



Research Article

Crops, caves, and bats: deforestation and mining threaten an endemic and endangered bat species (*Lonchophylla*: Phyllostomidae) in the Neotropical savannas

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Abstract

The Dekeyser's nectar bat (*Lonchophylla dekeyseri*) is a cave roosting bat endemic to the Brazilian Cerrado that is considered endangered according to the IUCN Red List. Even though it is likely highly threatened, there is no current assessment of its conservation status or the conservation of the caves within its distribution. Additionally, a change in the Brazilian law is causing increasing mining pressures to caves. In order to evaluate *L. dekeyseri* conservation status and the caves within its distribution, we made an extensive literature review looking for occurrence records within the Cerrado, which we used to generate species distribution model (SDM) to predict its potential distribution and understand the main environmental variables driving its occurrence. We also overlapped its potential distribution map and cave roosting sites with information on protected areas and mining pressures. We found that most of its potential distribution is located in the central portion of Cerrado, with a large proportion of this area already deforested (43.74%) or threatened due to mining (55.83%) between 2000 and 2019. Moreover, a large vegetation proportion around the caves within its potential distribution was already converted to pastures (67.50%) and soybean crops (22.03%). Our results revealed that only a small proportion of the species potential distribution (~4%) and a small share of caves suitable for roosting (~15%) are preserved within strictly protected areas. Thus, we call attention to the need of more strictly protected areas across suitable habitat locations in order to cover a larger proportion of the species potential distribution and the caves it might be using for roosting.

Introduction

Encompassing more than two million square kilometers, Cerrado is the second largest biome of the Neotropical region, the third-largest biodiversity hotspot, and the most biodiverse tropical savanna worldwide (Myers et al., 2000). It is located in the central region of South America, sharing its boundaries with many other Neotropical biomes, which have likely helped to boost its biodiversity, but decreased the proportion of endemic species for some taxa, such as mammals and plants (Paglia et al., 2012; Françoso et al., 2015). The Cerrado has 251 mammal species of which bats represent 40%, but only two cases of endemic bat species (*Lonchophylla bookermanni* and *Lonchophylla dekeyseri*) (Paglia et al., 2012; Gutiérrez and Marinho-Filho, 2017). However, the distribution of many bat species within the Cerrado is still poorly known. Species distribution models are one of the main methods used to describe the patterns of poorly sampled species (Stephenson et al., 2020; Zurell et al., 2020), including bats (Razgour et al., 2016; Scher-

rer et al., 2019). Even though efforts have been made to better describe bat distributions within the Cerrado (Rojas et al., 2018; Aguiar et al., 2020; Delgado-Jaramillo et al., 2020), estimates indicate that we would still need many decades in order to properly sample the whole biome (Bernard et al., 2011).

The bat fauna of the Cerrado is not only poorly known, but also highly unprotected and threatened. Cerrado deforestation happens mostly due to the conversion for pastures and soybean crops, and even though the rates of deforestation (~360000 ha/year – 2010/2011), are more than twice as high as those in the Amazon Forest (Brasil, 2015; Françoso et al., 2015; Strassburg et al., 2017), less than 10% of the native Cerrado ecosystems are inside protected areas (Françoso et al., 2015). In addition, many bat species can be heavily impacted by deforestation (Oliveira et al., 2017; Pereira et al., 2018; Oliveira et al., 2019). In particular, the conversion of land for agriculture reduces food resources for nectarivorous bat species and decreases abundance outside protected areas (Voigt et al., 2006; Oliveira et al., 2017). This poses a big challenge for bat conservation, since native Cerrado vegetation will be almost exclusively constrained to protected areas by 2030 (Machado

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et al., 2004). Thus, understanding the factors that influence the distribution of Cerrado bat species is essential in order to better evaluate possible threats of this rapidly disappearing biome, and to propose effective conservation measures.

The sharp agricultural expansion and intensification observed in the last decades, and the consequent increase in crop and animal production will expand agricultural use of antibiotics, water, pesticides and fertilizer (Calaboni et al., 2018; Soltangheisi et al., 2019; Rohr et al., 2019). Converting natural habitats for agricultural use can increase the abundance of artificial ecotones, change species composition, and decrease native biodiversity (Green et al., 2005; Crist et al., 2017), all of which play an important role in a number of emerging infectious diseases (Despommier et al., 2006; Borremans et al., 2019). Contact rates between humans and both wild and domestic animals will increase, with consequences for the emergence and spread of infectious agents (Jones et al., 2008; Rohr et al., 2019). These developments may, thus, influence the increasing incidence of zoonotic diseases or the deterioration of already endemic diseases (Jones et al., 2013; Cohen et al., 2016; Dobson et al., 2006; Rohr et al., 2019). This might pose a serious challenge for bat conservation, since they can be affected by zoonotic control policies, including endangered species (Aguiar et al., 2010; Gonçalves et al., 2021). This scenario reinforces the urgency of developing approaches for mapping the spatial distribution of native species worldwide, and analyzing its spatial context using Land Use and Land Cover (LULC) maps.

