Assessing mammal pollinators in the Eastern Amazon and the effects of climate change on endangered species

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Abstract

Although the importance of insects in pollination is well recognized, the role of vertebrates in this important ecosystem function remains to be addressed. The need to understand this role is especially urgent due to the risks posed by climate change, which threatens populations of native species and affects their interactions and the ecosystem services they provide. Our study aimed to define a novel list of criteria to analyse the role of Amazonian mammal species as pollinators and apply these criteria to all species present in the study area. We also predicted the effects of climate change on endangered mammal species that can act as pollinators. We defined 19 criteria to evaluate whether a mammal species can be considered an effective or potential pollinator and applied these criteria to a list of mammal species present in our study area. Sixty of the 281 species were classified as effective or potential pollinators according to our criteria. Three species were classified as under some degree of threat according to current red lists, with a fourth species being taxonomically divided and revalidated. Among the four threatened species selected for species distribution modelling, one species, *Saguinus niger* (É. Geoffroy), was unlikely to find climatically suitable habitats in the future scenarios analysed, suggesting the need to plan actions for conservation. Knowledge about the role of species in nature is important for designing conservation programs and making decisions aimed at protecting biodiversity.

Keywords

Pollination; mammals; vertebrates; endangered species; ecosystem services; climate change

Introduction

Pollination is one of the most important examples of mutualistic ecological interactions and is characterized by the transfer of pollen grains between flowers (Wilmer, 2011). This process is part of the sexual reproduction of angiosperms (Olerton et al., 2011) and consists of an important ecosystem service, as it generates direct and indirect benefits to humans, particularly in terms of food production (Potts et al., 2010; 2016). Different groups of animals are responsible for pollination, especially insects (Michener, 1962; Roubik, 1989), birds (Feinsinger, 1976; Stiles, 1981) and mammals (Sazima and

Sazima, 1977; 1978; Kunz et al., 2011). These species play a key role in maintaining biodiversity and floristic composition (Potts et al., 2016). Among invertebrates, the most common pollinating insects in tropical forests are wild bees (Heithaus, 1975; Roubik, 1989; Bawa, 1990), which depend on flowers for trophic resources (Michener, 2000). However, the role of vertebrates in pollination remains to be explored.

Identifying pollinators is a complex task, as floral visitors can benefit from resources without pollinating the flower. However, specific visitors can be defined as pollinators through direct observations or floral reproductive biology experiments (Inouye, 1980; Irwin et al., 2010). Characteristics such as body size and dispersion capacity point to certain mammal species as potential important pollinators (Fleming et al. 2009). Mammals can connect habitats due to their movement in the environment (Sekercioglu, 2006), also contributing to the important function of increasing genetic diversity. As static organisms, plants cannot move to find mates and instead rely on external vectors (pollinators) to reproduce and to avoid the loss of genetic diversity (Kunz and Fenton, 2005; Ollerton, 2017). Vertebrates are highly mobile pollinators that transport pollen across wider landscapes and promote outcrossing between genetically diverse individuals (Wessinger, 2021). Therefore mammals, including certain species of primates, rodents, marsupials and carnivores, can potentially perform pollination (Silvius and Fragoso, 2003; Buzato et al., 2012; Bizri et al., 2018), with bats being one of the most cited groups (Kunz et al., 2011).

Tropical forests are highly dependent on biotic pollinators (Bawa, 1990; Degen and Roubik, 2004; Ollerton et al., 2011). Previous studies have indicated that pollination by mammals can be more efficient than pollination by insects, especially in tropical environments (Sharma and Shivanna, 2011). Although tropical forests commonly harbour high richness of mammal species (Eisenberg and Thorington, 1973; Emmons, 1984; Janson and Emmons, 1990; Connor et al., 2018), little is known about their role as pollinators. This information is urgently needed since many species are threatened, and knowledge about the real consequences of the decline of their populations is scarce (Ratto et al., 2018).

The eastern Amazon, with its long history of deforestation, is particularly vulnerable to climate change (Flores et al., 2024). Climate change threatens native species populations, affecting not only their occurrence and geographic distribution but also their interactions (Valiente-Banuet et al., 2015). The reorganization of interaction forces between species, such as plant-pollinators, can have deleterious consequences for the functioning of ecosystems due to the drastic effects generated on species diversity (Paine, 1966; Terborgh et al., 2001; Romero et al., 2018). Climate change can also influence the behaviour of interacting species, such as their ability to disperse and pollinate (Kearns et al. 1998; Thomas, et al. 2004). Previous works addressing native species of the Amazon have predicted the effects of climate change on several taxonomic groups, such as flora (Gomes et al., 2019; 2020; Giannini et al., 2021), bees (Giannini et al., 2020), birds (Miranda et al., 2019), bats (Costa et al., 2018), amphibians (Silva et al., 2018), lizards (Teixeira et al., 2022), primates (Sales et al., 2020; Silva et al., 2022) and other groups of mammals (Ribeiro et al., 2018; Oliveira et al., 2023). In general, Amazonian mammals represent a group that may be significantly affected by climate change (Oliveira and Mendes-Oliveira, 2024), resulting in alterations in their migration patterns and consequently the availability of food resources.

Our study aimed to define a list of criteria to analyse the role of Amazonian mammal species as pollinators and apply these criteria to all species present in the study area. We also predicted the effects of climate change on endangered mammal species that can act as pollinators in the study area. This research may contribute to increasing awareness of the contribution of Amazonian mammal species to pollination, an essential ecosystem function, and direct efforts towards conservation strategies for endangered species facing climate change.

Methods

Study area

The study area is located in the eastern part of the Amazon biome (Figure 1). The eastern Amazon has historically been threatened by deforestation (Fearnside, 2005; Malhi et al., 2008; Nobre et al., 2016), which has caused this region to receive special attention for conservation. The study area considers the main rivers as biogeographic barriers (following Miranda et al. 2019). The study area is delimited by the right banks of the Tapajós and Juruena rivers to the west, by the marginal limits of the Amazon Biome and the Cerrado Biome to the east and south, and by the Atlantic Ocean coastline to the north.

