



Niche overlap between two sympatric frugivorous Neotropical primates: improving ecological niche models using closely-related taxa

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Abstract

Ecological niche models (ENMs) are widely used tools for predicting species geographic distribution as a function of environmental variables. The inclusion of biotic factors in the predictor suite can significantly increase the predictive power of such models, leading to a model closer to the realized niche for the species under investigation. In this study, we provide evidence of niche overlap between gray woolly monkeys (*Lagothrix cana*) and black-faced black spider monkeys (*Ateles chamek*) based on locality and ecological data covering their complete geographic range in the Amazon forests of Brazil, Peru and Bolivia. We also estimate the potential distribution of *L. cana* using environmental predictors, and the distribution of *A. chamek* as a biotic factor. Finally, we quantified current and future habitat loss and areas under legal protection. We found that only 39% of the *L. cana* area of occupancy is under legal protection and that the species could potentially lose up to 58% of habitat in the next 30 years. We also show that the use of a closely-related species that has a more robust dataset can improve ENMs of poorly studied, rare and/or cryptic species. The framework developed here can be applied to a wide range of sympatric species if they share similar ecological requirements. Since our focal species are the most frugivorous primates in our study region and especially vulnerable to habitat loss, the identification of highly suitable areas for both taxa can help to protect other forest-dwelling species, reducing the rate of overall biodiversity loss.

Keywords *Ateles chamek* · Biotic interactions · *Lagothrix cana* · Potential geographic distribution · Predicted habitat loss

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Introduction

The distribution of species is always limited by their dispersal ability, as well as a myriad of environmental and biotic constraints (Soberón and Nakamura 2009). Ecological niche models (ENMs) are now widely used as tools to predict species potential geographic distributions based on environmental variables (Phillips et al. 2006). However, biotic interactions also play a significant role in limiting species distributions, although these factors are often neglected in ENMs (Guisan and Thuiller 2005; Godsoe and Harmon 2012). The inclusion of biotic variables within the suite of predictor variables can significantly increase the predictive power of such models (e.g., Anderson et al. 2002), and can potentially lead to a more accurate realized niche being modeled for a species (Guisan and Thuiller 2005).

Biotic variables such as competition and other biotic interactions between species (e.g., predation, mutualism) can affect species distributions in different ways. For example, closely-related species can exclude each other from areas of otherwise environmentally suitable habitat, creating parapatric distributions in which the ranges are contiguous to each other but do not significantly overlap (Coyne and Orr 2004). Likewise, as a result of ecological niche conservatism, the ecological characteristics of a genetically related, but geographically isolated species (i.e. one showing an allopatric distribution) can be used to predict the geographic distribution of a respective sister taxon (Peterson et al. 1999).

The gray woolly monkey (*Lagothrix cana*) is an arboreal diurnal Atelinae species that occurs in the Amazonian forests of Peru, Brazil and Bolivia (Fooden 1963; Iwanaga and Ferrari 2002), although its range limits are poorly known. The species is considered as Endangered by the International Union for Conservation of Nature (Boubli et al. 2008). The black-faced black spider monkey (*Ateles chamek*) is another member of the Atelinae subfamily that is also Endangered. It is sympatric with *L. cana* in most habitats throughout its range (Iwanaga and Ferrari 2002). Although *L. cana* and *A. chamek* are not sister species, they are closely-related phylogenetically, highly frugivorous and are the most large-bodied genera within the Amazonian forests (Di Fiore and Campbell 2007; Di Fiore et al. 2014; Iwanaga and Ferrari 2001). Indeed, spider and woolly monkeys shared a common ancestor approximately 10 mya (Di Fiore et al. 2014). As a result, it has been suggested that niche overlap and competition may play an important role in the ecology of these species (Iwanaga and Ferrari 2001, 2002).