In addition to landscape characteristics, roost availability is also an important factor shaping the structure of Neotropical bat communities (Voss et al., 2016), acting as a filter and limiting bat species existence to areas where they can find available roosts (Voss et al., 2016). Caves represent an important roosting resource for almost 40% of Brazilian bat species, which use them to some extent during their life time (Oliveira et al., 2018). Even though Brazil is thought to have more than 300000 caves (Piló and Auler, 2011), only a small portion of this number has been officially recorded (20147 caves), and even fewer caves have been surveyed for bats (~220 caves) (ICMBio/CECAV 2015; Oliveira et al., 2018; Cruz et al., 2018). Still, almost half of all recorded Brazilian caves occur in the Cerrado (9225 caves), for which the use of 64 bat species out of the known 118 bat species (~54%) was recorded (Oliveira et al., 2018; Cruz et al., 2018). Many Brazilian caves and their associated fauna are under severe threat due to exploitation for mining (Delgado-Jaramillo et al., 2018; Gallão and Bichuette, 2018) and the number of mining projects are expected to more than double in the next years (Villen-Perez et al., 2018). Furthermore, the Brazilian act 6.640 has changed the conservation status of most Brazilian caves (Brasil, 2008, 2017), allowing the exploitation of several caves which were previously legally protected (Brasil, 1990). Therefore, understanding the association of caves and bats occurrence is crucial for adequate conservation priorities, since one of the criteria to determine the protection of a Brazilian caves is its use as an essential shelter for a threatened species (Brasil, 2008, 2017).

The Dekeyser's nectar bat (*Lonchophylla dekeyseri* Taddei, Vizotto & Sazima, 1983) is a small nectarivorous bat species with small home ranges (564–640 ha) that is endemic to the Brazilian Cerrado and known to only roost in caves (Aguiar et al., 2014; Aguiar and Bernard, 2016; Gutiérrez and Marinho-Filho, 2017). It is also considered to be threatened according to the IUCN Red List, with some of its main threats considered to be deforestation and the destruction of caves due to mining (Aguiar et al., 2016). According to the Brazilian act 6.640, the presence of this species inside caves would be an important factor in considering a cave legally protected against mining, which would also be beneficial for the species' survival. However, the potential distribution of *L. dekeyseri* has, so far, been poorly assessed. Current distribution maps do not take into consideration the importance of caves for its occurrence and also used fewer species records than those currently available in the literature (Torrecilha et al., 2017; Coura et al., 2018; Delgado-Jaramillo et al., 2020; Martins et al., 2020; Oliveira, 2020). Thus, there is still not a clear assessment of the conservation status of this species regarding the proportion of its distribution that is located

inside protected areas or the protection status and possible threats to the caves within its distribution. This lack of knowledge poses additional challenges for the conservation of *L. dekeyseri* and, thus, its long-term persistence in the Cerrado.

The main goal of our study was to assess the potential distribution of the Dekeyser's nectar bat (*Lonchophylla dekeyseri*) within the Cerrado and describe its conservation status. Specifically, our aims were fourfold: 1) model the potential distribution of the Dekeyser's nectar bat (*Lonchophylla dekeyseri*) in the Brazilian Cerrado, and describe the main factors that affect its occurrence; 2) evaluate the proportion of *L. dekeyseri* predicted distribution that is preserved inside protected areas or that has been deforested; 3) evaluate the impact of mining pressures and the role of protected areas on the conservation of caves that can be used as roosts by *L. dekeyseri*; and 4) assess the conservation priorities for the caves and the species within its potential distribution area.

Methods

Study area

The Cerrado is mostly located in central Brazil, with parts in Bolivia and Paraguay, and formed by a vegetation mosaic that ranges from open formations with low density of trees to dense forest formations (Ratter et al., 1997). However, most of its distribution (70%) is composed by savanna woodland, which is a xeromorphic savanna-like vegetation type formed by trees ranging from 2 m to 6 m high and an arboreal cover that ranges from 20% to 50% (Ribeiro et al., 1998). According to the Köppen's classification, most parts of the Cerrado have a tropical savanna climate (Aw) with an average annual precipitation of 1500 mm, ranging from 750–2000 mm, and an average temperature of 20.1 °C, with a minimum of 18.0 °C on the coldest month of the year (Ribeiro and Walter, 2008). It also presents a well-defined seasonal climate with a warm-wet season from October to April, when ~90% of the annual precipitation occurs, and a cool-dry season from May to September (Miranda et al., 1993).

The natural vegetation of the Cerrado started to be more intensively deforested in the 1950's, after the geopolitical decision to build a new Brazilian capital (Brasília) in the center of Brazil (Klink and Moreira, 2002; Lopes and Guilherme, 2016). However, the acid soils and their low fertility is one of the main challenges for the cultivation of grains (Castro and Crusciol, 2013), which changed in the 1970's, when low soil pH was compensated through liming, enabling the development of agriculture in the Cerrado (Goedert, 1983; Lopes and Guilherme, 2016). Nowadays, lime is the most used way to correct for soil pH in Brazil (Castro and Crusciol, 2013), and caves are one of the main lime sources in the country (Auler and Piló, 2015). Cerrado is home to 70% of all Brazilian agricultural production (Wickramasinghe et al., 2012) for which more than 88 million hectares of natural Cerrado vegetation have been converted (Scaramuzza et al., 2017). These land use change processes exert a high pressure not only on the ecosystem, but also on the caves that are exploited for the extraction of lime in order to correct soil pH for the conversion of savannas to agriculture.