List of species and criteria for determining pollinators

To compile the list of species, four data sources were consulted, as follows: [1] The Information System on Brazilian Biodiversity (SiBBr, 2021), whose platform integrates data on biodiversity and ecosystems from different sources. Specifically, to proceed with this query, we imported the shapefile of the study area into the platform to extract the list of mammal species with confirmed occurrences in the area. [2] The International Union for Conservation of Nature (IUCN) platform, from which we retrieved the available polygons (in shapefile format) of the extent of known occupation of each species from the "Terrestrial Mammals" database (Mammals found only in terrestrial habitats), available at https://www.iucnredlist.org/resources/spatial-data-download (IUCN, 2021). The polygons were subsequently cropped according to the study area, and a list of flying and nonflying mammal species was extracted from the vector data. [3] Two published studies (Martins et al., 2012; Costa et al., 2018); these studies were consulted to establish a list of species present in the Carajás National Forest, which is one of the largest continuous forest fragments in eastern Pará state and is home to a great diversity of fauna and flora. [4] An unpublished internal database (ACMO) developed through fieldwork, which includes data specific and relevant to the objective of this study. This final source eliminated some of the uncertainties associated with secondary data.

We followed the Taxonomic nomenclature of the Taxonomy Committee of the Brazilian Society of Mastozoology (SBMz) (Abreu et al., 2022) and the Brazilian Bat List Committee (CLMB/SBEQ) (Garbino et al., 2022). In the absence of information in both lists, we used the nomenclature described by Quintela et al. (2020) and/or available in the Global Biodiversity Information System database (GBIF, 2022). Data on the body size and natural history of species, such as their feeding habits, endemism and distribution within biomes, were obtained from Paglia et al. (2012).

Relying on previous studies, we classified mammalian species according to their potential role as pollinators on the basis of several criteria associated with the diet, morphology and behaviour of the species inside flowers (Buzato et al., 2012; Gribel, 1988; Prance, 1980; Janson et al. 1981; Regan et al., 2015; Costa et al., 2018; Bernard, 2001; González-Gutiérrez et al., 2022; Kalko, et al. 1996; Martins and Gribel, 2007; Datzmann et al., 2010; Kalko and Handley, Jr, 2001; Vieira and Carvalho-Okano, 1996; Simmons and Voss, 1998; Fleming et al., 2009; Sazima and Sazima, 1978; Freeman, 1994; Vieira et al., 1991; Kasso and Balakrishnan, 2013; Voigt, 2004; Datzmann, et al., 2010). The criteria were then categorized into five different classes as follows: (A) morphology or specialized behaviour; (B) contact with floral reproductive organs; (C) floral visitor and/or potential pollinator; (D) carrier of pollen; and (E) specialized in nectar exploration (details are provided in Table 1). Importantly, species whose behaviour was described as pillage or robber were not considered in this study since they can act as resource thieves, sometimes damaging the floral parts, without direct benefits related to pollination (Inouye, 1980; Irwin et al., 2010).

Endangered species

For the application of species distribution modelling (see below), we selected endangered species from the list of species with an effective or potential pollinating role. The species were selected according to the Official List of Species of the Brazilian Fauna Threatened with Extinction (MMA Nº 148/2022) and the Red List of Threatened Species (IUCN, 2022-2). In light of the revision of the taxonomical group of *Saguinus niger* and the revalidation of the species *Saguinus ursula* (Gregorin and De Vivo, 2013), we included both species in the analyses, although the latter remains under evaluation for its threatened status. We chose to model only the threatened species because there is growing recognition that the interplay between the effects of climate change and other threats may be extremely detrimental to species under threat (Brook et al. 2008), with tropical species being particularly vulnerable (Laurance and Useche 2009). Threatened species may be more susceptible to climate change for numerous reasons. For example, in Australia, almost half of threatened species are considered vulnerable to climate change, particularly those mammals also threatened by fire, drought, proximity to geographic barriers and/or low genetic diversity (Lee et al. 2015).

Occurrence Data

We retrieved the occurrence data of threatened species with potential pollinator roles from the Global Biodiversity Information Facility (GBIF) repository (https://www.gbif.org/occurrence). To adjust the scope of the data search to our objective, we applied three filters on the retrieved occurrence records. First, we used “Mammalia”, so that only records of species of this class were listed (DOI: https://doi.org/10.15468/dl.4kq7kc); then, only the records related to the species of interest were filtered. Second, we selected the “including coordinates” checkbox to obtain only data containing valid geographic coordinates. Third, we restricted the records listing to “North America” and “South America” to reduce the total number of records listed to those occurring exclusively in our area of interest. Species occurrence data were also retrieved from the SpeciesLink virtual repository, which is available at https://specieslink.net/search/. Two main filters were applied to survey the occurrence records; first, “Mammalia”, which was then filtered to retain only the records related to the species to be analysed, and second, “Countries of South America”. One of the authors (ACMO) also provided occurrence data for the target species from fieldwork records. After consolidating the different databases, we manually inspected the data and removed any questionable or clearly inaccurate records (e.g., over water bodies and divergently located records from the majority for each species) and records for species whose presence has not been confirmed in the scientific literature.

Species distribution modelling (SDM)

We used climate variables obtained from the WorldClim database (Fick and Hijmans, 2017), with a resolution of 2.5 minutes of arc (approximately 5x5 km cells) (Table S1). The values of such variables include means, extremes and combinations of temperature and precipitation for the period of 1970-2000 (Fick and Hijmans, 2017). For the same variables, projections were obtained for future scenarios comprising the period 2041-2060. Future bioclimatic variables were obtained from two CMIP6 global circulation models (GCMs), HadGEM3-GC31-LL and MIROC6; both GCM datasets are available from WorldClim. These methods were chosen because they showed good performance for tropical regions (unpublished data). The two shared socioeconomic pathways (SSPs) used were SSP2-4.5, which is considered a moderate scenario, and SSP5-8.5, which is a pessimistic scenario (IPCC, 2022). The set of variables was previously analysed for the risk of multicollinearity using the vifcor function of the usdm package (Naimi, 2017) in the R language platform (R Core Team, 2020). This function excludes variables with high collinearity, retaining a list of variables with low correlations for the modelling procedure (Table S2).