The major ecosystem where the two occur in sympatry is the Amazonian rain forests that comprises one of the greatest repositories of tropical biodiversity on Earth (Fearnside 1999). It is, however, severely threatened by deforestation (Hansen et al. 2008; Nobre et al. 2016; Lovejoy and Nobre 2018). Both primate species in this study are threatened principally by hunting and habitat loss, being especially vulnerable to fragmentation (Peres 1990, 1991). The extinction of such large atelins can affect forest structure (Stevenson and Aldana 2008), causing a cascade effect due to their role as seed dispersers (Peres and van Roosmalen 2002). This alarming situation requires the rapid deployment of practical methods to predict species distributions and quantify habitat loss. In this context, ENMs have been used in conservation planning and to advise decision makers on the creation of new biodiversity protection zones (Rabelo et al. 2018; Boubli et al. 2019). However, to the best of our knowledge, no study has attempted to quantify the similarity between the environmental requirements of the two primate species under study at large spatial scales, nor attempt to understand how the ecological requirements (or ecological niche) of one of these species might affect the geographic distribution of the other. The presence of these

primates in protection zones and fragmented landscapes can help protect other forest-dwelling species, so reducing the rate of overall biodiversity loss in the Amazonian forests.

Here, we quantify the similarity in environmental requirements for the two species of Atelinae, the gray woolly monkey (*L. cana*) and the black-faced black spider monkey (*A. chamek*). We estimate the potential distribution of *L. cana* as a function of environmental variables and the distribution of its putative competitor species, *A. chamek*. We then estimate the overlap between highly suitable areas for both species. Finally, we describe the conservation status of the areas with highest habitat suitability for *L. cana* by quantifying the current and future habitat loss, and areas under legal protection.

Previous studies have suggested that niche overlap and competition may have some important influence in the ecology of these sympatric species (Iwanaga and Ferrari 2001, 2002). Their close relatedness, specialization on fruits, and similarities in feeding ecology makes them a robust and useful primate-based model for testing hypothesis related to niche overlap. Thus, we hypothesize that, due to ecological niche conservatism, niche overlap and ecological similarity between these species would be expected (Peterson et al. 1999; Iwanaga and Ferrari 2001, 2002; Losos 2008). Therefore, we predict a high degree of ecological niche overlap and no significant differences in the fundamental niche between these two species. In this sense, the habitat suitability model for *A. chamek* should positively influence the habitat suitability for *L. cana*, due to the high similarity in ecological requirements between these species.

Methods

Study area and data compilation

The study area covered the complete geographic distribution of the two target species, which comprises three countries (Brazil, Peru and Bolivia), although most of the range of the species lies within the Amazon forests of Brazil (2° S, 55° W and 15° S, 75° W). Both species range south of the Amazonas and Solimões rivers. The current southern limit of *L. cana* known distribution is the Guaporé River valley between the Brazilian states of Rondônia and Mato Grosso, but *A. chamek* has a broader distribution that extends further south, north and west of the Solimões and Japurá River. While the Amazon rainforest is the major occupied ecosystem, the study region also encompasses the Cerrado and Pantanal biomes, including the ecotonal zone between the three types of biome in Brazil.

The database for *L. cana* occurrence was compiled by gathering information from field data collected for the current study, plus unpublished records and gray literature, as well as peer-reviewed scientific literature and online datasets [such as the Global Biodiversity Information Facility—GBIF (www.gbif.org); SpeciesLink (spling.cria.org.br); and Macaulay Library at the Cornell Lab of Ornithology (www.macaulaylibrary.org)]. Of the records obtained, we excluded those older than 1990, to avoid either uncertain species identification, inaccurate geographic location or localities in areas now deforested (Online Resource 1 Table S1). We randomly removed duplicate records within two classes of distance (5- and 10-km) in order to control for the sampling bias from highly sampled areas (Renner et al. 2015). We obtained a total of 77 occurrence records for *L. cana*, of which 69 and 64 were retained within 5- and 10-km buffering area, respectively (Online Resource 1 Table S1).

We plotted all records into a GIS environment and created a polygon layer that included all accepted records. We drew the boundaries for this polygon by following large rivers,

comprising the interfluvial regions that included species' records (see Online Resource 3 Fig. S2). As the ranges of Amazonian primates are usually limited by large rivers (Ayres and Clutton-Brock 1992; Boubli et al. 2015), this polygon was defined as the species' extent of occurrence. We also obtained 172 occurrence records of the black-faced black spider monkey (*A. chamek*), and the polygon of its extent of occurrence, as given in Rabelo et al. (2018).

