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Combining geospatial abundance and ecological niche models to identify high-priority areas for conservation: The neglected role of broadscale interspecific competition

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Ecological niche models (ENMs) have become a practical and key mechanism for filling major gaps in spatial information for targeted conservation planning, particularly when only occurrence data are available. Nonetheless, accounting for abundance patterns in the internal structure of species' ranges, and the role of biotic interactions in such models across broadscale, remains highly challenging. Our study gathered baseline information on abundance data of two Endangered Amazonian primates (*Ateles chamek* and *Lagothrix lagotricha cana*) to create geospatial abundance models using two spatial interpolation methods: Inverse distance weight (IDW) and Ordinary kriging (OK). The main goals were to: (i) test whether geospatial abundance models are correlated with habitat suitability derived from correlative ENMs; (ii) compare the strength of the abundance-suitability relationships between original and interpolated abundances; (iii) test whether interspecific competition between the two target taxa constrained abundance over broad spatial scales; and (iv) create ensemble models incorporating both habitat suitability and abundance to identify high-priority areas for conservation. We found a significant positive relationship between habitat suitability with observed and predicted abundances of woolly (*L. l. cana*) and spider (*A. chamek*) monkeys. Abundance-suitability correlations showed no significant differences when using original relative abundances compared to using interpolated abundances. We also found that the association between *L. l. cana* abundance and habitat suitability depended on the abundance of its putative competitor species, *A. chamek*. Our final models combining geospatial abundance information with ENMs were able to provide more realistic assessments of hotspots for conservation, especially when accounting for the important, but often neglected, role of interspecific

competition in shaping species' geographic ranges at broader scales. The framework developed here, including general trends in abundance patterns and suitability information, can be used as a surrogate to identify high-priority areas for conservation of poorly known species across their entire geographic ranges.

Introduction

Ecological niche models (ENMs; also referred to as species distribution or habitat suitability models) have become a practical and important mechanism for filling major gaps in spatial information for targeted conservation planning (Zurell et al., 2021), particularly when only occurrence data are available (Phillips et al., 2006; Sillero et al., 2021; Valavi et al., 2021). ENMs relate geo-referenced species observations to environmental variables to estimate suitable habitats in a geographical space, providing hypothesis for the geographic distributions of the species (Sillero et al., 2021). Although ENMs have proven useful to adequately describe the geographic distribution of species, their capacity to inform about the abundance patterns in the internal structure of species' ranges remains an unsolved problem (Weber et al., 2017; Dallas and Hastings, 2018; Jiménez-Valverde et al., 2021; Lee-Yaw et al., 2021). Therefore, incorporating species abundance information across broad spatial scales is a fundamental step toward effective conservation and management of species.

Abundance is not evenly distributed across space. It is expected that most species occur at low abundances in most of their range, and are highly abundant in relatively few locations (Brown et al., 1995). These patterns reflect population responses to local conditions in which the species meet its ecological requirements (de la Fuente et al., 2021). Another classical assumption of abundance distribution is that abundance variation is spatially autocorrelated, so that the probability of sites having similar abundance values is an inverse function of the distance between them (Brown et al., 1995). This is in line with the foundation of Tobler's first law of geography (Tobler, 1970), which poses that "everything is related to everything else, but near things are more related than distant things." This fundamental spatial dependence and autocorrelation concepts lies at the heart of methods of spatial interpolation (Li and Heap, 2008, 2011, 2014).

Spatial interpolation is the process of mapping a variable of interest at unsampled locations using the values present in a sampled set of known locations to generate spatially continuous surfaces (see Li and Heap, 2014 for topic review). Conservation scientists, policymakers and environmental managers usually require such kinds of spatially explicitly data to make effective and confident decisions over a region of conservation concern. Consequently, geostatistical techniques have been widely disseminated in different disciplines (e.g., mining engineering, soil sciences, anthropology: Li and Heap, 2008; Relethford, 2008; Li and Heap, 2014). Spatial interpolation has been used for characterizing the spatial distribution and mapping soil gradients and properties (e.g., Robinson and Metternich, 2006; Zuquim et al., 2019), generating climate surfaces of precipitation and temperature (e.g., Tan et al., 2021), and mapping epidemic vectors and diseases (e.g., Zhou et al., 2021). In ecological studies, they have also been applied, for example, to map temporal changes in live coral cover (Walker et al., 2012), predict forest stem volume (Wallerman et al., 2002), or to characterize the spatial structure of vegetation communities (Wallace et al., 2000). However, the use of interpolation methods for spatial conservation prioritization and abundance predictions has been considerably scarcer, especially for Amazonian data-deficient species.

Black faced black spider monkeys (*Ateles chamek*) and the gray woolly monkeys (*Lagothrix lagotricha cana*) are two Endangered Amazonian primate taxa with just such abundance-data limitations, and at a number of scales (Alves et al., 2021; Cornejo et al., 2021). These two taxa are members of the subfamily Atelinae (Platyrrhini, Atelidae). They are considered to be keystone dispersers, providing invaluable ecosystem services (Peres et al., 2016; Sales et al., 2020). The extirpation of such large-bodied forest-dwelling animals from ecosystems could critically alter long-term forest dynamics and maintenance of above-ground biomass and carbon storage (Peres et al., 2016). It is estimated that *Ateles* spp. and *Lagothrix* spp. (spider and woolly monkeys, respectively) shared a common ancestor approximately 10–11 mya (Di Fiore et al., 2014). They are highly frugivorous taxa, have large home ranges that can reach up to 1,021 hectares, and are the most large-bodied

genera within the Amazonian forests (Di Fiore and Campbell, 2007). Consequently, it has been suggested that a complex combination of ecological forces (e.g., regional and local variation in the degree of interspecific competition), historical biogeographical process (e.g., dispersal factors), and local hunting pressure have been shaping the current distributions of these species (Peres, 1990, 1991; Iwanaga and Ferrari, 2002; Peres et al., 2016; Rabelo et al., 2018; Cavalcante et al., 2020).