For SDM, we used two algorithms available in the biomod2 package (Thuiller et al. 2009): generalized linear models (GLMs; Mccullagh and Nelder, 1989) and maximum entropy (Maxent; Phillips et al., 2006). Both were chosen because they presented robust and reliable results (Li and Wang, 2013). Five rounds of modelling were performed per algorithm per species, and in each round, a different subset of the occurrence data was randomly selected (75% for model training and 25% for predictive quality testing). To measure the quality of the models, the true skill statistics index (TSS; Allouche et al., 2006) was used, and the threshold used for the TSS index was 0.9 for all species (Table S3). To generate pseudoabsences, we used five sets of randomly selected occurrences per modelling run with 10 times the number of presences recorded to achieve better predictive performance (Chefaoui and Lobo, 2008). For each species, models related to the GLM and Maxent algorithms were generated, the quantity of which varied according to the TSS index (Figure S1).

For the present study, individual binarized models were selected for each species (1 = suitable and 0 = unsuitable, considering the climate variables used). We used the TSS values to create binary maps by using thresholds that maximize the sensitivity and specificity of the models (Jimenez-Valverde and Lobo, 2007). For this procedure, a cut-off point was defined that equally balances the importance between specificity (proportion of true negatives correctly identified on the basis of pseudoabsences) and sensitivity (proportion of correct positives on the basis of the share of presences attributed to the test) (Hao et al., 2019; Allouche et al., 2006).

The models were subsequently grouped (between the GCMs and algorithms) into ensemble forecast models (EFMs) on the basis of the Committee Averaging method (Thuiller et al., 2009). This process resulted in maps with geospatial classes ranging from zero (where all the models agreed with the unsuitability of the area) to the total number of suitable habitats detected by all the models. After this process, the final models of each species and scenario (current, moderate future, and pessimistic future) were normalized considering the classification range from 0–1,000. Thus, all models per species have equivalent (scaled) predictive metrics per species and scenario, improving the comparison of results. The EFMs were subsequently reclassified, with values of <=500 being assigned as unsuitable, whereas values greater than this threshold were determined to be suitable. This procedure aims at direct comparison among scenarios and the reduction of noise from models with less convergent predictions (we only maintained prediction zones with 75% or more agreement). Next, the ensembles in the current scenario per species were compared to the ensembles projected for each future scenario (moderate and pessimistic) to identify the differences between the spatial conformations of the current suitability in relation to the future scenarios, which resulted from the effect of the estimated climate change. For this analysis, a binary comparison approach was performed. This procedure compares each cell of the projected raster model (map) against its current value and potential value changes in future scenarios. In this comparison, four possibilities can be expressed spatially per cell as follows: Zone gain: the cell is unsuitable in the current scenario but becomes suitable in the future scenario. Zone loss: the cell is suitable in the current scenario but becomes unsuitable in the future scenario. Remains suitable: the cell is suitable in both the current scenario and the future scenario. Remains unsuitable: the cell is unsuitable in both the current scenario and the future scenario. Areas of climatic suitability were projected on maps for the potential distribution area of each selected species, with the addition of a buffer of 100 km. Data related to losses and gains (in area – km^2) were subsequently extracted, and the relative percentages were computed.

Results

Species list of (effective or potential) pollinators

We recorded 310 mammal species occurring in our study area. However, we excluded 29 species: 16 that do not have a confirmed occurrence in the Amazon biome (Paglia et al., 2012); four species that do not have confirmed occurrence in the Eastern Amazon; one species that is endemic to Peru (Hurtado and Pacheco, 2017); three species with records that were considered erroneous by the Brazilian Bat List Committee (CLMB/SBEQ) (Garbino et al., 2022); two species with records that were considered doubtful by the Brazilian Bat List Committee (CLMB/SBEQ) (Garbino et al., 2022); one species that was excluded from the List of Mammals of Brazil, organized and updated by the Taxonomy Committee of the Brazilian Society of Mastozoology (Abreu et al., 2022); and two species that do not have a terrestrial habit, according to the List of Mammals of Brazil of the Taxonomy Committee of the Brazilian Society of Mastozoology (Abreu et al., 2022) (Table S4). Thus, 281 species were retained for the analysis (Table S5).

Using the previously mentioned criteria (Table 1), 60 species were categorized as pollinators (P) or potentially pollinators (PP) (Table 2). These species are from five orders: Chiroptera, Carnivora, Didelphimorphia, Primates and Rodentia. The most heavily represented order was Chiroptera (flying mammals), with 41 species, followed by Primates, Didelphimorphos, Carnivores and Rodents (nonflying mammals), with eight, six, three and two species, respectively (Table 2). Nine species (15%) were classified as effective pollinators, of which seven received this categorization on the basis of morphology and/or specialized behaviour, and two received this categorization because they were observed in contact with reproductive floral organs. Another 51 species (85%) were classified as potential pollinators. Among these, 46 species were described as floral visitors, 29 species were associated with nectar exploitation, and 13 species were observed to carry pollen (Table S6).

Among the 41 species of bats (order Chiroptera), seven were considered effective pollinators, and 34 were considered potential pollinators (Figure 2). Regarding the nonflying mammal orders, 100% of primates (Primates) (n=8), 100% of carnivores (Carnivore) (n=3) and 100% of rodents (Rodentia) (n=2) were classified as potential pollinators. Of the six species of marsupials recorded for the region (Order Didelphimorphia), two were considered effective pollinators, and four were considered potential pollinators (Figure 2).

