling units where each species was recorded (presence) relating to total sampling unit. The total abundance was the maximum number of individuals recorded in each sampling unit. Total abundance was used to estimate the Punctual Abundance Index (hereafter “abundance”), which is the ratio between the total number of individuals of each species and the total number of sampling units. It indicates species abundance as a function of their detection coefficient (Bibby et al. 2000). To estimate the abundance regarding the urbanization index, the number of individuals of each species recorded in the sampling units with an equal urbanization index value was divided by the number of sampling units with this value of the urbanization index. The abundance estimates for coast distance and protected area distance were determined at intervals of 200 m, based on the mean area of Tropical mockingbird territory (3.4 ha; L.C. Araujo, unpublished data); for example, the abundance-200 m comprised the ratio between the total number of individuals of each species and the total number of sampling units between zero and 200 m, and so on.

Statistical analyses

Prior to analysis, there was a weak correlation between the three predictive variables (Pearson correlation coefficient $r < 0.75$) (Bland and Altman 1990). The Chi-square Adherence test (χ^2) was applied to determine if there was a difference between the two species regarding total FO and total abundance. The individual relationship between each species' abundance and the predictive variables was assessed by simple linear regression (Zar 1984), using the BioEstat version 5.0 program (Ayres and Ayres 2000), at a significance level of $\alpha = 0.05$.

Generalized Linear Models (GLMs) were used to test how the numbers of individuals of each species varied in relation to the predictive variables (Gotelli and Ellison 2013). Eight models were generated for each species, and model selection followed Akaike Information Criteria (ΔAIC) values, where models with $\Delta AIC \leq 2$ were considered to have similar ability to explain the variation in the data (Burnham and Anderson 2002). The best models had lower ΔAIC values and higher strength of evidence (high values of w_i). Null models were also included (Zuur et al. 2009). The GLM with

Poisson distribution was employed using the `glm()` package in version 3.0.3 of R (R Core Team 2015).

Partial redundancy analysis (pRDA), spatial filtering using Moran's auto vector mapping (Moran's eigenvector maps [MEMs] – see Dray et al. 2006, Griffith and Peres-Neto 2006), and spline correlograms were utilized to partition the abundance of the two species into spatial MEM and environmental components and to quantify univariate and bivariate species patterns. The MEMs were designed to detect spatial structures of variable scale in response data. These structures, understood as scale measures, were then decomposed into a new set of independent spatial variables, which were incorporated into the analysis of variance partitioning (Legendre and Legendre 2013). The species abundance matrix ('A') per sample unit was used in this analysis. Another matrix (X) was elaborated using local spatial coordinates, longitude (x) and latitude (y) of each sampling unit, which, after being expanded to Moran's auto vector predictors, resulted in a 'M' matrix and a third 'E' matrix, representing a gradient with the three predictive variables. Prior to partitioning, a forward selection of variables was run on these explanatory matrices.

Spline-type Moran's I and univariate and cross-correlation functions were calculated using an abundance matrix of the species per sample unit and a matrix of geographic coordinates (x, y) (Bjørnstad and Falck 2001, Fortin and Dale 2005, Borcard et al. 2018). They were used to determine the autocorrelation scale (univariate analysis) and the cross-correlation (bivariate analysis) between the species Tropical mockingbird and Chalk-browed mockingbird. Spatial autocorrelation is obtained from mean deviations and provides evidence of autocorrelation intensity, influence zone size, and the type of spatial pattern of the studied variable (Legendre and Fortin 1989). Differently from the commonly used discrete correlograms, the spline correlogram is a continuous estimator (Bjørnstad and Falck 2001). For univariate correlograms, values close to zero indicate randomness in species abundances, whereas values above zero indicate an aggregate distribution pattern. For the cross-correlograms, values below zero indicate a segregated pattern among the individuals of both species. This segregation can be used as an indicator of competitive interactions between the two species. The uncertainty of the cross-spline correlograms was estimated using the bootstrapping method (10 thousand iterations) with 95% confidence intervals. The correlograms were created at a distance of 6,665 m, approximately one-third of the maximum amplitude. All analyses were performed in R (R Core Team 2015). MEMs were created using the PCNM package (Legendre et al. 2013), variable

selection was carried out using the ordistep function from the vegan package (Oksanen et al. 2017), and the univariate and cross-correlograms were run with the ncf package (Bjørnstad 2017).