Ateles chamek has a broader distribution range that extends south, north and west of the Solimões and Japurá rivers, while *L. l. cana* is limited by the Guaporé River valley to an area between the Brazilian states of Mato Grosso and Rondônia (Iwanaga and Ferrari, 2002; Rabelo et al., 2018; Cavalcante et al., 2020). The geographic distribution of *L. l. cana* is entirely embedded within the range of *A. chamek*. This extensive sympatric area (1,791,200 km^2) falls within the southwestern Brazilian Amazon, a region that has been called the "arc of deforestation" due to habitat loss and ongoing deforestation (Michalski et al., 2008; Trancoso, 2021). Therefore, identifying high-priority areas for conservation of these taxa across their geographic distributions can help to protect other forest-dwelling species, so reducing the rate of overall Amazonian biodiversity loss.

Our study gathered baseline information on abundance data of two Endangered Amazonian primates (*Ateles chamek* and *Lagothrix lagotricha cana.*) to create geospatial abundance models and assess abundance patterns across the entire range of each taxon. The main goals of this study were to: (i) test whether geospatial abundance models are correlated with habitat suitability derived from correlative ENMs; (ii) test whether interspecific competition between the two target taxa constrained abundance over broad spatial scales; (iii) compare the strength of the abundance-suitability relationships between original and interpolated abundances; and (iv) create ensemble models incorporating both habitat suitability and abundance to identify high-priority areas for conservation.

We hypothesized that geospatial abundance models are positively correlated with habitat suitability derived from ENMs, and that interspecific competition between our two target taxa will be an important factor in limiting their abundances across their geographic distributions. We predicted a negative correlation between *A. chamek* and *L. l. cana* abundances due to their close relatedness, comparable body sizes, specialization on ripe fruits as the principal diet component, and other similarities in their feeding ecology and ecological niche requirements (Iwanaga and Ferrari, 2001, 2002; Cavalcante et al., 2020). Finally, we expected that there would be no difference in the correlation strengths between geospatial abundance models and original abundance estimates with habitat suitability, which would support the viability of using geospatial abundance
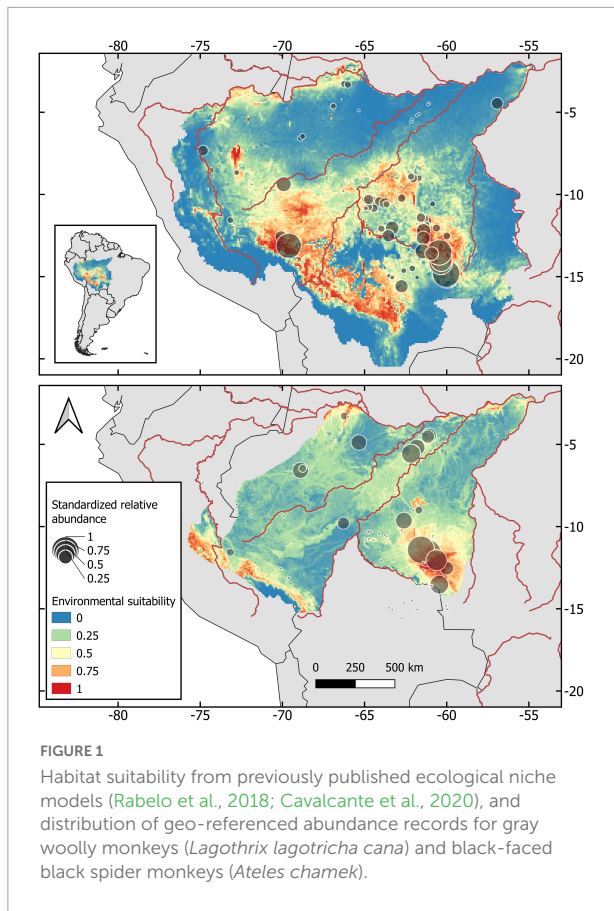
and ENMs as a surrogate to identify high-priority areas for conservation of poorly known species across their geographic distributions.

Materials and methods

Relative abundance and ecological niche models

Our study area lies within the Amazon forests of Brazil, Peru and Bolivia (2°S, 55°W and 15°S, 75°W), and covers the whole geographic distribution of the two target taxa. We gathered 77 geo-referenced abundance records from the literature for the two taxa of Amazon atelins. Our abundance dataset comprises 18 different studies addressing community structure and species diversity of primates and other mammals that spanned from 1983 to 2018 across different habitat types in all three countries where both taxa occur (**Figure 1** and **Supplementary Table 1**). To avoid bias in abundance estimation, we selected abundance data only from those studies using standard line transect surveys (see Brockelman and Ali, 1987; Peres, 1999). This standard sampling protocol documents encounter rates (sightings per 10 km surveyed), which are commonly used as indices of relative abundance for diurnal mammals (Scheel, 1993; Iwanaga and Ferrari, 2002; Gray et al., 2016). Abundance gathered from the selected studies varied from 0 (i.e., local absence) to 7.97 sightings per 10 km (mean = 0.78 ± SD 1.43), indicating that the selected studies were not biased to areas with known high primate abundance.

Ecological niche models used in this study were previously constructed by Rabelo et al. (2018) and Cavalcante et al. (2020) using spatially explicit variables that could reasonably be expected to influence a primate species' distribution (see **Supplementary Material**). These variables consisted of climatic, topographic, edaphic, and vegetation layers. The estimated area of occupancy for *A. chamek* was 927,754 km^2. Temperature seasonality, net primary productivity and potential evapotranspiration were the most important variables in the final model (Rabelo et al., 2018). Suitable habitats for the species are distributed in the Amazonas-Javary interfluvial region in Peru, and along the Lower-Jutaí and Juruá rivers in Brazil. The estimated area of occupancy for *L. l. cana* was 412,250 km^2. The most important variables in the final model were mean annual temperature, temperature seasonality, occurrence of arenosols, and a layer of habitat suitability for *A. chamek* as a biotic predictor variable (Cavalcante et al., 2020). A wide area with high habitat suitability for *L. l. cana* is located within the southwestern Brazilian Amazonia, and also in the Amazonas-Javary interfluvial region in Peru. The two taxa show a high proportion of habitat suitability overlap (Cavalcante et al., 2020), due to similar ecological niche requirements (Iwanaga and Ferrari, 2001, 2002; Cavalcante et al., 2020).

Habitat suitability from previously published ecological niche
models (Rabelo et al., 2018; Cavalcante et al., 2020), and
distribution of geo-referenced abundance records for gray
woolly monkeys (*Lagothrix lagotricha cana*) and black-faced
black spider monkeys (*Ateles chamek*).