Study species

The Dekeyser's nectar bat (*Lonchophylla dekeyseri*; Chiroptera: Phyllostomidae) is a small nectarivorous bat (average body weight = 10.7 g; average forearm length = 35.3 mm) considered to be endemic of the Cerrado of Brazil, and caves are its only known roost (Aguiar et al., 2014; Gutiérrez and Marinho-Filho, 2017). It has a high roost fidelity in some caves, with the same individuals being recaptured over the course of several years (Aguiar et al., 2006). Its diet is known to include invertebrates, fruits, and nectar from flowers (Kissling et al., 2014), and it is considered to be a pollinator of the following plant species: *Pseudobomba* sp., *Luehea* sp., *Bauhinia* sp., *Lafoensia* sp., *Ruellia* sp., *Inga* spp.; and the seed disperser of *Piper* sp. and *Cecropia* sp. (Coelho and Marinho-Filho, 2002). Also, bats from the genus *Lonchophylla* are known to have the smallest distribution ranges among the Phyllostomidae (e.g., 23 309 km² for *L. bokermanni*, Mello et al., 2019), a trait

connected to vulnerability to extinction. *L. dekeyseri* is considered endangered according to the IUCN red list, and its main threats are related to cave mining, the rapid deforestation and degradation of the Cerrado, and rabies control programs, which can affect not only the populations of the common vampire bat, but also kill *L. dekeyseri* individuals that could be sharing the same roosts (Aguiar et al., 2014; Aguiar and Bernard, 2016; Oliveira et al., 2017).

Dekeyser's nectar bat occurrence data

We compiled species records from the literature using Google Scholar and the keywords “*Lonchophylla dekeyseri*” in order to search for occurrences to build our species distribution models. In addition, we also added occurrences from Specieslink (<http://www.splink.org.br>), the Global Biodiversity Information Facility (GBIF), and an unpublished record where the species was captured by one of the authors of the current study during a field campaign. We found a total of 181 occurrences of *L. dekeyseri* in 44 references published from 1983–2020. We followed Gutiérrez and Marinho-Filho (2017) in our study, and considered *L. dekeyseri* to be an endemic species of the Cerrado of Brazil due to inability to morphologically classify individuals outside of the biome distribution as *L. dekeyseri*. Thus, we excluded from our analysis any occurrences of *L. dekeyseri* that were found outside the distribution of the Cerrado, including records from the Caatinga biome and the Bolivian savanna, which could have not been formally assigned to *L. dekeyseri*. In order to reduce spatial autocorrelation, these records were submitted to spatial filtering, delimiting a minimum distance of 1 km between each locality data. This procedure was performed using SDMtoolbox Brown (2014), resulting in a total of 96 unique occurrence records.

Environmental data

As potential environmental predictors for our habitat suitability model, we obtained climate data from the Chelsa database at the resolution of 1 km² (Karger et al., 2017). We developed a kernel density estimation with a resolution of 1 km² of all georeferenced cave locations to represent refuge/roost availability. Cave occurrences were obtained from the National Register of Speleological Information (NRSI) (<https://www.icmbio.gov.br/cecav/canie.html>), which is regularly updated with new cave discoveries with a total of 9225 caves for the Cerrado. NRSI follows the Brazilian act 99.556 (1990) for cave definition, which is defined according with the following: “any and all underground space accessible by human beings, with or without identified opening, popularly known as cave, grotto, burrow, abyss, or hole, including its environment, mineral and water content, the fauna and flora found there and the rocky body where they are inserted, as long as they were formed by natural processes, regardless of their dimensions or type of enclosing rock”. We used the *spatstat* R package (Baddeley et al., 2015), which computes an isotropic kernel intensity estimate of the point pattern, with a bandwidth of 20 km to represent cave availability in the range of the dispersal ability of this species (Aguiar et al., 2014), and a Gaussian smoothing function.

We also included Normalized Difference Vegetation Index (NDVI) as a surrogate of primary productivity (1982–2015; GIMMS AVHRR Global NDVI; Pinzon and Tucker, 2014; Pettorelli et al., 2011). Finally, to account for the habitat and vegetation preferences of the Dekeyser's nectar bat, we considered a vegetation map which was produced for the year 2014, and encompasses 12 of the main vegetation physiognomies as described by Ribeiro and Walter (2008). A combination of Landsat Enhanced Vegetation Index (EVI) time series, phenological metrics and several environmental variables that influence the occurrence of vegetation physiognomies were used in a machine learning approach to create the map. To date this is the most detailed map in terms of vegetation physiognomies for the entire Cerrado with 30 m spatial resolution. The map was developed within the framework of the Cerrado Monitoring Project (<http://fip.mma.gov.br/projeto-fm/>), and details of the methodology are described in (Bendini et al., 2020). The map and related data are available in a public repository (Bendini et al., 2021).

Species distribution model

We used the maximum entropy modelling approach (MaxEnt) to represent habitat suitability (Phillips, 2017). MaxEnt is a nonparametric species distribution modelling algorithm that shows a high performance across several niche modelling methods for presence-only data and small samples (Elith and Leathwick, 2009). We fitted models using MaxEnt (v3.4.1), and used 10000 background points distributed randomly in the study area. We built a series of the model to avoid over- and under-fitting, and selected the optimal model by using the ENMva1 package in R (Muscarella et al., 2014). For each model, we combined six separated feature classes, including L, LQ, H, LQH, LQHP and LQHPT (L=linear, Q=quadratic, H=hinge, P=product and T=threshold), and two regularisation values (1 and 2). We used AIC for model selection, and AUC for model evaluation. The best model was chosen based on the minimum AICc values (Muscarella et al., 2014). We evaluated model performance by employing a 10-fold cross-validation (Muscarella et al., 2014) and used the area under the curve of the testing data (AUC) to evaluate the model. AUC values range from 0 to 1; a value of 0.5 indicates the model did not perform better than random, while values >0.7 indicate high performance (Peterson et al., 2011). We selected the highest presence threshold (Maximum training sensitivity plus specificity) to determine suitable/unsuitable habitats (binary habitat; Pearson et al., 2006). To account for potential multicollinearity we used variance inflation factor (VIF) to remove the most correlated variables using a VIF threshold of 5.