Of the total number of species of flying mammals (Chiroptera), eight are endemic to the Amazon biome (Paglia et al., 2012). None of these species is threatened at the national level (MMA, 2022), and all are classified as “least concern” globally according to the IUCN Red List of Threatened Species (2022-2) (Table 3; Table S6). Among nonflying mammals, the following are listed: a) eight species of primates, seven of which are endemic to the Amazon biome (Paglia et al., 2012) and one (*Mico humeralifer*) of which has a restricted distribution (Paglia et al., 2012) in the south of the Amazon River, between the Maués River to the west and the Tapajós River to the east (Rylands and Mittermeier, 2013); b) six species of marsupials (Didelphimorphia), two of which are endemic to the Amazon (Paglia et al., 2012); c) three species of the order Carnivora, one of which is endemic to the Amazon (Paglia et al., 2012); and d) two species of rodents endemic to the Amazon biome (Paglia et al., 2012). Only three primate species are classified as under some degree of threat according to the red lists of endangered species (MMA, 2022; IUCN, 2022-2) (Table 3; Table S6).

Potential impact of climate change

As mentioned above, three threatened species of mammalian pollinators or potential pollinators were identified: *Alouatta belzebul, Ateles marginatus* and *Saguinus niger*. Considering that the taxonomy of *Saguinus niger* has been revised, with the species *Saguinus ursula* separated and revalidated (Gregorin and De Vivo, 2013), we included the latter in the analyses. Therefore, four species were selected for SDM. Data on the occurrence of these four targeted species resulted in 163 unique records. The number of occurrence points varied between 26 and 67 per species.

In the moderate future scenario (SSP2-4.5), the primates *Ateles marginatus* and *Saguinus ursula* will be able to maintain more than 60% of their climatically suitable habitats; however, 94% of the climatically suitable area for *Saguinus niger* may be lost. Considering the net gain (balance between loss and gain of climatically suitable areas), only the primate species *Ateles marginatus* exhibited a potential gain of suitable area in this future scenario, of 6% (Table 4A; Figure 3).

A similar trend was observed in the pessimistic future scenario (SSP5-8.5), with *Ateles marginatus* and *Saguinus ursula* having the potential to retain more than 60% of their climatically suitable habitats in this future scenario and *Saguinus niger* potentially losing almost all of its climatically suitable area (95%). In this scenario, none of the four species presented a net gain in suitable area (Table 4B; Figure S2).

Discussion

On the basis of the pollinator definition criteria used here, our study area and the total number of 281 species analysed, 21% of the species were considered effective or potential pollinators (60 species). We considered 15% of the mammal species as effective pollinators and 85% as potential pollinators. Among the pollinator species, 33% are endemic to the Amazon biome, and four species are threatened (one of which was separated and revalidated) (MMA, 2022; IUCN, 2022-2) and require greater attention. Special attention should be given to the primate species *Saguinus niger*, which will probably not find climatically suitable habitats in the future scenarios analysed.

Species list of (effective or potential) pollinators

In this study, we considered mammal species that act as floral visitors, explore nectar, or have been reported in the literature to have pollen adhering to the body to be potential pollinators, even if there is no guarantee that pollination occurs due to these behaviours. Determining pollination behaviour is complex and often depends on direct observations of the animal in the flower or floral reproductive biology experiments. In general, pollination is considered legitimate when the animal approaches the flower and contacts the anthers and stigmas (Alves-dos-Santos et al., 2016), which ultimately produce fruits and seeds. However, contact with reproductive structures can produce varying effects depending on the temporal availability of floral resources (Biesmeijer et al., 1999; Dworschak and Blüthgen, 2010). We also highlight that pollination is one of the functional roles of mammals, and this group also participates in several other ecological processes in tropical forests (Vale et al. 2023), such as seed dispersion (Belo et al. 2015), which places them among the indispensable organisms in the regeneration of tropical forests (Carthew and Goldingay, 1997; Brewer and Rejmanek, 1999; Forget and Vander Wall, 2001). Some species listed in the present work act predominantly as frugivores, but they may also present other feeding habits (Henry, 1999; Paglia et al., 2012). Nectar, in particular, is an important high-calorie resource (Welch et al. 2008) and may represent an important alternative for primates and other nonflying mammals when fruit abundance in their habitats reaches its annual minimum (Janson et al., 1981). In Central America, the diet of frugivorous bats has been observed to shift to predominantly nectarivorous when fruit is scarce in the dry season (Heithaus et al. 1975). Thus, it is likely that these species can adapt their predominant diets to exploit other resources (Mello et al., 2007; Barros et al., 2013) and visit resources opportunistically (Tschapka and Von Helversen, 1999), characterizing them as nonspecialists.

In our study area, 21% of the Amazonian mammal species were categorized as pollinators (P) or potential pollinators (PP), filling a considerable knowledge gap concerning the vertebrate species that perform pollination services. In particular, pollination by nonflying mammals (terophily) has received little attention (Janson et al., 1981). We showed that bats represented approximately 68% of the total species defined as pollinators or potential pollinators. Morphologically adapted species with an elongated snout and tongue or that exhibit specialized behaviours, such as hovering flight, as in the case of glossophagous bats, are more likely to achieve pollination (Howell and Hodgkin, 1976). The scarcity of data on the eating and behavioural habits of species occurring in the Amazon region hinders the full comprehension of interactions between animals and plants (but see Hinojosa et al., 2021). According to Lopes et al. (2021), the neglected diversity of vertebrate pollinators could reach as high as 95.2%, indicating that many plant–pollinator interactions have not yet been mapped.

We also highlight that three species of primates analysed and considered potential pollinators are classified as under some threat (one being separated and revalidated, totalling four threatened species) (MMA, 2022; IUCN, 2022-2). An assessment of the conservation status of Brazilian mammals characterized habitat loss and fragmentation resulting from agricultural activities as the main threats to continental mammals (ICMBio, 2018). Mammalian conservation has benefited from several initiatives, such as the definition of priority areas for conservation and management plans for several endangered species (ICMBio, 2018). However, considering the conservation status of the species and their occurrence in areas of the Eastern Amazon, which is characterized as one of the main deforested regions in the Amazonian biome due to its history of land cover modification (Fearnside, 2005), other conservation strategies to minimize the population decline of these species are urgently needed.