RESULTS

At least one species (Tropical mockingbird and/or Chalk-browed mockingbird) was present in 64% (n = 933) of the sampling units. The frequency of occurrence of Tropical mockingbird (FO = 73%) was significantly higher than Chalk-browed mockingbird (FO = 39%) ($\chi^2 = 97.94$; df = 1; $p < 0.001$). Tropical mockingbird (n = 1019; 0.91 ind.ha⁻¹) had 1.9 times more individuals than Chalk-browed mockingbird (n = 543; 0.49 ind.ha⁻¹) ($\chi^2 = 128.82$; df = 1; $p < 0.001$).

The abundance of the Tropical mockingbird was negatively correlated with the urbanization index ($r^2 = 0.42$; $p < 0.001$), whereas the Chalk-browed mockingbird showed a weak correlation with the urbanization index ($r^2 = 0.01$; $p = 0.67$) (Fig. 2). The abundance of Tropical mockingbird decreased with increasing coast distance ($r^2 = 0.46$; $p < 0.001$), whereas Chalk-browed mockingbird showed a weak correlation with coast distance ($r^2 = 0.01$; $p = 0.73$). The abundance of Tropical mockingbird showed a weak correlation with protected area distance ($r^2 = 0.01$; $p = 0.21$), whereas Chalk-

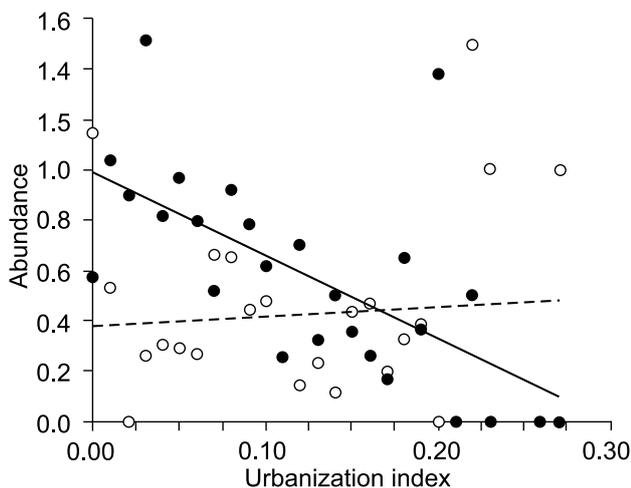


Figure 2. Abundance (Punctual Abundance Index) of Tropical mockingbird (*Mimus gilvus*, closed circle and continuous line) and Chalk-browed mockingbird (*M. saturninus*, open circle and dashed line) regarding urbanization index (Normalized Difference Built-up Index) in a coastal region of southeastern Brazil. Urbanization increases toward a higher urbanization index.

browed mockingbird increased with protected area distance ($r^2 = 0.19$; $p < 0.001$).

The model with all three predictive variables was the best fit to the abundance of both species, explaining 63% of the abundance variation of the Tropical mockingbird and 97% of the Chalk-browed mockingbird (Table 1). For the Tropical mockingbird, the second best-fitting model had the urbanization index and coast distance explaining 37% of the data. These two models explained 100% of the abundance of the Tropical mockingbird and the Chalk-browed mockingbird (Table 1).

Table 1. Model selection of abundance of Tropical mockingbird and Chalk-browed mockingbird regarding the predictive variables (Normalized Difference Built-up Index – NDBI, coast distance – CD, and protected area distance – PAD) based on Akaike’s Information Criteria (AIC). Total AIC, the difference of AIC of each model relative to the top model (ΔAIC), Akaike model weight (w_i).

Models	AIC	ΔAIC	w_i
Tropical mockingbird			
NDBI + CD + PAD	746.95	0.00	0.63
NDBI + CD	748.05	1.10	0.37
CD + PAD	763.24	16.29	0.00
NDBI	773.13	26.18	0.00
NDBI + PAD	773.69	26.74	0.00
CD	783.66	36.70	0.00
PAD	817.19	70.24	0.00
Null	824.53	77.58	0.00
Chalk-browed mockingbird			
NDBI + CD + PAD	577.99	0.00	0.97
NDBI + PAD	584.76	6.77	0.03
NDBI	593.92	15.93	0.00
NDBI + CD	594.92	16.93	0.00
CD + PAD	647.92	69.94	0.00
PAD	651.86	73.88	0.00
CD	653.45	75.47	0.00
Null	659.87	81.89	0.00

The partitioning between environment and space explained 22% of the variation ($p = 0.001$). The greater proportion (11%; $p = 0.001$) of the abundance variation of Tropical mockingbird and Chalk-browed mockingbird was associated with the spatial component (MEMs), whereas the environment explained a relatively lower fraction (6%, $p = 0.001$). The shared variation between both components was 5%.