Threats on Dekeyser's nectar bat distribution

Initially, we analyzed the potential threat of deforestation on the species distribution by using a deforestation layer. Deforestation and land use change can hamper bat distribution by reducing potential suitable habitat (Frick et al., 2019), and deforestation and habitat fragmentation in the Cerrado are among the main threats to biodiversity identified by the IUCN. We used a deforestation layer from PRODES project (“Desmatamento no Bioma Cerrado – Geotiff (2000/2019)”) (INPE, 2019). Based on these maps, we analyzed deforestation patterns within a radius of 1.5 km around the caves between 2000 and 2019. We calculated total deforestation area within this radius and additionally estimated the share of deforested areas around each individual cave. Furthermore, we used a land use map for the year 2019 from the Mapbiomas project (version 5; Souza et al., 2020) to identify the post-deforestation land use around the caves.

Moreover, there is plenty of evidence that bats that roost in caves are particularly vulnerable to activities such as mineral extraction and mining. Mining and quarrying activities threaten bats by destroying subterranean habitats used for roosting as well as degrading habitat by intentional (e.g., persecution, hunting, vandalism, etc.) and unintentional (e.g., noise, contamination, etc.) disturbance (Frick et al., 2019). We used mining activity occurrence as a variable for the potential threat to the bat distribution in the zonation analysis (DNPM, 2012) (see below for more details). Moreover, we have also used mining activity map in order to estimate the proportion of the distribution of *Lonchophylla dekeyseri* and the caves that occur inside it that are threatened due to mining.

Finally, we assessed the protection status using terrestrial protected areas from the World Database on Protected Areas (UNEP-WCMC 2019), which is one of the most comprehensive data sets available for protected areas worldwide. Protected areas are divided into seven categories: Strict Nature Reserve (Ia), Wilderness Area (Ib), National Park (II), Natural Monument or Feature (III), Habitat/Species Management Area (IV), Protected Landscape/Seascape (V), Protected Area with Sustainable Use of Natural Resources (VI) (Dudley, 2008). We considered strictly protected areas those from categories I–IV and less strictly protected areas those from categories V and VI. Strict Nature Reserves (Ia) are strictly protected areas with a specific focus to preserve the biodiversity and geological/geomorphological features, with restricted visitation, use, and impacts by humans (Dudley, 2008). Wilderness Areas (Ib) are usually larger and less strictly protected from human influence than Strict Nature Reserves, but they also have a primary

focus on nature preservation (Dudley, 2008). National Parks (II) have as a main goal to preserve ecological processes in a large scale together with the species and ecosystems of the area, which are also important for a range of compatible scientific, spiritual, scientific, educational, recreational, and visitor activities (Dudley, 2008). Natural Monuments or Features (III) are generally small protected areas that focus primarily on the management and protection of a natural feature Dudley (2008). Habitat/Species Management Areas (IV) are focused on the protection of specific habitats or species, which in many cases will require regular interventions in order to address the particular management requirements of this kind of protected areas Dudley (2008). Protected Landscape/Seascape (V) are usually areas that have been transformed due to anthropogenic activities over time, where regular interventions are needed in order to protect and maintain the conservation of the area and other associated values Dudley (2008). Protected Areas with Sustainable Use of Natural Resources (VI) are generally large protected areas, which are mostly in preserved conditions, but a variable proportion is focused on the sustainable use of natural resources Dudley (2008).

Conservation and gaps on Dekeyser's nectar bat distribution

In order to identify priority areas for the conservation of *Lonchophylla dekeyseri*, we used the software Zonation 4.0 (Lehtomäki and Moilanen, 2013). It produces a hierarchical prioritization of the landscape based on entrance factors and a rule to remove pixels that allows for the retention of only those pixels that more specifically contribute to conservation goals (Moilanen et al., 2014). The entrances used were: i) potential distribution map of *Lonchophylla dekeyseri* as estimated by the MaxEnt model, as a starting point; ii) a kernel distance map of the caves as potential places where the species could inhabit; iii) the mining exploitation map to indicate the condition of the landscape, taking into account habitat loss or degradation resulting from current human pressures; and iv) finally, the deforestation map 2000-2020 as a retention layer, which describes habitat adequability that will be retained for the species in the absence of conservationist interventions. In this case, we attributed the retention mode that habitat quality will be improved by management intervention. We applied the Central Area Zoning removal rule (CAZ), which minimizes biological loss (see Moilanen et al., 2005, 2011, Moilanen, 2007). We used the integration of these data layers to allow for a more robust assessment in identifying ideal locations to expand currently protected areas in the Cerrado.