Potential impact of climate change

Our results revealed that more than 60% of climatically suitable habitats are maintained in patches scattered throughout the distribution area of two species, *Ateles marginatus* and *Saguinus ursula*, with the former having a net gain of 6% of areas adequate in the moderate future scenario in relation to the current climatically suitable extent. One species, *Saguinus niger*, presented a significant potential loss of climatically suitable habitats from 2041-2060 under both scenarios.

Our future forecasts point to the maintenance of 30% of suitable areas (moderate scenario) for *Alouatta belzebul* in the eastern and southern portions of northeaster Brazil. Future projections by Moraes and collaborators (2020) indicate that 23% of its distribution areas, which are currently protected, will remain climatically suitable, corroborating our results. The literature indicates, however, that the areas normally considered suitable for the species have a low percentage of forest cover, mainly due to the high degree of fragmentation that the biome has experienced over the years (Ribeiro et al., 2011). Our study also revealed a net loss of 7% of suitable areas in the moderate scenario and 10% in the pessimistic scenario for *Alouatta belzebul*, contrary to previous modelling (Moraes et al., 2020). The authors maintain that the results of climatic habitat suitability for this species can be affected by several factors, including geomorphology, which directly influences the structure and composition of the vegetation (Shi-Kui et al., 2019).

The species *Saguinus ursula* and *Ateles marginatus* may maintain 62% and 72% of their climatically suitable habitats, respectively, in a moderate future scenario, especially in the northern region of their potential current distribution. Our results also indicate a net loss of 6% for *S. ursula* in the moderate scenario, 3% in the pessimistic scenario, and 2% for *A. marginatus* in the pessimistic scenario; these values are relatively lower than those obtained by Silva et al. (2022). These authors reported a loss of up to 98% of the area of occurrence, considering both climate change and deforestation. It is important to highlight that the two species mentioned here can tolerate some degradation of their habitats but cannot survive in areas without forests (Boyle and Smith, 2010) since they are essentially arboreal. In this sense, the loss of climate suitability in the areas of occurrence can be greatly aggravated in the face of a coupled scenario of forest loss.

As discussed above, *Saguinus ursula* has been revalidated as a distinct species, having been separated from *Saguinus niger* on the basis of coat colour and corroborated by molecular data (Gregorin and De Vivo, 2013). The authors concluded that those two species are allopatric and that the Tocantins River acts as a barrier to gene flow. On the one hand, our projections point to a low percentage of loss for *S. ursula*; on the other hand, our results indicate a significant loss of suitable habitats for *S. niger* in the period 2041-2060 (94% in the moderate scenario and 95% in the pessimistic scenario), considering exclusively climate change predictions. *S. niger* occurs in the state of Pará, south of the Amazon River, east of the Rio Xingu and Rio Fresco, to the Rio Tocantins and lower Rio Araguaia. It also occurs in the western two-thirds of the forest of Marajó Island (north of Pará state) in the estuary of the Amazon River (Ferrari and Lopes, 1996). The species is distributed in a densely populated region of the Brazilian Amazon, overlapping one of the most developed regions of the Brazilian Amazon (Ferrari and Lopes, 1996). The species suffers from habitat loss and fragmentation, especially in the area known as the deforestation arc (east and south of the Amazon biome; Fearnside, 2005), and its potential distribution areas can be severely reduced if both climate change and loss of forest cover are considered (Silva et al. 2022).

In this sense, our projections indicate that climate change could pose an additional threat to the local persistence of this species in its current distribution areas. The loss of climatically suitable habitats can result in two main consequences: inducing the species to expand its distribution area to other areas that are less vulnerable to climate change, forcing it to face new environmental challenges, or culminating in severe population reductions due to its inability to colonize new suitable environments. As species expand or retract, their interactions are also redistributed, affecting ecosystem functions locally (Tylianakis et al., 2008; Gonçalves et al., 2020; Gonçalves et al., 2021) and potentially leading to biotic homogenization and altering the trophic structure of assemblages (Moura et al., 2023). While climate change presents its own set of risks, the consequences of its synergy with factors such as habitat loss need to be investigated. The combined scenario between climate change and loss of forest cover could be strictly worse, since fragmentation can make it difficult for species to move across the landscape and thus prevent them from following ideal climatic conditions in space (Thomas et al., 2004).

Considering the synergy between climate change and the loss of forest cover, the most effective way to protect these species includes proactive conservation through habitat restoration and enhancing the connectivity of fragments of native vegetation (Silva et al., 2022; Miranda et al., 2021). The creation of protected areas, which aim to halt habitat loss and fragmentation, in addition to the continuous monitoring of species' responses to climate change, is of paramount importance. Notably, long-term monitoring of responses to climate change is necessary to detect functional changes related to the expansion or contraction of the species' distribution area. A future step for our study consists of analysing the potential effects of climate change on the other species mentioned here, aiming to anticipate scenarios of potential loss of species and changes in interaction patterns.

Conclusion

The present work categorized and classified 60 species of terrestrial and flying mammals as effective or potential pollinators, of which three are classified in some threat category, and a fourth species has been separated and revalidated. Considering the complexity of pollinator species interactions and the knowledge gap among vertebrates, our approach allowed us to identify, for the first time, a set of mammal species that may contribute to this important ecosystem function. With respect to the potential impact of climate change, *Saguinus niger* will potentially not find climatically suitable habitats in the future scenarios analysed. The overlap of its distribution area with highly anthropized areas suggests the urgent need for habitat restoration and protection. Although our results indicate that climate change constitutes its own set of risks, the consequences of its synergy with factors such as habitat loss need to be investigated, as this combined scenario could culminate in worse effects. Furthermore, the identification of species for which climate change will have the least potential impact is also an important result, since resources dedicated to conservation actions are limited and need to be assertively directed to protect the most vulnerable species. In this sense, our results can guide the management of mammal species with potential roles in pollination and direct conservation efforts to neotropical mammals threatened by climate change. Conservation planning that maximizes ecosystem connectivity and promotes the pervasiveness of specific species will ensure the safeguarding of ecosystem functions and services.

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Conflicts of interest

There are no conflicts of interest.