We used 49 freely available, spatially explicit environmental variables that could reasonably be expected to influence a primate species distribution (Online Resource 1 Table S2). These variables consisted of climatic (19), topographic (4), edaphic (20), and vegetation (6) layers at 5-km resolution. We chose this resolution because *Lagothrix* spp. are known to have long daily travel distances (up to 3,582 m; Di Fiore and Campbell 2007), and estimated home ranges that can reach up to 1,021 ha in *L. cana* groups (Peres 1996), thus, matching the spatial resolution with the biology and ecology of the species. Also, our study scale is in accordance with the scale considered by decision makers when developing most environmental conservation policies, i.e., the landscape scale (Monjeau 2010).

We also included a layer concerning *A. chamek* habitat suitability (Rabelo et al. 2018), to evaluate its effect as a potential predictor of *L. cana* distribution. We created a ~ 55-km buffer of the convex hull of all *L. cana* records and used this polygon to crop the stack of all predictor layers. We then removed all highly correlated variables ($r > 0.7$) to avoid collinearity effects. After running preliminary models, we also removed predictor variables that were negatively dropping the model training gain and reducing model performance. We used a final set of twelve environmental layers to model *L. cana* potential geographic distribution (Online Resource 1 Table S3).

Niche overlap

We extracted the values of all environmental variables at *L. cana* and *A. chamek* occurrence locations, using all 77 *L. cana* and 172 *A. chamek* records. These values represent the range of environmental requirements for both species. We then built a matrix with all records of both species on the rows and their respective values of environmental variables in columns, with column values centered and scaled to the same range of variation (mean = 0, standard deviation [SD] = 1, Legendre and Legendre 2012). We then used a principal coordinate analysis (PCoA), based on the Euclidean dissimilarity index, to condense the environmental requirements of each species into a smaller number of axes. Since principal component analyses are computed from the eigenvectors using a matrix of covariance or correlation (Legendre and Legendre 2012), we retained all environmental variables for this analysis. Scores from the first two axes derived from this ordination were used to represent the environmental niche of the species in a bi-dimensional space. We used a permutational multivariate analysis of variance (PERMANOVA) to evaluate whether the environmental requirements (or environmental niche) differed between the two species.

Species distribution modelling and threats assessment

We used the maximum entropy algorithm in MAXENT 3.3.3, to map habitat suitability for *L. cana* and estimate its potential distribution (following Phillips and Dudík 2008). This algorithm seeks non-random relationships between species occurrences and environmental

variables, building a model that can be used to estimate a potential species distribution according to the most relevant variables. We chose this algorithm because MaxEnt has consistently demonstrated modelling accuracy with limited datasets (e.g. < 25 localities, Thorn et al. 2009).

We used 5,000 random background records and divided the occurrence data into training and testing (30% for training and 70% for testing), using a cross-validation technique to validate the model (Phillips et al. 2006). We performed an AIC model selection procedure to evaluate the best buffer scale for occurrence record filtering (i.e., 0-, 5- or 10-km radius), and the inclusion of the layer representing the *A. chamek* distribution among the predictor variables. Since records can also be biased by spatial clustering in better-surveyed areas (Oliveira et al. 2016), and because these are generally influenced by ease of access, we also included the distance to rivers and roads as a layer of bias control, which would indicate the habitat suitability for the species independent of such proximity (Warton et al. 2013). We then used the ENMevaluate function from ENMeval R package (Muscarella et al. 2014) to evaluate and choose the best model parametrization (features and regularization multiplier), according to the AIC (see Online Resource 2 for further details).

After having built the model, we chose a threshold of habitat suitability above which we considered that the species is likely to be present. We achieved this by finding the threshold in the receiver operating characteristic (ROC) curve that has maximum sensitivity (i.e., the proportion of observed presences that are predicted as such) and specificity (i.e., the proportion of correctly predicted absences). We then evaluated model accuracy with the true skill statistic (TSS), an effective and well-accepted measure of accuracy for binary predictions (Allouche et al. 2006). TSS is obtained from sensitivity and specificity ($TSS = \text{Sensitivity} + \text{Specificity} - 1$). It ranges from -1 to $+1$ and values close to $+1$ indicate accurate predictions, whereas values $\leq$ zero are no better than random predictions.