Results

Dekeyser's nectar bat distribution model

Overall, eight models with different combinations of feature classes and regularization were evaluated for predicting the *L. dekeyseri* potential distribution. All models perform well, reaching AUC values >0.82. Based on the lowest AICc criteria, the best model with the lowest AICc value included linear, quadratic, product, threshold and hinge features, regularization multiplier of 2, and showed AUC values of 0.893 with the training data. The most important variables for the prediction of *L. dekeyseri* suitable habitat in the Cerrado were the kernel of cave distribution (28.65%), temperature seasonality (22.33%), annual mean temperature (14.49%), precipitation of the coldest quarter of the year (13.03%), and precipitation of the warmest quarter (8.07%) (Tab. 1). Potential distribution maps with continuous and binary outputs with the threshold of 0.346 showing suitable habitat are shown in Fig. 1.

Patterns of deforestation and land use/cover in Dekeyser's nectar bat distribution

We found that 43.74% of the potential distribution area of *L. dekeyseri* has been deforested since 2000, but only 15.40% is located inside protected areas (Fig. 1). From the total area of *L. dekeyseri* located inside protected areas, Protected Landscapes (IUCN category V) (10.86%), National Parks (IUCN category II) (3.15%), and Strict Nature Reserve (IUCN category Ia) (0.74%) are the ones that encompass the highest proportion of its potential distribution (Tab. 2). In addition, 6.66% of

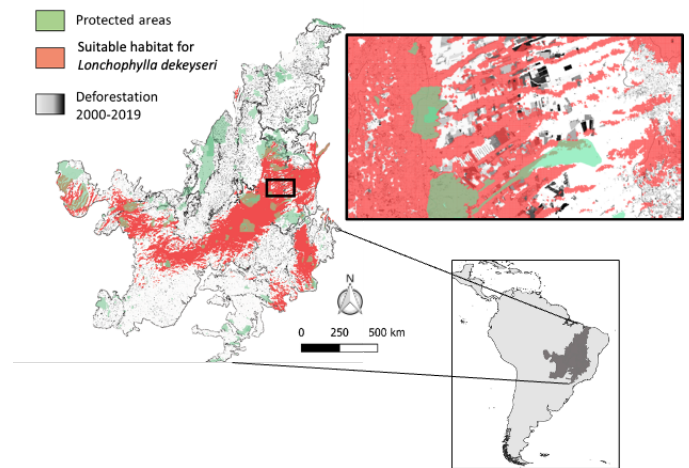


Figure 1 – Potential distribution of the Dekeyser's nectar bat (*Lonchophylla dekeyseri*) and the deforestation in the Brazilian Cerrado between 2000-2019.

Table 1 – Contribution of different environmental variables for the prediction of the occurrence of the Dekeyser's Nectar bat (*Lonchophylla dekeyseri*) in the Cerrados of Brazil.

Variable	Contribution (%)	Permutation importance (%)
Kernel of cave distribution	28.65	21.11
Temperature Seasonality (standard deviation *100)	22.33	30.53
Annual mean temperature	14.49	17.73
Precipitation of Coldest Quarter	13.03	14.13
Precipitation of Warmest Quarter	8.07	5.92
Annual Precipitation	4.21	0.95
Precipitation Seasonality (Coefficient of Variation)	4.11	5.88
Normalized Difference Vegetation Index (NDVI)	2.44	0.10
Mean Diurnal Range (Mean of monthly (max temp - min temp))	1.75	3.13
Vegetation map	0.91	0.52

the caves within *L. dekeyseri* distribution were affected due to deforestation since 2000.

We found that approximately 587000 ha of forest were cleared around the caves between 2000 and 2019. The individual evaluation of each cave, regardless of buffer overlaps, showed that the surroundings of almost 50% of the considered caves were deforested during the time period under investigation. Our analysis revealed that land in a radius of 1.5 km around the caves was mainly converted to pasture, urban in-

Table 2 – Percentage of the potential distribution and caves of Dekeyser's Nectar bat (*Lonchophylla dekeyseri*) within different protected areas categories of IUCN in the Cerrados of Brazil.

Protected area category - IUCN	Distribution (%)	Caves (%)
Strict Nature Reserve (Ia)	0.74	0.00
National Park (II)	3.15	12.15
Natural Monument or Feature (III)	0.46	3.68
Habitat/Species Management Area (IV)	0.05	0.91
Protected Landscape (V)	10.86	33.10
Protected area with sustainable use of natural resources (VI)	0.14	0.67
Total	15.40	50.51 (1442)

Table 3 – Vegetation types covering the potential distribution of the Dekeyser’s Nectar bat (*Lonchophylla dekeyseri*) in the Cerrados of Brazil.

Vegetation types	Area in hectares	
Savanna woodland	10 690 436.61	(40.84%)
Riparian forests	4 554 644.04	(17.40%)
Grassland	3 276 506.25	(12.52%)
Rupestrian grassland	2 615 404.50	(9.99%)
Dry forest	1 689 650.37	(6.46%)
Dry woodland	1 580 705.10	(6.04%)
Shrubland	821 397.60	(3.14%)
Rupestrian cerrado	502 211.97	(1.92%)
Ipuca	1 622.16	(0.01%)
Palmeira	968.40	(~0.00%)
Total	26175449.71	(100.00%)

frastructure, agriculture (particularly soybean), and forest plantations. Considering the whole potential distribution area of *L. dekeyseri*, the classes pasture and soybean were most prominent (Fig. 2). Finally, we analyzed the occurrence of the main vegetation physiognomies in the potential distribution areas of *L. dekeyseri* and found savanna woodland (40.84%), riparian forests (17.40%), and grasslands (12.52%) were most prominent (Tab. 3).