Author contributions

CBN and TCG: Conceptualization; CNB, ALA, LCT, ACMO: Data curation; CBN. ALA: Formal analysis; TCG: Funding acquisition; CBN: Writing - original draft; all authors: Writing - review & editing

Supplementary data

- Table S1
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Table 1. Criteria associated with diet and behaviour in the flower to determine the role of mammal species as effective pollinators and potential pollinators in the Eastern Amazon.

ID	Criteria	Class
	(PE) EFFECTIVE POLLINATOR	
1	Elongated snout and tongue	**A. Morphology and/or specialized behaviour**
2	Features hover flight	
3	Observed landing on the inflorescence and touching a large part of the anthers	**B. Touches the floral reproductive organs**
4	Observed holding the inflorescence and touching the anthers and stigmas with the head	
5	Observed touching the stamens with the head	
	(PP) POTENTIAL POLLINATOR	
6	Specifically defined as potential pollinator by the authors	**C. Floral visitor and/or potentially pollinator**
7	Specifically defined as floral visitor by the authors	
8	Observed feeding on flowers	
9	Consumes pollen	**D. Carries pollen**
10	Observed with the face stained with pollen	
11	Observed carrying pollen load on skin	
12	Observed grabbing the inflorescence with pollen attached to the face and body	
13	Observed with a load of pollen adhered to the snout	
14	Consumes nectar	**E. Specialized in nectar exploration**
15	Defined as nectarivorous (opportunistic)	
16	Defined as nectarivorous (predominant)	
17	Observed feeding on nectar	
18	Observed licking nectar	
19	Observed sucking or licking nectar from flowers	

Table 2. Flying and nonflying mammal species defined as pollinators (P) or potentially pollinators (PP) for the eastern Amazon tropical forest biome.

Order	**Species (author)**	**Effective pollinators (PE) or potential pollinators (PP)**
Carnivora	*1.* *Bassaricyon alleni* Thomas, 1880	PP
Carnivora	*2.* *Nasua nasua* (Linnaeus, 1766)	PP
Carnivora	*3.* *Potos flavus* (Schreber, 1774)	PP
Chiroptera	*4.* *Ametrida centurio* Gray, 1847	PP
Chiroptera	*5.* *Anoura caudifer* (É. Geoffroy St.-Hilaire, 1818)	PE
Chiroptera	*6.* *Anoura geoffroyi* Gray, 1838	PE
Chiroptera	*7.* *Artibeus (Dermanura) anderseni* Osgood, 1916	PP
Chiroptera	*8.* *Artibeus (Dermanura) cinereus* (Gervais, 1856)	PP
Chiroptera	*9.* *Artibeus (Koopmania) concolor* Peters, 1865	PP
Chiroptera	*10.* *Artibeus (Dermanura) gnomus* Handley, 1987	PP
Chiroptera	*11.* *Artibeus (Artibeus) lituratus* (Olfers, 1818)	PP
Chiroptera	*12.* *Artibeus (Artibeus) obscurus* (Schinz, 1821)	PP
Chiroptera	*13.* *Artibeus (Artibeus) planirostris* (Spix, 1823)	PP
Chiroptera	*14.* *Carollia brevicauda* (Schinz, 1821)	PP
Chiroptera	*15.* *Carollia perspicillata* (Linnaeus, 1758)	PP
Chiroptera	*16.* *Chiroderma trinitatum* Goodwin, 1958	PP
Chiroptera	*17.* *Chiroderma villosum* Peters, 1860	PP
Chiroptera	*18.* *Choeroniscus minor* (Peters, 1868)	PE
Chiroptera	*19.* *Gardnerycteris crenulatum* (É. Geoffroy St.-Hilaire, 1803)	PP
Chiroptera	*20.* *Glossophaga soricina* (Pallas, 1766)	PE
Chiroptera	*21.* *Glyphonycteris sylvestris* Thomas, 1896	PP
Chiroptera	*22.* *Hsunycteris thomasi* (Allen, 1904)	PE
Chiroptera	*23.* *Lampronycteris brachyotis* (Dobson, 1879)	PP
Chiroptera	*24.* *Lichonycteris degener* Miller, 1931	PE
Chiroptera	*25.* *Lionycteris spurrelli* Thomas, 1913	PE
Chiroptera	*26.* *Lophostoma silvicola* d'Orbigny, 1836	PP
Chiroptera	*27.* *Mesophylla macconnelli* Thomas, 1901	PP
Chiroptera	*28.* *Phylloderma stenops* (Peters, 1865)	PP
Chiroptera	*29.* *Phyllostomus discolor* (Wagner, 1843)	PP
Chiroptera	*30.* *Phyllostomus elongatus* (É. Geoffroy St.-Hilaire, 1810)	PP
Chiroptera	*31.* *Phyllostomus hastatus* (Pallas, 1767)	PP
Chiroptera	*32.* *Phyllostomus latifolius* (Thomas, 1901)	PP
Chiroptera	*33.* *Platyrrhinus brachycephalus* (Rouk & Carter, 1972)	PP
Chiroptera	*34.* *Platyrrhinus lineatus* (É. Geoffroy St.-Hilaire, 1810)	PP
Chiroptera	*35.* *Rhinophylla fischerae* Carter, 1966	PP
Chiroptera	*36.* *Rhinophylla pumilio* Peters, 1865	PP
Chiroptera	*37.* *Sturnira lilium* (É. Geoffroy St.-Hilaire, 1810)	PP
Chiroptera	*38.* *Sturnira tildae* de la Torre, 1959	PP
Chiroptera	*39.* *Trinycteris nicefori* (Sanborn, 1949)	PP
Chiroptera	*40.* *Uroderma bilobatum* Peters, 1866	PP