To assess the overlap between highly suitable areas for both species, we extracted the values of predicted habitat suitability for each species from 5000 random points across the area of overlap within the species' extents of occurrence. We then used these values to perform a Pearson's correlation. Finally, we mapped the combined habitat suitability to identify highly suitable areas for both species.

To quantify the areas under legal protection, the area of occupancy estimated by our final model was projected on the protected areas and indigenous land maps published by Juffe-Bignoli et al. (2015). We then calculated the extent of areas currently covered by protected areas and indigenous lands within *L. cana* area of occupancy. We calculated habitat loss by the same procedure using the current and future forest cover layers modelled by Soares-Filho et al. (2006). Forest cover projections across the Amazon basin were modelled by these authors under two different scenarios. At one end is the "Business-as-Usual" (BAU) scenario, which essentially considers current deforestation trends, plus the combined effects of low effectiveness of legislation on private land, infrastructure development, and no implementation of new protected areas. At the other end, the "Governance" (GOV) scenario assumes an improved level of environmental laws enforcement across the Amazon basin, imposing that no more than 50% of forest in private land can be deforested, and ensuring the expansion of the protected areas network. Using these projections, we calculated how much of the available habitat for *L. cana* was lost up until 2002, and how much would be lost by 2050 under each scenario. We used the R 3.3.3 software (R Core Team 2018) for all data processing and modelling.

Results

The representation of the ecological niche of the gray woolly monkey (*L. cana*) and the black-faced black spider monkey (*A. chamek*) using the two first PCoA axes based on 49 environmental variables shows a high degree of niche overlap between the two species (Fig. 1). Also, in accordance with our hypothesis, we did not observe significant difference between the environmental niche of *L. cana* and *A. chamek* (PERMANOVA, $F = 10.9$, $P = 0.44$), showing that the two species share very similar environmental niche requirements.

The model that most likely explained the distribution of *L. cana* was the one including the environmental variables and the habitat suitability layer for *A. chamek* among the predictor variables (Table 1). The selected filtering distance was 10-km, resulting in the use of 64 occurrence records. Chosen model parametrization indicated by the ENMevaluate function was based on linear, quadratic and hinge features, and a regularization multiplier of 1.5, which generates a more restricted/conservative prediction (see Online Resource 2 for further details). Model averaged TSS score was 0.53 ± 0.01 (mean $\pm$ SD). Habitat suitability and predicted species distribution are shown in Fig. 2.

The maximum sensitivity–specificity mean threshold was 33%, above which we considered the species to be present. According to our model, the species can potentially occupy an area of 412,250 km², which constitutes only 23% of its extent of occurrence (1,791,200 km²). The species is more likely to occupy the south-eastern, south-western and northern regions of its range, areas we estimated as having higher habitat suitability (Fig. 2).

The most important variables in the model were mean annual temperature, temperature seasonality, occurrence of arenosols, and the distribution of *A. chamek*, which jointly contributed 70% to model gain in all iterations (32%, 17%, 12% and 9%, respectively;

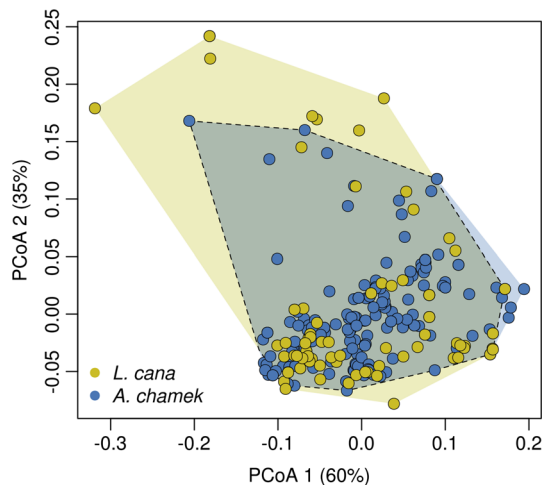


Fig. 1 Environmental niche overlap between *L. cana* and *A. chamek*. The graph shows the bi-dimensional space of environmental conditions used by woolly and spider monkeys at the occurrence locations (points), which was accessed by a principal coordinate analysis (PCoA). Fawn and blue polygons represent the environmental volume occupied by woolly and spider monkeys, respectively. Dashed lines highlight the overlap between the species niches. The observed overlap area was not different from the expected overlap area over a null distribution (see main text for statistical results)