Patterns of mining on Dekeyser’s nectar bat distribution

The number of caves in the *L. dekeyseri* potential distribution is 2855, which is 30.95% of the total number of caves found within the Cerrado. In addition, 55.83% of the potential distribution of *L. dekeyseri* is threatened due to mining (Fig. 3). However, only 1442 caves within the distribution of *L. dekeyseri* are located in protected areas, which represents 50.51% of the total number of caves within its distribution. Moreover, caves were not equally represented inside different protected area IUCN categories, with Protected Landscapes (category V) (33.10% – 945 caves); National Parks (category II) (12.15% – 347 caves); National Monuments (category III) (3.68% – 105 caves) encompassing the highest proportion of the caves within its potential distribution (Tab. 3). On the other hand, 59.16% of the caves are affected by mining activity. Among the main mining threats are: industrial mining (350), cement factory (225), coating (163), soil broker (103), limestone factory (105), and fertilizers (93). For numerous caves, no information on the specific threat was available (605 caves).

Conservation and gaps on Dekeyser’s nectar bat distribution

The zonation analyses showed that most of the caves are located in sites with low quality for the conservation of *Lonchophylla dekeyseri*, while the sites where *L. dekeyseri* occurs are mostly intermediate, extremely high- or low-quality (Fig. 4).

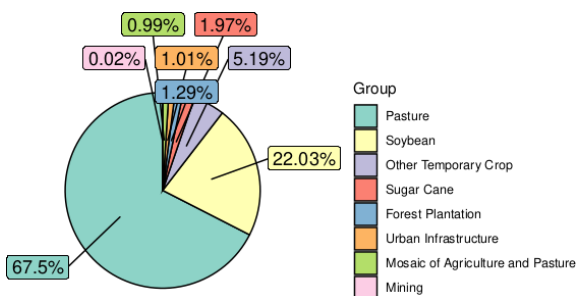


Figure 2 – Main land cover types driving land use change between 2000 to 2019 around caves (within a radius of 1.5km) inside the potential distribution of the Dekeyser’s nectar bat (*Lonchophylla dekeyseri*) in the Cerrados of Brazil.

Discussion

This is the first comprehensive study evaluating the main threats to *L. dekeyseri* within its putative whole distribution, after using a representative set of known species records from the literature and caves, together with other important environmental variables as predictive factors to estimate its potential distribution. Cave availability and temperature seasonality were the most important factors to predict species occurrence in the landscape. In addition, we found that *L. dekeyseri* is under serious threat within the Cerrado due to deforestation and mining, which are threatening 43.14% and 55.83% of its potential distribution, respectively, and also due to the low quality of conservation of caves within its estimated distribution.

Dekeyser’s nectar bat distribution model

We found that the kernel of cave distribution, temperature seasonality, and annual mean temperature were the three most important variables to predict the distribution of *L. dekeyseri* in our study. In contrast to another study estimating the potential distribution of *L. dekeyseri* from 28 occurrences and bioclimatic covariates among other bat species occurring in Brazil (Delgado-Jaramillo et al., 2020), our study was focused in *L. dekeyseri*. Also, we used more than three times the number of records than the previous study (n=96) to estimate *L. dekeyseri* distribution including landscape descriptors that are essential for the species

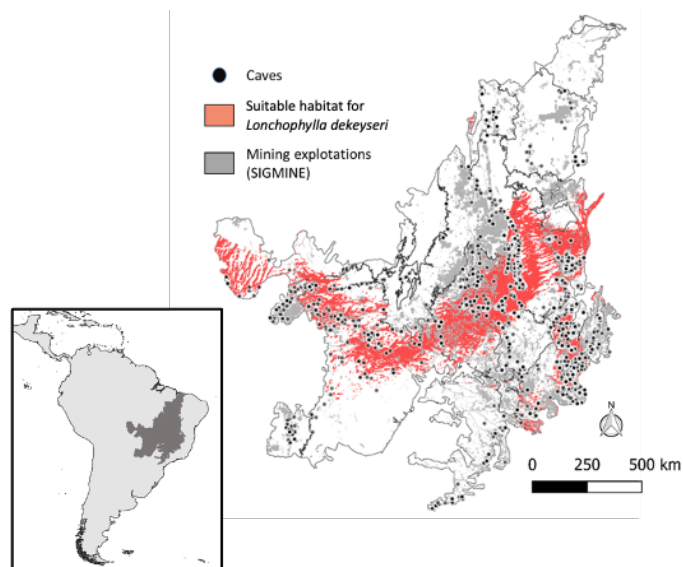


Figure 3 – Mining threats to the caves within the potential distribution of the Dekeyser’s nectar bat (*Lonchophylla dekeyseri*) in the Brazilian Cerrado.