Spatial interpolation analyses

We plotted all geo-referenced abundance records for each
taxon into a GIS environment and created a polygon layer by
drawing the boundaries using the previously published ENMs
(Rabelo et al., 2018; Cavalcante et al., 2020). We then created
a grid of 0.09° × 0.09° latitude-longitude cells to interpolate
species abundance. The spatially referenced original abundance
estimates data were used to interpolate the abundances across
their geographic ranges, producing spatially explicit predictions
of species abundance.

We created the geospatial abundance models using Inverse
distance weight (IDW) and Ordinary kriging (OK). Both
methods are based on the principle of spatial autocorrelation
where the greater the distance, the less influence the cell
has on the interpolated values, while closer cells have greater
influence (Li and Heap, 2011). IDW is a simpler method which
uses arbitrary exponential weighting according to distance
(Watson and Philip, 1985), while OK is a more powerful
and sophisticated statistical method that takes into account
spatial autocorrelation of the data to assign interpolation
weights based on automated variogram modeling (Pebesma
et al., 2011). This later method is a reliable and highly
recommended univariate method with unbiased estimates that

minimize prediction errors with relatively low variances (Laslett
et al., 1987; Oliver and Webster, 1990; Li and Heap, 2011).
We used these two different methods because (i) they are
suitable for irregularly spaced samples (Li and Heap, 2014),
as in our training dataset and (ii) we intended to combine
methods from different families [geostatistical (OK) and simpler
non-geostatistical methodologies (IDW)] to overcome inherent
biases from each individual model. Both spatial interpolation
methods were implemented in ArcGIS 10.5 using the default
parameter settings. Specifically, for IDW, we used a weighting
power of two and for OK, we used spherical semivariogram
for modeling the distance decay and infer lag, nugget and
sill (Meek and Sauer, 2003; Fletcher and Fortin, 2018). More
details about the OK variograms and fitted models are available
in **Supplementary Figure 1**. Abundances predicted by the
IDW and OK technique will be hereafter referred to as IDW-
abundance and OK-abundance, respectively.

Correlation tests and comparisons

We tested the association between habitat suitability derived
from the two previous published ENMs (Rabelo et al., 2018;
Cavalcante et al., 2020) with the original relative abundance,
and IDW- and OK-abundances using Pearson product-moment
correlation. We aimed to determine if a significant positive
relationship existed between predicted habitat suitability and
predicted and original local relative abundance. Correlation
methods are widely used to measure the relationship between
abundance and habitat suitability derived from occurrence
data (see Weber et al., 2017 for an overview). We explored
other correlation coefficients that do not assume linearity (e.g.,
Spearman's r_s and Kendall's tau) during data exploration but
Pearson's r provided the best fit for the correlations between
abundance and suitability. We log-transformed $[\log(x + 1)]$
abundance data to match Pearson's correlation assumptions.

We compared the ENMs to the original relative abundance
data by extracting the values of predicted habitat suitability in
the geo-referenced abundance points. We excluded localities
with small sampling effort (i.e., <35 km of line transects
surveyed, $N = 11$), as localities with less accurate abundance
data may hide or weaken the abundance-suitability correlation
(see for discussion Weber et al., 2017), especially because
such possible outliers may have undesirable effects on Pearson
correlation coefficient estimates (Schober et al., 2018). In case
of the predicted abundances, we sampled 1,000 random points
across the complete range within the extents of occurrence of
both taxa to extract the values of predicted habitat suitability
and predicted relative abundance for each taxon. We performed
a randomization approach for spatial thinning using the "thin"
function in the R package *spThin* (Aiello-Lammens et al., 2015)
to avoid the clustering of random points in geographic space.
This function returns a dataset with the maximum number

of records for a given thinning distance. We used 30 km as the filter distance, following the largest control radius used in previous ENMs for the taxa of this study (Rabelo et al., 2018). The thinning process resulted in a sample of 597 random points for *L. l. cana*, and 751 random points for *A. chamek*.

We performed a set of tests of significance to compare the magnitude and strength between the correlations with the purpose of testing whether the associations differed when using original and predicted abundances. First, we compared the correlations between the original relative abundance and habitat suitability vs. the correlation between the IDW-abundance and habitat suitability. Second, we compared the same original relative abundance correlation vs. the correlation between the OK-abundance and habitat suitability. To ensure a valid and interpretable comparison, we directly contrasted the two correlations under investigation using Fisher's z and Zou's confidence interval (Zou, 2007) within the R package *cocor*, version 1.1-0 (Diedenhofen and Musch, 2015). Fisher's z is commonly used to test the significance of the difference between two correlation coefficients, while Zou's test considers the magnitude and precision of an estimated effect. The latter test is based on the computation of confidence intervals, which is considered to be superior to significance tests used by most of the other available approaches (Olkin and Finn, 1990; Zou, 2007; Diedenhofen and Musch, 2015). Since we expected no differences between the correlations and no *a priori* expectation of directionality, we used a two-tailed test of significance. Statistical difference is assigned for Fisher's z test when $P < 0.05$ and Zou's (2007) confidence intervals are considered significant different when there is no overlap with zero. A null hypothesis is retained when confidence intervals overlap zero.

Broadscale interspecific competition hypothesis

To assess the role of broadscale interspecific competition, we tested if abundance variation is related to an interaction between habitat suitability and a putative interspecific competition between the two target taxa (see Braz et al., 2020; Cavalcante et al., 2020). After validating the geospatial abundance models using the tests of correlation and strength of association, we decided to use the modeled abundances to test the competition hypothesis because it was possible to make use of a large and well distributed random sample of locations within the area of sympatry of the two target taxa, providing a robust test; an approach that would not be possible using the original compiled abundance data. We used only the OK-abundances because they showed the strongest relationship with habitat suitability (see results below). For this purpose, we sampled 1,000 random points within the area of sympatry of the two target taxa. We applied the same thinning process used for the correlation tests. We extracted the values of predicted habitat

suitability and predicted abundance from 607 random points to fit a generalized linear model (GLM) using the *glmmTMB* package (Brooks et al., 2017). To build the model, we used *L. l. cana* OK-abundance as the response variable, and habitat suitability and *A. chamek* OK-abundance extracted at the same localities as predictor variables. We decided to assess the effect of competition for only one of the two taxa because the geographic distribution of *L. l. cana* is entirely embedded within the range of *A. chamek*. Thus, the geographic distribution of *L. l. cana* is our main area of interest (i.e., their sympatric area).