Table 1 Ranking of *L. cana* candidate models according to AIC selection procedure

Model	#par	AICc	Δ AICc	AICw
Buffer 10-km (with <i>A. chamek</i>)	11	1400.15	0	0.82
Buffer 10-km (without <i>A. chamek</i>)	10	1403.15	3.00	0.18
Buffer 5-km (with <i>A. chamek</i>)	11	1506.32	106.17	0.00
Buffer 5-km (without <i>A. chamek</i>)	10	1510.65	110.50	0.00
Buffer 0-km (with <i>A. chamek</i>)	12	1680.02	279.87	0.00
Buffer 0-km (without <i>A. chamek</i>)	10	1681.26	281.11	0.00

We built candidate models considering: three buffer distances (0-, 5- and 10-km), within which we filtered duplicate records in order to control for the effect of spatial intensity of points; and with or without the inclusion of *A. chamek* distribution among the predictor variables. In all models, *L. cana* occurrences (with different spatial scales of filtering) are the response variable as a function of combinations of environmental variables with or without *A. chamek* distribution

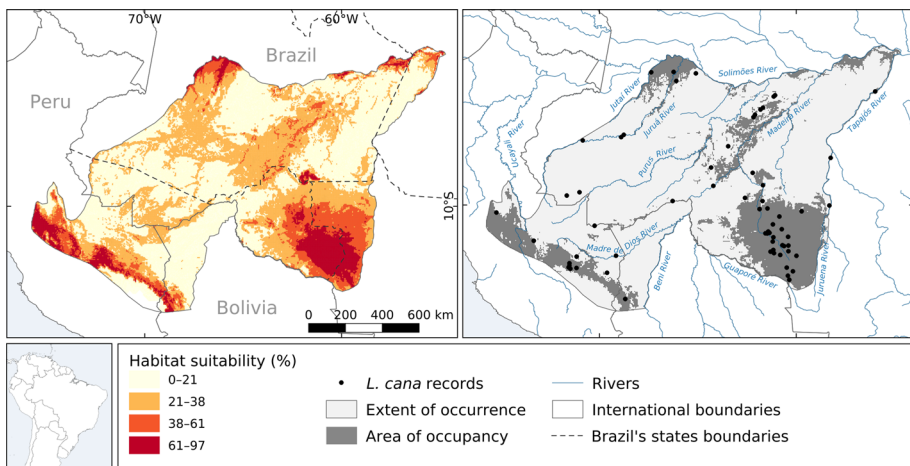


Fig. 2 Habitat suitability and predicted distribution for *L. cana* in Amazonia. The darker the red, the higher the habitat suitability for the species within its extent of occurrence (map left). The predicted species' area of occupancy (i.e., areas with habitat suitability > 33%) is shown on the right hand map. The species' area of occupancy (dark gray areas) correspond to 23% of its extent of occurrence

Online Resource 1 Table S3 and Fig. S1). According to the model, higher annual temperature and temperature variation were associated with lower habitat suitability for the species. On the other hand, the higher the percentage of arenosols and habitat suitability for *A. chamek*, the higher the habitat suitability for *L. cana*.

We found a positive correlation between habitat suitability for *L. cana* and *A. chamek* ($R = 0.27$, $p < 0.01$; Fig. 3), which implies some level of spatial overlap in the suitable habitat for both species. The combined habitat suitability for both species allowed us to identify the areas with a high habitat suitability for both species (Fig. 3).