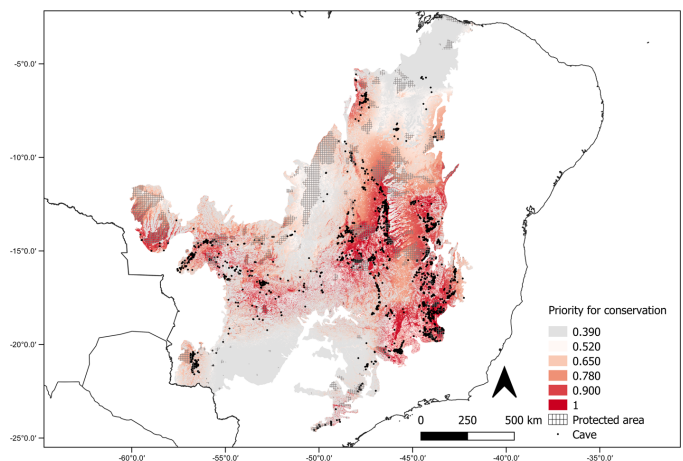


Figure 4 – Zonation analysis ranking priority areas for the conservation of the Dekeyser’s nectar bat (*Lonchophylla dekeyseri*) within its potential distribution in the Cerrados of Brazil.

habitat use, such as karst and deforestation. This addition of new occurrences probably improved the species distribution models performance (here, AUC >0.82) and validity, as models based on low number of records inherently present more uncertainty to potential suitable area calculation. Improving model performance in ecological niche modeling can lead conservationists and decisions makers to make better decisions (Aguiar et al., 2016; Delgado-Jaramillo et al., 2018). In addition, we found that cave availability is an important predictor for its distribution in the Cerrado and should be incorporated in future studies for cave-dwellers distribution. Caves, as roost availability, play an important role to predict the presence of the species in the Cerrado (Aguiar and Bernard, 2016), emphasizing the importance of the protection of this natural formation for the conservation of this species.

The Cerrado has a wide latitudinal range, from 3° to 22° (Albuquerque and Silva, 2008)), but *L. dekeyseri* distribution is concentrated on its central portion, which has intermediate to warm temperatures, and intermediate values of precipitation in comparison with the distribution of the whole biome (Albuquerque and Silva, 2008). The relationship between the occurrence of *L. dekeyseri* and temperature seasonality, precipitation of the coldest quarter of the year, and precipitation of the warmest quarter might be related to the seasonality in the diet of nectarivorous species (Ayala-Berdon et al., 2009; Sperr et al., 2011; Barros et al., 2013).

Patterns of deforestation and land use/cover in Dekeyser's nectar bat distribution

Even though *L. dekeyseri* is able to persist in highly modified savannah woodlands, which accounts for 70% of the whole Cerrado distribution (Oliveira et al., 2017; Pereira et al., 2018), the high deforestation rates within its potential distribution (43.74%) together with the low percentage of protected areas coverage (15.40%) can be a major threat to its conservation. In addition, most of the protected areas covering the distribution of *L. dekeyseri* belong to Protected Landscapes (10.86%), which is one of the less strictly protected IUCN categories in terms of the actual preservation of the landscape, as it can allow for activities such as traditional agriculture (Phillips & World Conservation Union 2002; Dudley, 2008). Thus, they might be less effective in helping to promote the conservation needs of *L. dekeyseri*. Even though we did not evaluate the role of Indigeneous Territories within the Cerrado for the conservation of *Lonchophylla dekeyseri*, they might play a significant importance since they cover 4.8% of the total area of the Cerrado and promote a significant reduction in deforestation (Carranza et al., 2014; Resende et al., 2021).

Nectarivorous bat species are sensitive to deforestation in the Cerrado (Oliveira et al., 2017), and *L. dekeyseri* seems to be impacted by more intense deforestation in some habitat types, such as gallery forests and dry woodlands (Pereira et al., 2018). In addition, a large proportion of its distribution is located within fragmented and disconnected areas where deforestation has largely advanced in the last two decades (Grande et al., 2020). *L. dekeyseri* has also a small home range and it is unlikely to be able to move across deforested areas due to its high metabolic rates, small size, and dependence on caves to roost (Tschapka, 2004) is also one of the predictors of *L. dekeyseri* occurrence, has been linked with a higher chance of deforestation in the central-east portion of the Cerrado (Trigueiro et al., 2020) (Tab. 1), which overlaps with *L. dekeyseri* potential distribution. Thus, further deforestation is still likely to occur within the species range, which might deteriorate even more its conservation status in the near future.

Even though only a small percentage of the caves in the distribution of *L. dekeyseri* are within deforested landscapes (6.66%), close to half of the caves had more than 50% of the natural vegetation around them deforested, which can have a high impact on roost occupancy and survival of *L. dekeyseri* in the landscape. Habitat degradation around caves has been shown to negatively impact the presence of some species, including some nectarivorous and endangered species (Sousa et al., 2020; Vargas-Mena et al., 2020). Since the small home range of *L. dekeyseri*, and deforestation around caves can hamper bat distribution on larger scales (Aguiar et al., 2014; Sousa et al., 2020), it is urgent

that the vegetation around the caves potentially used by *L. dekeyseri* are protected or restored in order to increase the suitability of roosts for the species.

A large proportion of the deforestation in the Cerrado has been linked with the expansion of cattle ranching (Lahsen et al., 2016), which has an impact on many other bat species, including the common vampire bat (*Desmodus rotundus*) (Greenhall and Schmidt, 1988; Ávila-Gómez et al., 2015; Gonçalves et al., 2017). The presence of the common vampire bat in the landscape has been shown to also be a threat to *L. dekeyseri*, due to the conflict with farmers because of the economic risk of losing their livestock to bat transmitted diseases (Shapiro et al., 2020). Cattle ranchers are known to poison cave bats and cause roost destruction to kill hematophagous bats, but this activity can also affect the survival of other bat species, such as *L. dekeyseri* (Aguiar et al., 2010). Thus, resolving bat-human conflicts is crucial for the conservation of *L. dekeyseri* in deforested landscapes.