We fitted the models with untransformed abundance data using a Tweedie error distribution with a logarithmic link function to compensate for overdispersion and to handling the zero data in our abundance models (**Supplementary Figure 2**; Tweedie, 1984; Dunn and Smyth, 2005). For the hypothesis testing, we compared full vs. null models using analysis of variance (ANOVA) with a chi-square test. For the full model, we used the fixed effects with an interaction term (i.e., habitat suitability**A. chamek* OK-abundance). We tested the final model performance by checking residual diagnostics using the R package *DHARMa* (Hartig and Lohse, 2020). We used cross-sectional plots in the R package *visreg* (Breheny and Burchett, 2017) to visualize and identify the directionality of the interaction between habitat suitability and the abundance of the putative competitor. For this purpose, we took cross-sections at the 10, 50, and 90th percentiles of habitat suitability. Finally, given that we tested our hypothesis by comparing the full vs. null models and by testing the significance of the interaction term, we did not perform a *post-hoc* analysis to identify the individual effects of low, medium, and high habitat suitability.

Final ensemble models

To combine the ecological niche and geospatial abundance models, the output from each model's predictions (i.e., habitat suitability, IDW-abundance, and OK-abundance) were united in an ensemble model, which is an effective approach to overcome any biases inherent to each individual model (Araújo and New, 2007; Anderson et al., 2017; Abrahms et al., 2019; Brodie et al., 2020). The two abundance models (IDW- and OK-abundance) were rescaled between zero and one to match the habitat suitability models. Ensemble projections were then created using the averaged index across all three models, which provides a robust consensus output of an abundance-informed ENM, where one represents greatest abundance-suitability and agreement among the models.

Finally, to identify high-priority areas for conservation of the two target taxa accounting for the broadscale interspecific competition between them, we binarized the ensemble models (*L. l. cana*: 0 and 1; *A. chamek*: 0 and 2; where 1 and 2 represent suitable-abundant areas) by setting a threshold of abundance-suitability. For this purpose, we used the threshold

that has maximum sensitivity (i.e., the proportion of observed presences predicted as such) and specificity (i.e., the proportion of correctly predicted absences) in the original ENMs (Rabelo et al., 2018; Cavalcante et al., 2020), which were considered as the species' area of occupancy (sensu IUCN: Alves et al., 2021; Cornejo et al., 2021). We then summed the binarized maps to represent how suitable-abundant areas for each taxon alone (values of 1 or 2) and coincident suitable-abundant areas (values of 3) were distributed.

Results

Our abundance dataset based on 18 studies and 77 geo-referenced records resulted in a mean sighting rate for *L. l. cana* of 0.36 sightings per 10 km surveyed (SD = 0.69, range = 0–3.20). Overall, *A. chamek* had a higher mean sighting rate (mean = 1.19 ± SD 1.80, range = 0–7.97). The areas with higher abundances predicted by the IDW- and OK-abundance models for *L. l. cana* were mostly distributed in the south and northeastern Amazonia, especially in Brazil, while *A. chamek* had areas with higher abundances extending toward the southwestern edges of the Amazon basin (Figure 2). The IDW-abundance predicted density estimates for *L. l. cana* ranged from 0 to 2.99 individuals per ~10 km^2 and from 0 to 1.14 per ~10 km^2 in the OK-abundance. The mean predicted density estimated for *L. l. cana* by IDW were slightly smaller than OK mean estimates (mean = 0.40 ± SD 0.36 and mean = 0.42 ± SD 0.31 individuals per ~10 km^2, respectively). The IDW-abundance predicted density estimates for *A. chamek* ranged from 6.05 to 7.83 individuals per ~10 km^2 and from 4.54 to 4.72 per ~10 km^2 with OK-abundance. The mean predicted density estimated for *A. chamek* by IDW was also slightly smaller than OK mean estimates (mean = 1.24 ± SD 1.25 and mean = 1.29 ± SD 1.13 individuals per ~10 km^2, respectively).

Regarding the abundance-suitability relationships, we found a significant positive relationship between habitat suitability and predicted and original abundances in all cases evaluated (Table 1 and Figure 3). We observed a relatively low correlation coefficient ($r < 0.30$) in the correlations using IDW-abundances and in the OK-abundance model for *A. chamek*. The strongest relationship between original relative abundance and habitat suitability was observed for *L. l. cana*. Between the geospatial abundance models, OK-abundances have strongest correlations with habitat suitability.

For the differences in magnitude and significance of the relationships between the correlations, the null hypothesis was retained in all cases in the two types of tests (Fisher's z and Zou's test; Table 2). Therefore, we found no significant differences between the correlations of the original relative abundances and IDW- and OK-abundances. For both taxa, the abundance-informed ENMs generated more conservative
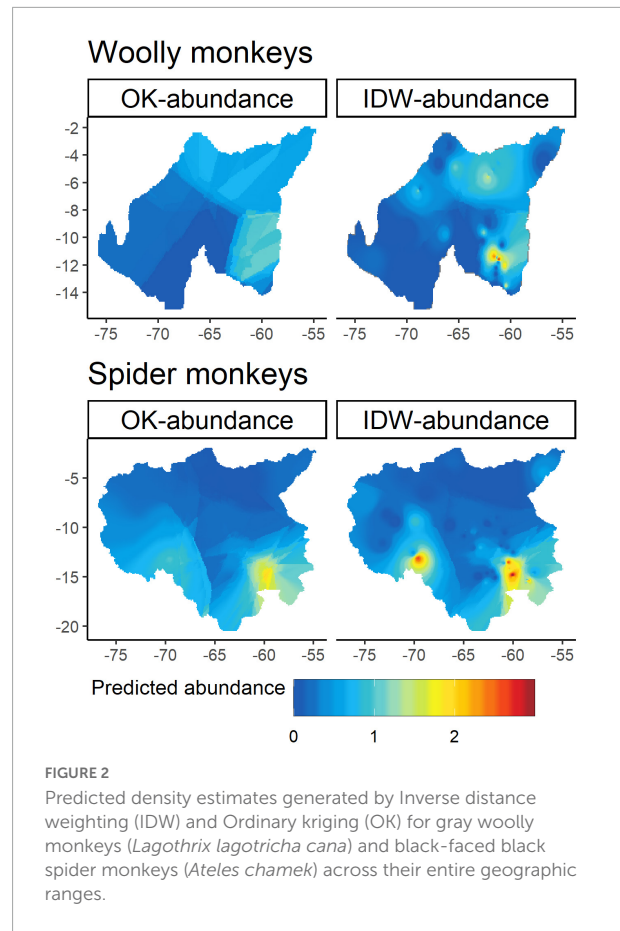

FIGURE 2
Predicted density estimates generated by Inverse distance weighting (IDW) and Ordinary kriging (OK) for gray woolly monkeys (*Lagothrix lagotricha cana*) and black-faced black spider monkeys (*Ateles chamek*) across their entire geographic ranges.

values with smaller concentrated areas of greatest abundance-suitability in comparison to the original ENMs (Figure 4).