We found that only 39% (159,250 km²) of the species area of occupancy is within protected areas (81,400 km² – 20%) and indigenous lands (77,850 km² – 19%). Based on deforestation estimates, the species had already lost 23% of its highly suitable habitat by 2002 (Table 2), with most of the forest loss occurred in the Rondônia State, in southern

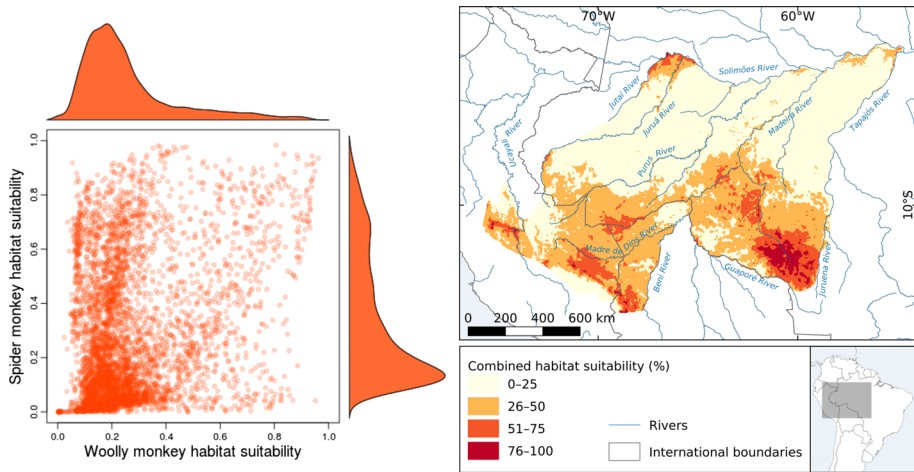


Fig. 3 Geographical niche overlap between *L. cana* and *A. chamek*. Correlation between the spatial habitat suitability for both species (graph, left) with 5000 randomly chosen points across the area of overlap within the species' extents of occurrence. The distribution curves of habitat suitability for both species are shown in the graph margins. The combined habitat suitability for both species is shown in the right hand map. The darker the red, the higher the habitat suitability for both species

Amazonian Brazil (Fig. 4). In the coming decades, the species is expected to lose up to 58% of the forest cover available in 2002 (Table 2; Fig. 4).

Discussion

In this study, we set out to test hypotheses regarding niche overlap between *L. cana* and *A. chamek*, and whether species with more robust datasets can improve ENMs of poorly studied, rare and/or cryptic species, when they share similar ecological requirements. We found a high similarity in the environmental niche of the two species at the broader scale (i.e. encompassing the species' complete geographic distributions). Preliminary evidence also suggests that there might be considerable niche overlap at the local scale when the two species occur in sympatry (Iwanaga and Ferrari 2001). While niche overlap in primates is usually evaluated at small scales, investigations at broader or combined spatial resolutions can help to infer the processes that have shaped species distributions (Cardillo and Warren 2016). Our results suggest that the high similarity between these species niches is

Table 2 Current and future forest cover within the species estimated area of occupancy (AOO), based on two future scenarios of deforestation (governance, business as usual) in the Amazon basin (Soares-Filho et al. 2006)

Forest cover	2002 area, km ² (%)	2050 area, km ² (%)	
		(Governance)	(Business as usual)
Available forest	340,959	340,959	340,959
Forest loss	79,465 (23)	132,922 (39)	196,255 (58)
Remaining forest	261,494 (77)	208,037 (61)	144,704 (42)

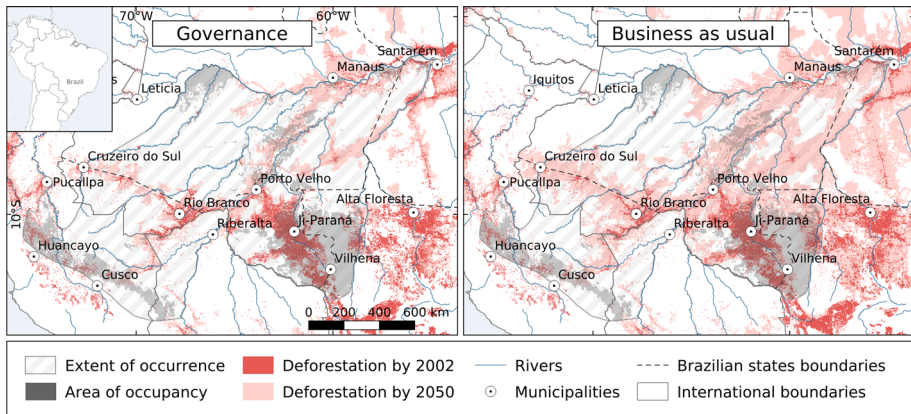


Fig. 4 Current and future habitat loss within *L. cana* predicted distribution in Amazonia. Maps show the accumulated forest loss until 2002 and the predicted forest loss by 2050 according to the ‘Governance’ (map, left) and ‘Business as usual’ (map, right) scenarios. Deforestation scenarios data from Soares-Filho et al. (2006)