Order	**Species (author)**	**Effective pollinators (PE) or potential pollinators (PP)**
Chiroptera	*41.* *Uroderma magnirostrum* Davis, 1968	PP
Chiroptera	*42.* *Vampyressa thyone* (Thomas, 1909)	PP
Chiroptera	*43.* *Vampyriscus bidens* (Dobson, 1878)	PP
Chiroptera	*44.* *Vampyrodes caraccioli* (Thomas, 1889)	PP
Didelphimorphia	*45.* *Caluromys (Mallodelphys) lanatus* (Olfers, 1818)	PE
Didelphimorphia	*46.* *Caluromys (Caluromys) philander* (Linnaeus, 1758)	PE
Didelphimorphia	*47.* *Didelphis marsupialis* Linnaeus, 1758	PP
Didelphimorphia	*48.* *Marmosa (Micoureus) demerarae* (Thomas, 1905)	PP
Didelphimorphia	*49.* *Marmosa (Stegomarmosa) lepida* (Thomas, 1888)	PP
Didelphimorphia	*50.* *Marmosa (Marmosa) murina* (Linnaeus, 1758)	PP
Primates	*51.* *Aotus azarae* (Humboldt, 1812)	PP
Primates	*52.* *Alouatta belzebul* (Linnaeus, 1766)	PP
Primates	*53.* *Ateles marginatus* É. Geoffroy St.-Hilaire, 1809	PP
Primates	*54.* *Mico argentatus* (Linnaeus, 1771)	PP
Primates	*55.* *Mico humeralifer* (É. Geoffroy St.-Hilaire, 1812)	PP
Primates	*56.* *Saguinus (Saguinus) niger* (É. Geoffroy St.-Hilaire, 1803)	PP
Primates	*57.* *Saimiri sciureus* (Linnaeus, 1758)	PP
Primates	*58.* *Sapajus apella* (Linnaeus, 1758)	PP
Rodentia	*59.* *Guerlinguetus aestuans* (Linnaeus, 1766)	PP
Rodentia	*60.* *Sciurus gilvigularis* Wagner, 1842	PP

Table 3 – Quantitative species of effective pollinating mammals (PE) or potential pollinators (PP), by taxonomic order.

Order	**Number of species**		**Endemic to the Amazon**	**Restricted distribution**	**Endangered**
	Effective pollinators (PE)	**Potential pollinators (PP)**			
Primates	-	8	7	1	3
Carnivora	-	3	1	-	-
Rodentia	-	2	2	-	-
Didelphimorphia	2	4	2	-	-
Chiroptera	7	34	8	-	-

Table 4. Changes in climate suitability under the current scenario, (A) future moderate scenario (SSP5-4.5) and (B) future pessimistic scenario (SSP5-8.5). Gain: Current scenario: unsuitable; Future scenario: suitable. Loss: Current scenario: suitable; Future scenario: unsuitable. Remain suitable: Current scenario: suitable; Future scenario: suitable. Remain unsuitable: Current scenario: unsuitable; Future scenario: unsuitable.

ID	Species	Gain		Loss		Remain suitable		Remain unsuitable		Total
		Area (10^3 km^2)	%	Area (10^3 km^2)	%	Area (10^3 km^2)	%	Area (10^3 km^2)	%	Area (10^3 km^2)
A. Moderate scenario										
1	*Alouatta belzebul*	11	1%	102	8%	385	30%	803	62%	1,301
2	*Ateles marginatus*	76	8%	15	2%	653	72%	164	18%	908
3	*Saguinus niger*	-	0%	531	94%	24	4%	10	2%	565
4	*Saguinus ursula*	29	5%	56	11%	323	62%	115	22%	522
B. Pessimistic scenario										
1	*Alouatta belzebul*	9	1%	140	11%	349	27%	805	62%	1,302
2	*Ateles marginatus*	72	8%	87	10%	581	64%	168	18%	908
3	*Saguinus niger*	-	0%	538	95%	17	3%	10	2%	565
4	*Saguinus ursula*	27	5%	39	8%	339	65%	117	22%	522

Figure 1. Study area in the eastern Amazon tropical forest biome.