We finally found that the full model (with the interaction term) predicting *L. l. cana* OK-abundance performed significantly better than the null model (ANOVA: χ^2 = 320.45, df = 3, $P < 0.005$), supporting our hypothesis of broadscale interspecific competition (Figure 5). Additionally, we found a significant interaction term in the full model indicating that the association between *L. l. cana* abundance and habitat suitability also depends on the abundance of its putative competitor species (see Supplementary Table 2 for GLM summary statistics). Our final reclassified map also reinforces the broadscale competition hypothesis showing a pervasive pattern of spatial segregation within the area of sympatry of the two target taxa (Figure 6).

Discussion

This study presents an innovative approach to identify important areas for conservation taking as examples two threatened sympatric Amazonian lowland primate species. By incorporating abundance information in ENMs and, especially,

TABLE 1 Pearson's correlation coefficients between habitat suitability and log-transformed abundance data for gray woolly monkeys (*Lagotrhix lagotricha cana*) and black-faced black spider monkeys (*Ateles chamek*).
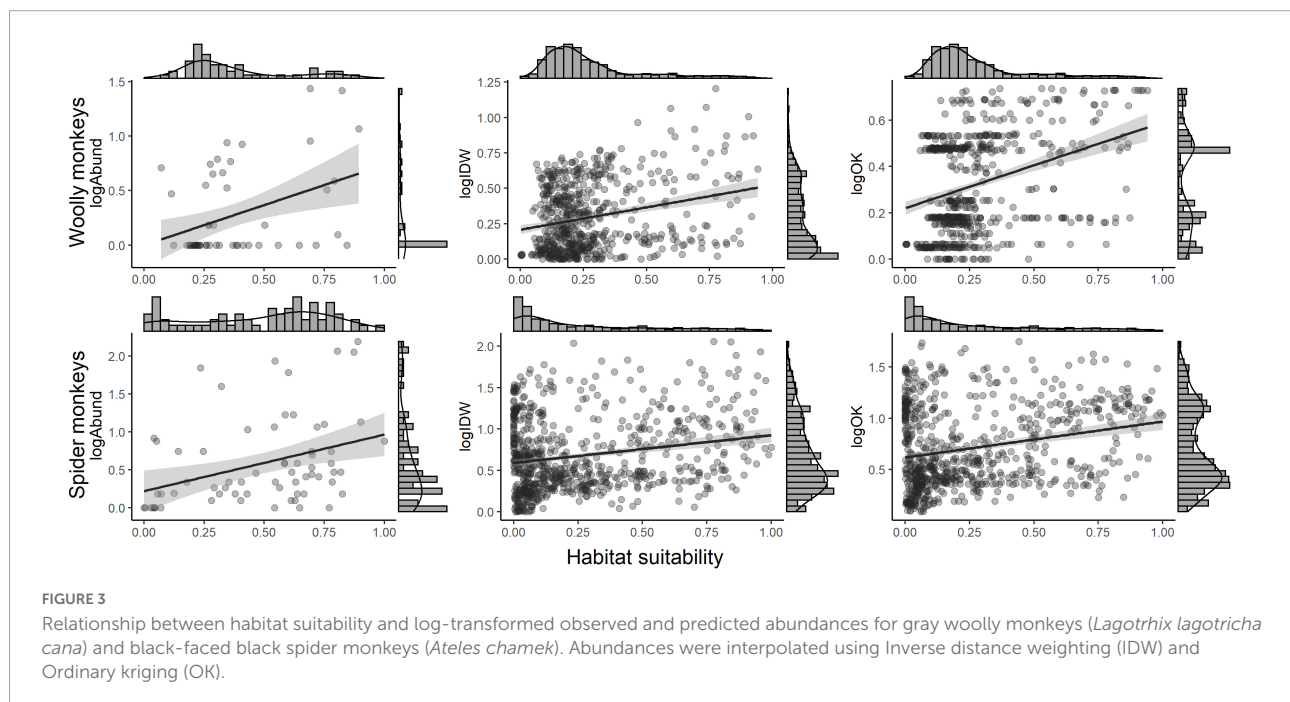
Observed and predicted abundances	Habitat suitability			
	Lagothrix l. cana		*Ateles chamek*	
Original relative abundance	0.39**	N = 53	0.36**	N = 66
IDW-abundance	0.25**	N = 597	0.21**	N = 715
OK-abundance	0.33**	N = 597	0.25**	N = 715

Modeled abundances were interpolated using Inverse distance weighting (IDW) and ordinary kriging (OK).
**Significant at $P < 0.005$.