compatible with the conservatism of ecological niches and phylogenetic signal across moderate time scales (Peterson et al. 1999; Losos 2008), since spider monkeys diverged from the remaining atelins about 10.6 mya (Di Fiore et al. 2014). Additionally, although the distribution of *L. cana* is entirely embedded within the range of *A. chamek*, sympatry of these species is not syntopic across the entire range, as considerable areas of allopatry also occur (Iwanaga and Ferrari 2002). Therefore, a complex combination of ecological forces (e.g., regional and local variation in the degree of interspecific competition), together with historical biogeographical process (e.g., dispersal factors), and local hunting pressure may have shaped the current distributions of these species.

Our analysis produced a clear potential distribution area with predicted habitat suitability for *L. cana*. Mean annual temperature, temperature seasonality, arenosols and the distribution of *A. chamek* were the most important variables within the model. Patterns of temperature are widely used as a surrogate for net primary productivity (Schloss et al. 1999), while seasonal fluctuations associated with soil moisture cycles are known to affect fruit, flower and leaf phenology in tropical rain forests (van Schaik et al. 1993). Changing patterns in these variables could have significant influence on temporal reliability and productivity of resources (e.g., Schloss et al. 1999), which is of paramount importance for both woolly and spider monkeys, two of the most frugivorous primate genera of the Neotropics (Chapman and Chapman 1990; Di Fiore et al. 2008; Hawes and Peres 2014; Gonzalez et al. 2016). Therefore, we can expect that climate variables can indirectly influence primate species distribution through direct effects on plant phenology and distribution (Stevenson 2014). Additionally, Amazonian endemic species such as *L. cana*, is likely to be tightly linked to climatic, hydrological and/or soil conditions (Sombroek 2000), restricting its occurrence to specific areas within the Amazon biome, where such species should have a relative advantage in competition with, and ecological adaptations over, other species.

Both *L. cana* and *A. chamek* are already facing the threat of extinction due to such human activities as deforestation and hunting (Boubli et al. 2008; Peres 1990). Additionally, they are also exposed to projected future temperature changes that could reach 1.5 °C greater than global average warming rates (Graham et al. 2016). Precipitation is

also predicted to vary dramatically across these primate ranges and may reach more than 7.5% increases or decreases per °C of global mean warming (Graham et al. 2016). Therefore, in the future deforestation scenarios predicted here, these species will be at risk of being also dangerously impacted by climate changes. The other threat that was also predicted to increase is that of wildfires which, under the same BAU scenario used in this study for 2050 predictions, are expected to be exacerbated by extreme weather events and land use in southern Amazonia in the coming decades (Brando et al. 2020).

Ateles chamek habitat suitability was among the most important predictors positively affecting *L. cana* distribution and habitat suitability. Biotic interactions are an important theoretical mechanism, but one that is frequently absent from most ENMs, even though it can potentially lead to a more accurate estimation of the realized niche for the species being modeled (e.g., Anderson et al. 2002). Our study clearly demonstrates this improvement in model performance, as inclusion of *A. chamek* distribution enhanced model's goodness-of-fit (Table 1; see Guisan and Thuiller 2005 for discussion). In addition to being applied to primates, this approach provides a bottom-line for optimizing conservation planning of poorly studied, rare and/or cryptic species. Ecologically equivalent taxa with robust datasets can be used as a tool to predict species distribution and determining conservation status of less studied endangered species due to the urgency of conservation planning (Shekelle and Salim 2009).