The spatial pattern analysis (univariate spline correlograms) of each species showed positive spatial autocorrelation for Tropical mockingbird until ca. 2,000 to 3,000 m (Fig. 3A), while Chalk-browed mockingbird (Fig. 3B) is aggregated up to a 3,500 m spatial scale. The cross-spline correlogram indicated segregation of the two species at scales up to 5,000 m. At greater distances, the test value and its confidence interval were at the zero line, denoting a random spatial distribution pattern (Fig. 3C).

DISCUSSION

The native restinga specialist Tropical mockingbird is more abundant than the invader Chalk-browed mockingbird in the study area. Considering the closest relationship between the Tropical mockingbird and the restinga ecosystem, this result corroborates the hypothesis of higher abundance at the center of species distribution (Brown 1984). Restinga patches still remain around higher urbanization centers and near the coastline. Thus, the specialization of Tropical mockingbird on restinga may influence its presence and abundance in the coastal-urban region (Crates et al. 2011), explaining the decreasing abundance of the Tropical mockingbird with coast distance and the weak relationship of Chalk-browed mockingbird abundance with this variable. However, habitat loss in restinga may be influencing the historical reduction of Tropical mockingbird abundance (i.e., 30% and 46% in a 10-year period; see Zanon et al. 2015) and the expansion of Chalk-browed mockingbird.

Apparently, the Tropical mockingbird is more sensitive to urbanization than the Chalk-browed mockingbird. The sensitivity of the Tropical mockingbird to urbanization has also been reported for other populations (Zanon et al. 2015), suggesting the need for conservation of the remaining restinga to maintain viable populations. Urbanization may be the main threat affecting the reduction of the Tropical mockingbird abundance across the Brazilian coast. The Tropical mockingbird is a threatened species in the coastal region of Southeastern Brazil (Alves et al. 2000, Chaves et al. 2019). It is also considered a key species due to its seed dispersal function in restinga ecosystem (Naranjo et al. 2003, Gomes et al. 2007), being essential in the conservation and recovery of degraded areas in coastal environments (Gomes et al. 2008). To safeguard the long-term presence of the Tropical mockingbird, a sustainable land use plan for the coastal region is required by combining urbanization and protection of restinga remnants (Rocha et al. 2007). We highlight the importance of the restinga strip as a permanent preserva-

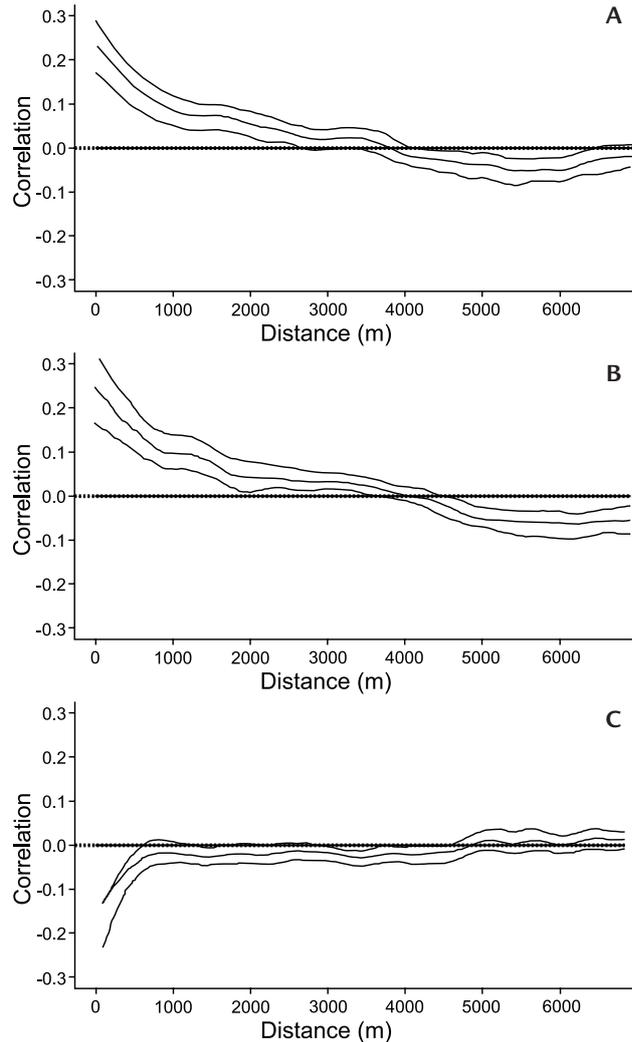


Figure 3. (A,B) Univariate spline correlogram: (A) Tropical mockingbird; (B) Chalk-browed mockingbird. Superior and inferior lines represent a 95% confidence interval. The confidence intervals below or above zero in splines indicate negative and positive spatial structures, respectively. (C) Cross-spline correlogram of the two species denoting spatial segregation between the two species (negative values) regarding distances of up 1,000 m.

tion area (Brasil 2012) on the coast as a way to mitigate the impacts of urbanization on the Tropical mockingbird population. We also suggest restinga restoration could be useful for the Tropical mockingbird recovery and Chalk-browed mockingbird control.