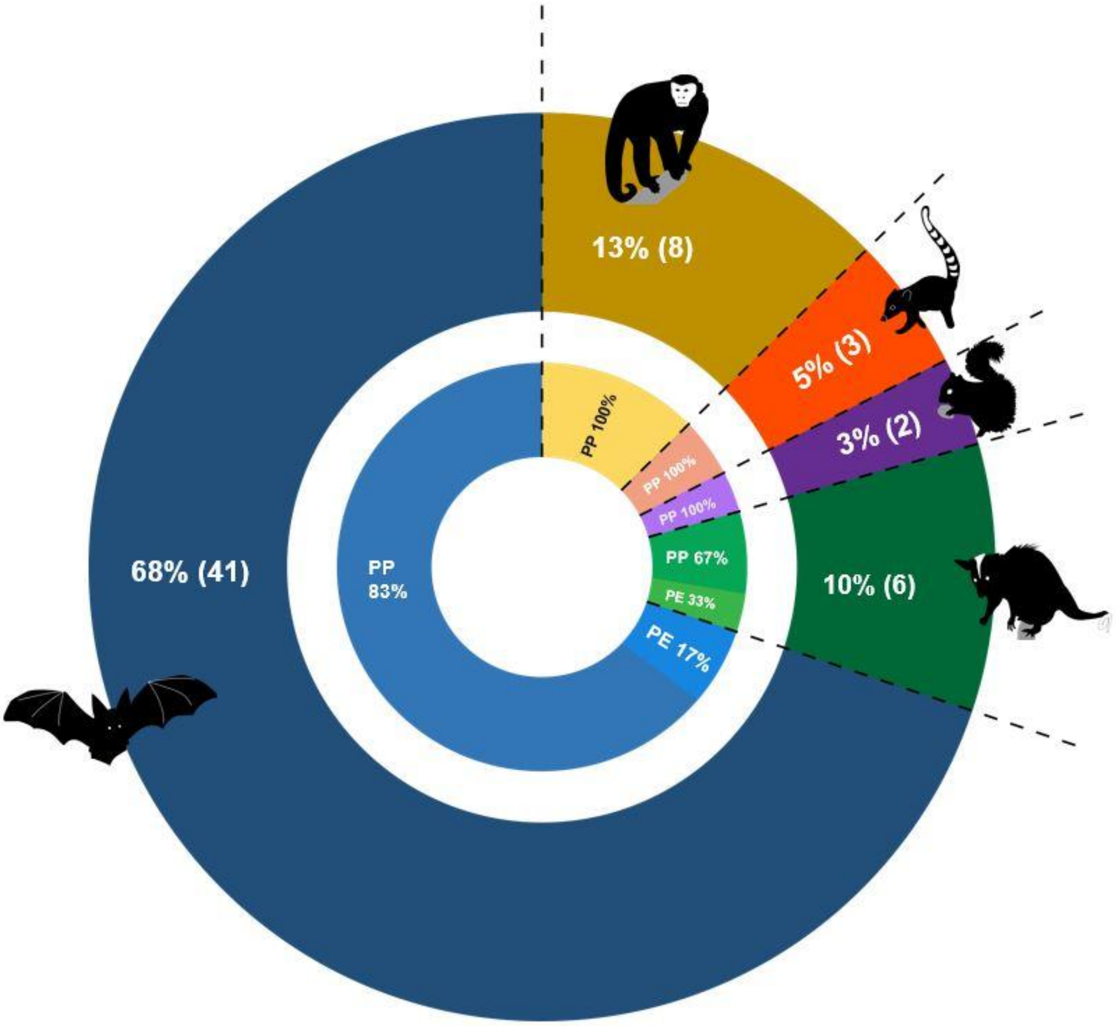

Figure 2. Mammal species as effective pollinators (PE) or potentially pollinators (PP) by taxonomic order.

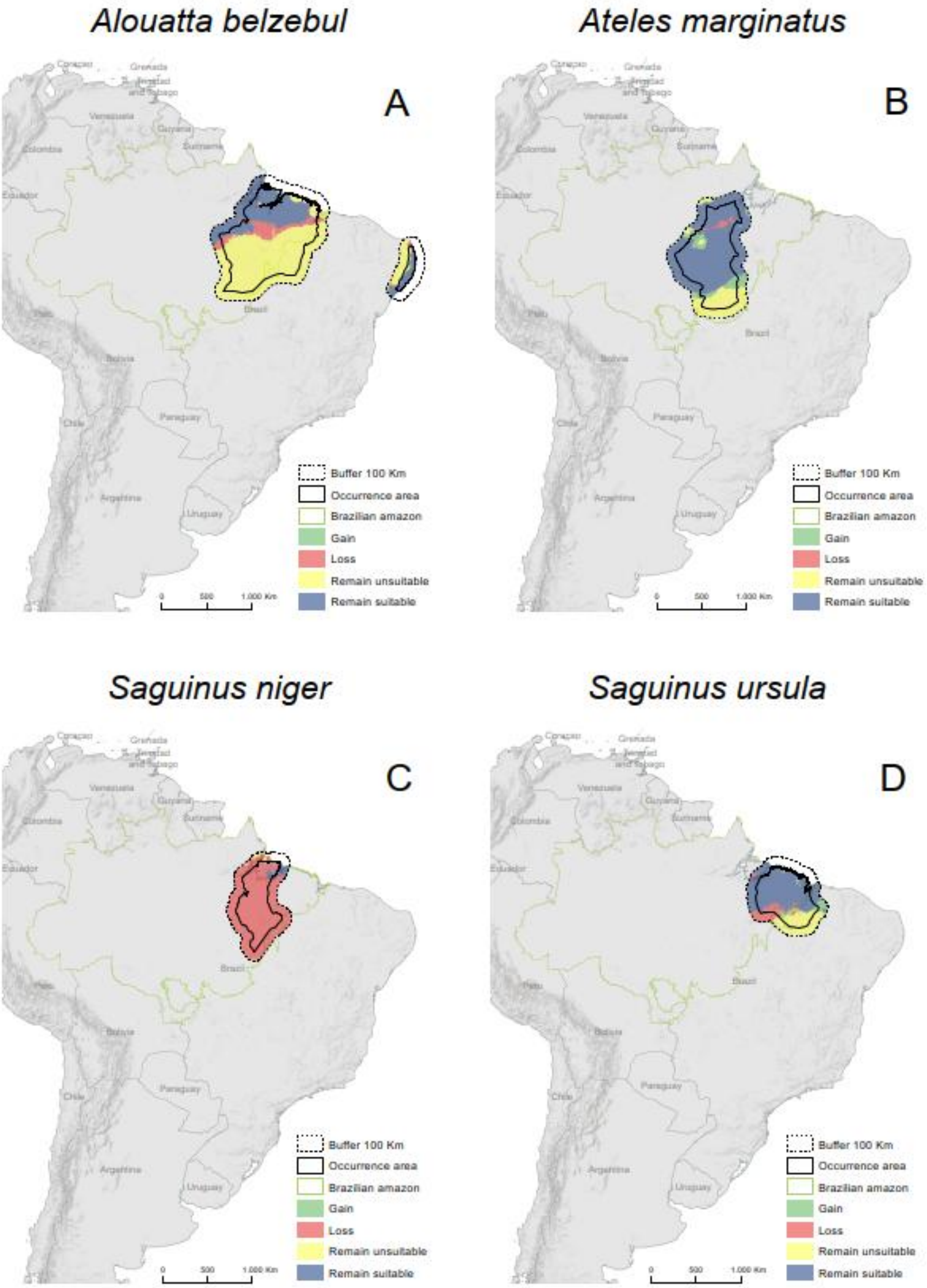

Figure 3. Potential impact of climate change on endangered species (moderate scenario - SSP2-4.5). (A) *Alouatta belzebul*, (B) *Ateles marginatus*, (C) *Saguinus niger* and (D) *Saguinus ursula*. Gain: Current scenario: unsuitable; Future scenario: suitable. Loss: Current scenario: suitable; Future scenario: unsuitable. Remain suitable: Current scenario: suitable; Future scenario: suitable. Remain unsuitable: Current scenario: unsuitable; Future scenario: unsuitable. A pessimistic scenario can be found in Figure S2.