TABLE 2 Differences between the abundance-suitability correlations when using original relative abundances compared to using Inverse distance weighting (IDW) and Ordinary kriging (OK) for gray woolly monkeys (*Lagotrhix lagotricha cana*) and black-faced black spider monkeys (*Ateles chamek*).
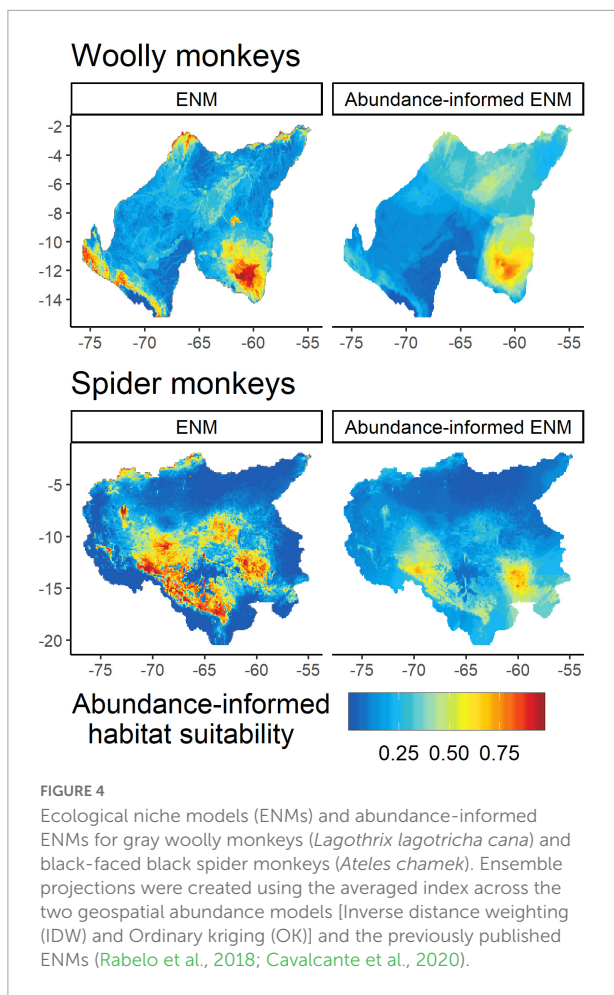
		Observed abundance x ENM			
		Zou's (CI)		Fisher's z	
		95% CI		Z	P
Lagothrix lagotricha cana	IDW × ENM	−0.1278	0.3597	1.0531	0.2923
	OK × ENM	−0.2048	0.2805	0.4734	0.6359
Ateles chamek	IDW ENM	−0.0762	0.3440	1.3177	0.1876
	OK × ENM	−0.1120	0.3074	1.0070	0.3139

FIGURE 3
Relationship between habitat suitability and log-transformed observed and predicted abundances for gray woolly monkeys (*Lagotrhix lagotricha cana*) and black-faced black spider monkeys (*Ateles chamek*). Abundances were interpolated using Inverse distance weighting (IDW) and Ordinary kriging (OK).

accounting for the important, but often neglected, role of interspecific competition in shaping species' geographic ranges at broader scales, our analytical framework was able to provide more realistic assessments of spatial information yielding targeted biodiversity management efforts and conservation planning at large scales.
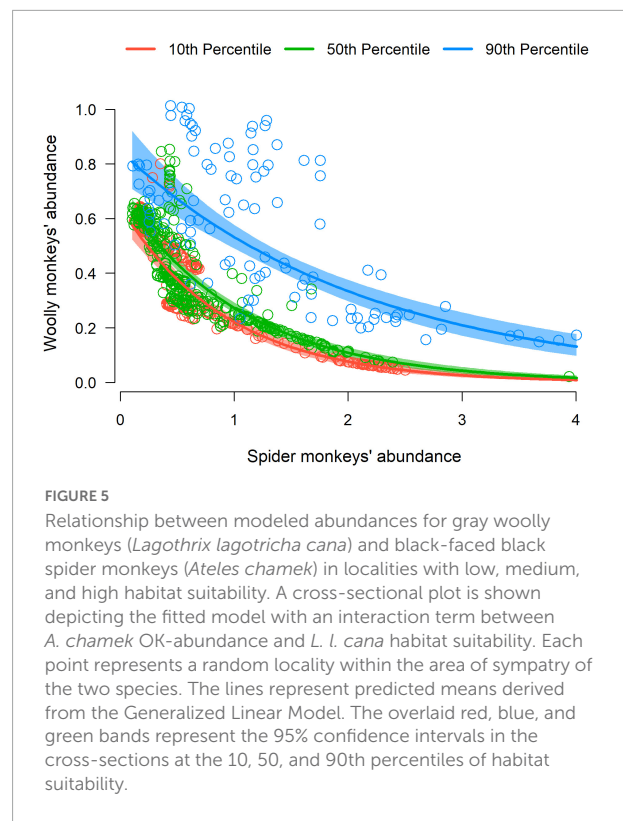
Abundance-suitability relationship

The abundance-suitability relationship is not new to ecology and substantial efforts have been made to explore the capacity of ENMs to predict abundance patterns in the internal structure of species' ranges (Brown et al., 1995; VanDerWal et al., 2009;

Ecological niche models (ENMs) and abundance-informed ENMs for gray woolly monkeys (*Lagothrix lagotricha cana*) and black-faced black spider monkeys (*Ateles chamek*). Ensemble projections were created using the averaged index across the two geospatial abundance models [Inverse distance weighting (IDW) and Ordinary kriging (OK)] and the previously published ENMs (Rabelo et al., 2018; Cavalcante et al., 2020).

Relationship between modeled abundances for gray woolly monkeys (*Lagothrix lagotricha cana*) and black-faced black spider monkeys (*Ateles chamek*) in localities with low, medium, and high habitat suitability. A cross-sectional plot is shown depicting the fitted model with an interaction term between *A. chamek* OK-abundance and *L. l. cana* habitat suitability. Each point represents a random locality within the area of sympatry of the two species. The lines represent predicted means derived from the Generalized Linear Model. The overlaid red, blue, and green bands represent the 95% confidence intervals in the cross-sections at the 10, 50, and 90th percentiles of habitat suitability.