Regarding the conservation status of *L. cana*, we found that only 39% of its area of occupancy occurred within indigenous lands and protected areas. Both these protected area categories are of paramount importance for ensuring in situ protection of wildlife and preventing deforestation (Nepstad et al. 2006). The parsimonious scenario ("Governance", Soares-Filho et al. 2006) predicts a loss of more than one third (39%) of the species area of occupancy (most included in Brazil's territory) in the next five decades. However, although Brazil's Forest Code has brought some optimistic possibilities to deforestation reduction in Amazonia, controversial revisions were made in 2012 (Soares-Filho et al. 2014), which may reduce its effectiveness. These included, for example, reducing the protection of sensitive areas and amnesty for illegal deforestation (Brançalion et al. 2016). Also, environmental legislation is under threat of being rolled back with the cloudy future of the political instability in Brazil. Recently, a Provisional Measure was passed on January 1st (PM N° 870, 2019), transferring the responsibility of identifying, delimiting and demarcating indigenous lands from the National Indigenous Foundation (Fundação Nacional do Índio—FUNAI) to the Ministry of Agriculture, an organ of executive power widely known to be heavily influenced by the Brazilian agribusiness lobby. Another Law Project (PL No 1551, 2019) proposes to revoke Chapter IV of Da Área de Reserva Legal, Law Number 12.651, of May 25, 2012, which in its Article 12 says that "All rural properties must maintain an area of native vegetation cover, as a Legal Reserve", observing minimum percentages stipulated based on the property size and vegetation type. Therefore, the BAU scenario seems to be more realistic for the near future, this being one in which the gray woolly monkey will lose more than half (58%) of its forest habitat available in 2002 over the next 30 years.

A wide area with high habitat suitability for *L. cana* and *A. chamek* falls within the southwestern Brazilian Amazon, in a region that has been called the "arc of deforestation". Habitat loss and ongoing deforestation within this region are the main threats, which is an important area of endemism for a wide variety of taxa (Gascon et al. 2001; da Silva et al. 2005; Michalski et al. 2008). Although both analysed ateline primates are highly susceptible to habitat fragmentation and hunting (Robinson and Redford 1986; Peres 1990), they are relatively abundant in this region's forests (Iwanaga and Ferrari 2002), even in

relatively small fragments (Iwanaga and Ferrari 2001; Cavalcante et al. 2018). This reinforces the conclusion that hunting pressure on these populations is currently low and that privately-owned forests have great potential to contribute to in situ conservation strategies for these species (Peres 1990; Iwanaga and Ferrari 2001, 2002; Cavalcante et al. 2018). Therefore, these regions should be a priority area for the implementation of new protected areas and corridors for both species, as has been repeatedly proposed (Iwanaga and Ferrari 2001, 2002; Cavalcante et al. 2018; Rabelo et al. 2018). Also, an improvement in the regulation of land-use in private properties should be put into practice for conservation purposes, since approximately 53% of Brazil's native vegetation exists on private land (Soares-Filho et al. 2014).

Our model represents the first attempt to estimate the geographic distribution of *L. cana* across its complete range using ENM with the largest representative sample published to date. We have shown that the species has lost a significant portion of its highly suitable habitat, and it is expected to lose much more in the next three decades, especially because most of the species area of occupancy is unprotected. The results of our study can help to direct conservation efforts by providing valuable information for the conservation of the gray woolly monkey, as required by the Brazilian National Action Plans (Jerusalinsky et al. 2011). We also found strong evidence of ecological niche overlap between sympatric *L. cana* and *A. chamek*, and show the importance of using a closely-related species with more robust datasets to improve ENMs of poorly studied, rare and/or cryptic species. The multi-species framework developed here can be applied to a wide range of sympatric species if they have similar ecological requirements. Our two focus species are the most frugivorous primate species in our study region, and particularly vulnerable to habitat loss. Therefore, the identification of highly suitable areas for both taxa can help to protect other forest-dwelling species, so reducing the rate of overall biodiversity loss; a model applicable to other communities similarly threatened.

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Author contributions Contributions to the early planning of the study were made by TC, ACG and DF. TC, ASJ and RMR developed the overall research framework and designed the methodology. TC, MRZ, JV, DF, ACG, ODS, LF provided new species occurrence data. All data was gathered by TC, ASJ and RMR. RMR performed all the statistical models and data analyses. TC, ASJ, RMR and AAB led the writing of the manuscript. All authors gave final revision and approval for publication and are accountable for all aspects of the work.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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