The Tropical mockingbird and the Chalk-browed mockingbird showed different responses to coast distance.

The abundance of Tropical mockingbird decreased toward the inland and Chalk-browed mockingbird did not show any trend. These spatial distributions are corroborated by the literature for both species (Ridgely and Tudor 1989, Argel-de-Oliveira 1994). The Chalk-browed mockingbird is less selective regarding coast distance due to its behavioral plasticity to use different habitats (see Argel-de-Oliveira 1994, Rodrigues et al. 2017). Invader species are usually benefited by urbanization and increase their presence in suburban and urban areas (e.g., van Rensburg et al. 2009, Grarock et al. 2014).

The Tropical mockingbird had similar abundance in relation to the protected area distance, whereas the Chalk-browed mockingbird had an increase toward urban areas. There are patches of restinga between the protected and urban areas that could increase habitat connectivity, mainly near the coast. Nonetheless, these remaining restinga patches are private properties under continuous human modification, which may promote the isolation of the Tropical mockingbird population. So, it is possible that Tropical mockingbird is not subjected to fragmentation effects on the study area yet, due to the still high restinga vegetation cover of the landscape, but it is also possible that it will be affected by restinga fragmentation in short to middle term.

The urbanization and the isolation of populations may influence the absence of Tropical mockingbird in some restinga patches. In other two populations, the Tropical mockingbird has also been absent in preserved areas (Zanon et al. 2015, C. Duca pers. obs.). Apparently, Tropical mockingbird is sensitive to high-density urbanization, leading to population isolation (Zanon et al. 2015), which would impede the recolonization of metapopulation dynamics (McDonnell et al. 1997). The fragmentation of the restinga may reduce displacement between sites and consequently recolonization (Rocha et al. 2007). On the other hand, the Chalk-browed mockingbird is likely more resistant to the effects of fragmentation, showing good adaptive plasticity in altered environments.

The Chalk-browed mockingbird does not occur only in developed urban areas nor it is restricted to regions occupied by exotic or native vegetation, showing that this species can inhabit both natural and altered environments (Vallejos et al. 2016). Low levels of urban development (e.g., areas with empty lots, small houses, squares, and gardens) increase the variety and quantity of resources available for birds (Blair 1996). Therefore, low rates of urbanization alter the environment less significantly compared to large urban centers. This low-intensity modification may occur through changes in the composition of the plant community, the introduction

of ornamental species, and changes in structure (e.g., replacement of tree species with herbaceous plants) (Rudnický and McDonnell 1989). These alterations may be associated with increased water sources, primary productivity, and habitat fragmentation (Kark et al. 2007). Alterations in resource availability may also alter community patterns, interfering with species composition as well as abundance (Blair 1996).

Habitat variability can lead to spatial segregation or species grouping. The results showed that at small scales (0 to 3,500 m), Tropical Mockingbirds and Chalk-browed Mockingbirds displayed individual aggregated spatial patterns, showing that the spatial variable explains the abundance variance of the two species. Apparently, the two species exhibited segregated spatial patterns in response to competition, suggesting that they would be potential competitors in syntopy. Congeneric species with similar niches tend to reduce competition by segregating in space, as discussed in the Principle of Competitive Exclusion (Gause 1932, Bringle et al. 2016). It is known that niche overlap can affect populations of both species (Chen et al. 2022) and this seems to be the ecological scenario for Tropical mockingbird and Chalk-browed mockingbird in the study area. The observed spatial differentiation may also be a result of past competition, a principle known as the “ghost of competition past” (Connell 1980). Future studies on habitat selection may provide important insights into how these species are segregating in space.

Our study showed that the Chalk-browed mockingbird has ecological plasticity in altered environments and is possibly benefiting from habitat modification, thus increasing its geographical distribution. The results corroborate studies showing that the Tropical mockingbird is susceptible to urbanization and fragmentation of the restinga (Alves et al. 2000, Zanon et al. 2015). Because the Tropical mockingbird is a threatened species in southeastern Brazil (Alves et al. 2000, Chaves et al. 2019) and also plays a critical role in the restinga ecosystem (Gomes et al. 2008), it can be a useful bioindicator of environmental quality in these areas. The monitoring of Tropical mockingbird populations can be considered a suitable tool for assessing the conservation status of restinga at local (remnant) and regional (landscape) scales and also to evaluate the efficiency of restoration of degraded areas in the restinga ecosystem.

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