Weber et al., 2017; Dallas and Hastings, 2018; de la Fuente et al., 2021; Jiménez-Valverde et al., 2021; Lee-Yaw et al., 2021). Previous studies have been corroborating a general positive trend between predicted habitat suitability from ENMs and species abundance regardless of taxonomic group and modeling methods (see Weber et al., 2017 for an overview). In our current study, we are extending these findings for abundance estimates predicted by two interpolation methods. More importantly, comparisons between abundance-suitability correlations using original and interpolated values showed no significant differences, validating the use of the two geospatial methodologies in our study case. This lack of significant differences in abundance-suitability correlations comparing original relative abundances against IDW- and OK-abundances have broad implications for conservation biology.
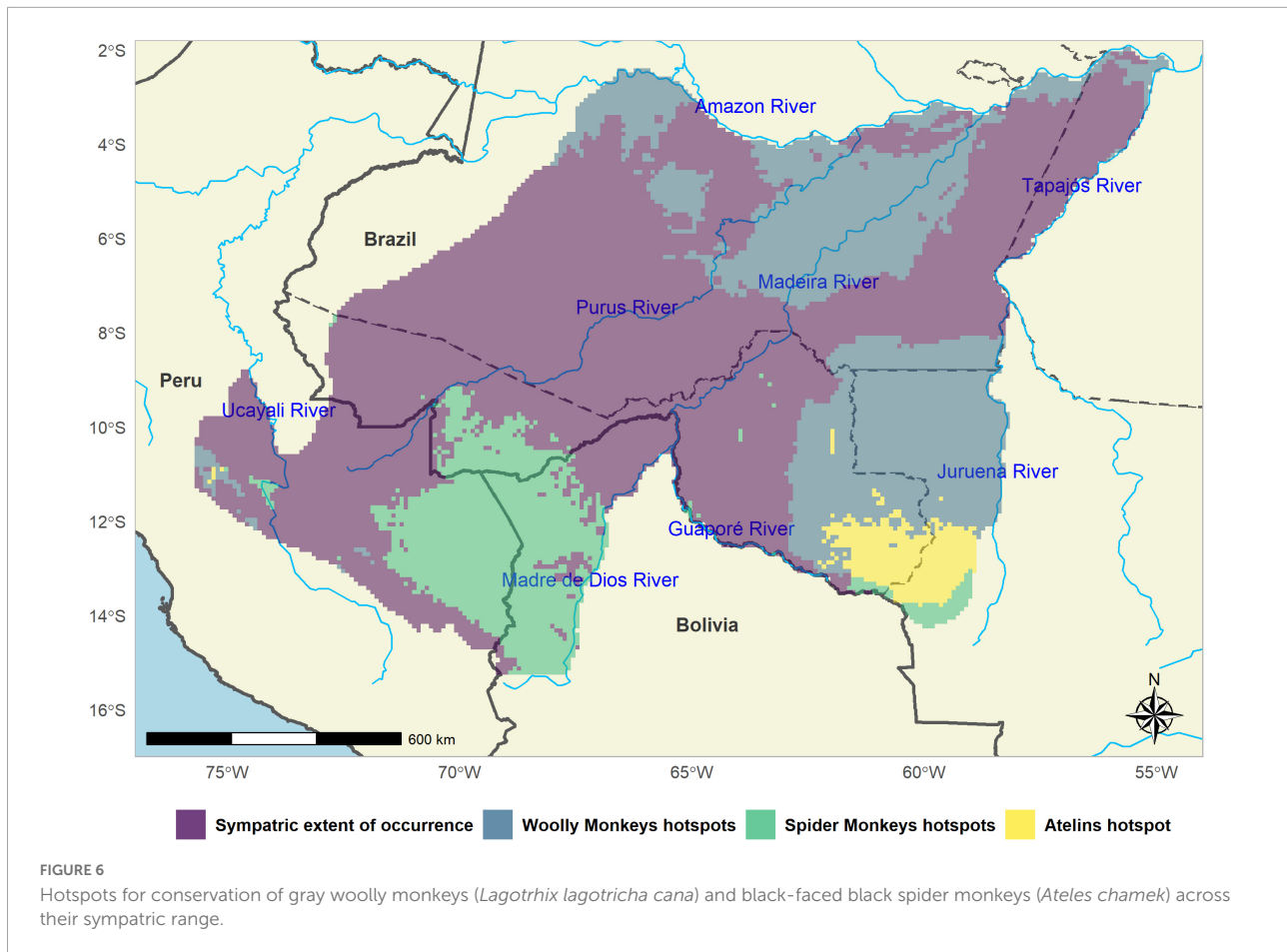
For instance, broadscale abundance estimates of declining species for input into ENMs are difficult to acquire, but are urgently required for conservation efforts. The geospatial models explored here, in addition to giving insightful and useful information concerning trends in abundance patterns for the two taxa, were combined with ENMs to identify high-priority areas for conservation of poorly known Amazonian species across their entire geographic range. Since recent studies are challenging the inherent capacity of ENMs to inform abundance patterns and other biological aspects of real populations (see Jiménez-Valverde et al., 2021; Lee-Yaw et al., 2021), the framework developed by this study, implicitly incorporating abundance proxies in ENMs, can be applied to a wide range of other species and with different approaches. For instance, using geospatial models as input or response variables to build ENMs and/or during modeling exercises, including setting up and interpreting results (e.g., Bahn and McGill, 2007).

The importance of interspecific competition for conservation prioritization

Biotic interactions are important theoretical mechanisms limiting species distributions across different spatial scales, but they are frequently absent from most ENMs (Anderson et al., 2002; Guisan and Thuiller, 2005; Godsoe and Harmon, 2012). This is especially true for interspecific competition, since this type of biotic interaction is often neglected in ENMs when considering broadscale patterns (but see Braz et al., 2020; Novella-Fernandez et al., 2021 for exceptions). There is substantial evidence and previous efforts showing that interspecific competition can scale up to broad spatial

Hotspots for conservation of gray woolly monkeys (*Lagotricha lagotricha cana*) and black-faced black spider monkeys (*Ateles chamek*) across their sympatric range.

scales, affecting and shaping species' geographic ranges and abundance variation (e.g., Gotelli et al., 2010; Braz et al., 2020; Novella-Fernandez et al., 2021; Braga et al., 2022). In agreement, we found evidence for our hypothesis of broadscale interspecific competition unraveling a pervasive pattern of spatial segregation across the geographic distribution of our two target taxa.

Interspecific competition has been previously suggested to affect the local-scale patterns of coexistence between *L. l. cana* and *A. chamek* (Iwanaga and Ferrari, 2001, 2002). Also, previous studies at broader scales have identified strong similarities in the environmental niche between these taxa (Cavalcante et al., 2020). Interestingly, we found that the abundances of the two taxa are negatively related, conditional on estimated habitat suitability (Figure 5), suggesting that interspecific competition between them constrains local abundance at different strengths in low, moderate and highly suitable areas. In addition to the ecological perspective, this pattern is extremely important from a conservation standpoint since using information based only on habitat suitability could mislead efforts and affect our ability to efficiently guide resource allocation toward areas likely to be strongholds for atelins populations. For example, a previously published ENM for *A. chamek* (Rabelo et al., 2018) predicted

that highly suitable areas would be present in the northeastern part of the species' distribution (see Figure 4). However, the gray woolly monkey's high density and suitability predicted by our abundance-informed ENM is liable to significantly affect spider monkey's populations in this region. The opposite is true for gray woolly monkeys at the southwestern part of its geographic distribution. This pattern of competitive exclusion at the broadscale clearly emerged when we binarized and summed our abundance-informed ENMs, indicating a clear distinction between the eastern and western parts of the areas of sympatry for these species.

The hottest hotspot

We identified priority areas for woolly and spider monkeys' conservation in our study region as those containing highly suitable habitats with high predicted densities for each taxon. Notably, we identified an interesting high-priority area that falls within the southwestern Brazilian Amazon between the Juruena and Guaporé rivers (see Figure 6). This area holds jointly suitable habitat and high predicted densities for both taxa, in addition to some key factors and biological criteria

(e.g., irreplaceability and vulnerability) that can be invoked for priority-setting purposes. First, it falls within the Rondônia center of endemism, an important component of Amazonian diversity given the high number of endemic species (Cracraft, 1985; Silva and Oren, 1996; Braga et al., 2022). Additionally, this region is located along the southern border of the Amazon rainforest in Brazil, within a region known as the arc of deforestation, where nearly half of the world's deforestation occurs (Gascon et al., 2001; da Silva et al., 2005; Michalski et al., 2008; Silva Junior et al., 2021).

Other major threats leading to deforestation and habitat loss in this region include fire (Brando et al., 2020; Feng et al., 2021), road construction (Fearnside, 2015), mega-dam construction (Cochrane et al., 2017), and mining (Rudke et al., 2020). Our two focal taxa are part of the largest-bodied highly frugivorous clade of primates within the Amazonian forests, have large area requirements, are particularly vulnerable to habitat loss, and play major roles in ecosystem functioning (Peres, 1994; Di Fiore and Campbell, 2007; Peres et al., 2016; Rabelo et al., 2018; Cavalcante et al., 2020; Sales et al., 2020). Therefore, the identification and conservation of this high-priority area can extend protection to a large number of naturally co-occurring forest-dwelling species, reducing the rate of overall biodiversity loss and helping to stem the biodiversity crisis in the Amazonian arc of deforestation.

Geospatial model limitations and conclusions

When comparing the interpolation techniques, we found that the resultant correlation coefficients of OK-abundances have stronger relationships with habitat suitability than IDW-abundances, which showed relatively low correlation coefficients (Table 1). Although these differences between both procedures were small, these results were expected because geostatistical methodologies (e.g., OK) are broadly considered better interpolators than simpler non-geostatistical methodologies, such as IDW (Li et al., 2011). Particularly, IDW tends to respond more strongly to discrepant values at individual data points, rather than the smoothness underlying the distance-based averaging approach in kriging methods.

Besides the interpolation techniques, the strength of the abundance-suitability relationships in our study case will also depend on distinctly factors that initially affect the ENMs and the geospatial models (e.g., the sampling distances and the density of samples in the training datasets; Li and Heap, 2008; Zarco-Perello and Simões, 2017). The sampling gaps across the taxon's geographic distributions and a mismatch between the ENMs and geospatial models' distribution of samples can be related to the small differences between the interpolation methods. In areas with such gaps, interpolation accuracy can significantly vary, being lower where data density is low. In

this sense, our abundance predictions for the western part of the distribution of both taxa should be carefully considered and validated *in situ* before and alongside any conservation or management action. For these reasons we are avoiding drawing strong conclusions from our geospatial abundance models alone (e.g., estimating species populations at a geographical range scale based on spatial predictions). However, when we combined the ecological niche and geospatial abundance models using the output from each model's predictions (i.e., habitat suitability, IDW-abundance, and OK-abundance), we are "feeding" the final models with suitability data. In other words, we are providing habitat requirements information for areas that have few or no abundance data, and these final models are the ones being used to draw the main conclusions of this study, making the case for abundance-informed ENMs as important tools for conservation purposes.

The ENMs and geospatial models exhibited similar sampling gaps across the Amazon basin. These shortfalls are intrinsically related to the lack of knowledge of species' geographic distribution and abundance in space and time, which are often scarce and inadequate at most scales (Hortal et al., 2015). Such shortfalls notably include the highly remote regions of the Amazon basin, such as the forests of southwest Amazonia (Bush and Lovejoy, 2007; Hopkins, 2007). We expect that more sophisticated interpolation methods, which are becoming increasingly available [e.g., Euclidean distance fields in machine-learning (EDM): Behrens et al., 2018; Random forest (RF): Hengl et al., 2018], could possibly be used to partially overcome these caveats by using covariates and machine-learning methods that can improve the accuracy of the maps and the strength of the abundance-suitability relationship. Future expeditions to those remote areas are also necessary to improve geospatial models and ENMs with new field-collected abundance and occurrence records, consequently affecting the correlation coefficients of these abundance-suitability relationships.

In conclusion, the framework developed in this study can be used as a surrogate to identify high-priority areas for conservation of poorly known species across their entire geographic distributions. This procedure integrates the relationship between general trends in abundance patterns and suitability information across broader spatial scales. We confirmed a significant positive relationship between woolly (*L. l. cana*) and spider (*A. chamek*) monkeys' habitat suitability with observed abundances and predicted abundances from geospatial abundance models. Most importantly, abundance-suitability correlations showed no significant differences when using original relative abundances against using IDW- and OK-abundances. We also found that the association between *L. l. cana* abundance and its habitat suitability depends on the abundance of its putative competitor species, *A. chamek*. Therefore, disregarding interspecific competition between our two focus taxa could affect our ability to accurately and efficiently guide resource allocation toward priority areas for

conservation actions for these two large arboreal mammals that inhabit the Amazonian arc of deforestation. Finally, fundamental spatial dependence and autocorrelation concepts and principles, which lies at the heart of spatial interpolation, are pervasive in natural ecosystems and biological aspects of real populations (Koenig, 1999; Dormann, 2007). This can be seen by the widespread use of interpolation methods in several environmental disciplines (Li and Heap, 2011, 2014). We argue that the use of interpolation methods should be extended for spatial conservation prioritization since its use has been considerably scarce in conservation biology, especially for Amazonian data-deficient species, such as the two we have studied.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical review and approval was not required for the animal study because the study is based on data gathered from the literature.

Author contributions

TC conceived the core ideas with important insights from MMW, gathered all data, and led the wrote of the manuscript. TC and MMW developed the overall research framework, designed the methodology, and performed all statistical analyses. All authors significantly contributed with interpretation, writing, and gave final approval for submission.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.915325/full#supplementary-material

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