Patterns of mining on Dekeyser's nectar bat distribution

Mining is the sixth major threat to bats worldwide, while deforestation is considered the first (Frick et al., 2019)). However, since 55.83% of its potential distribution and 59.16% of the caves found within its distribution are threatened due to mining, this is an important threat to *L. dekeyseri*. Although caves are considered important bat roosts, cave management is still poorly represented in interventions focused on bat conservation, with only a small proportion of papers published about the impact of mining on biodiversity (Furey and Racey, 2016; Sonter et al., 2018). Mining activities represent an important portion of Brazilian gross domestic product (5%) (MME, 2018). Although mining activities in the Cerrado represent only close to 10% (20509 ha) of the total area of mining activities in Brazil (MAPBIOMAS 2020), this impact is likely to be stronger for Cerrado caves, since most Brazilian caves were recorded in this domain (Jansen and Pereira, 2015). While only a small proportion of the types of mining activities on the caves in our study were shown to be indirectly related to deforestation (17.82% – soil broker, limestone factory, and fertilizers), extensive deforestation resulting from mining activities can extend up to 70 km from the source in some Brazilian forests (Sonter et al., 2017). This impact is mainly due to pollution, deforestation, and urbanization resulting from mining (Sonter et al., 2018). Thus, the impact of mining activities on the caves used as roosts by *L. dekeyseri* is likely to have synergistic effects on the landscape and contribute to the deforestation pressures that the species is facing.

Since the presence of genetically viable populations of an animal species threatened with extinction is one of the criteria in the Brazilian legislation to consider a cave as a high priority for conservation and receive full protection (Brasil, 2017), our study is extremely important to highlight which caves within the Cerrado could be hosting viable populations of *L. dekeyseri*, and should therefore be carefully surveyed in order to have its conservation status established. Interestingly, the relationship between the conservation of *L. dekeyseri* and the caves it roosts is reciprocal. Not only caves are important to be preserved as roosts for the conservation of *L. dekeyseri*, but the presence of *L. dekeyseri* in caves is also an important factor in promoting cave preservation. Besides, since *L. dekeyseri* also share caves with at least 27 other bat species, which represents 42.19% of all bat species known to roost in caves within the Cerrado (Bredt et al., 1999; Coelho, 1999; Portella, 2010; Bredt et al., 1999; Oliveira et al., 2018). Thus, the conservation of caves for *L. dekeyseri* is also likely to promote the conservation of many other cave roosting bat species in the Cerrado. However, the legislation and the criteria used for the protection of Brazilian caves is rapidly changing, due to increasing pressure from the mining sector, threatening even the caves that are considered of maximum priority for protection and their associated fauna (Ferreira et al., 2022; Oliveira et al., 2022).

Conservation and gaps on Dekeyser's nectar bat distribution

Our study clearly shows that caves play an important role in the conservation of *L. dekeyseri*. Protecting caves and the habitats around them should be a priority to counteract the pressure that mining and the agribusiness exerts on caves and the cave-dwelling fauna. However, caves within the potential distribution of *L. dekeyseri* and the sites where the species has been recorded showed clear differences in their quality for species conservation. According to the zonation analysis, most of the species potential species distribution is located in sites that have intermediate priority for the species conservation, but caves are more often located in low priority ones. This poses a complicated scenario for the conservation of the species, as the low roost availability in high quality sites might act as a bottleneck for the conservation of the species, since *L. dekeyseri* is known to roost exclusively in caves, and the quality of cave surroundings can potentially impact its conservation (Souza et al., 2020). Thus, urgent interventions are needed not only to survey high quality caves within the potential distribution of *L. dekeyseri*, but also to protect their surroundings from safeguarding potential future colonization events and population establishments of the species within these caves. Finally, there is anecdotal evidence that *L. dekeyseri* might be a species complex composed of a few cryptic species (Coutinho, 2007). Further work is still needed to assess intraspecific genetic and evolutionary divergence within the species, which might change its conservation status, as has been suggested by research on other Cerrado endemic organisms (Domingos et al., 2014; Silva et al., 2014).

Conclusions

The Dekeyser's nectar bat (*Lonchophylla dekeyseri*) faces a challenging situation in terms of its conservation within the Cerrado since more than half of its potential distribution has already been deforested with a small portion present within strictly protected areas. Additionally, its only known roost (caves), which is also one of the main predictors of its occurrence in the landscape, are heavily threatened due to mining across its distribution with only ~15% of them preserved inside strictly protected areas. More cave and field surveys are needed in order to better understand which factors are important for the occupation of the caves by *L. dekeyseri* (cave length, mean cave temperature, cave isolation, number of caves clustered together, etc.) and how important for its conservation are factors such as deforestation around the caves and mining pressures. These surveys are essential for the species conservation in the face of the rapidly changing Brazilian legislation regarding cave protection, which has been constantly weakened in the last years due to increasing mining pressures. Moreover, high Cerrado deforestation rates are an important threat for the conservation of the species across its distribution, which is already highly deforested. Furthermore, deforestation is likely to decrease the genetic flux between populations and reduce the suitable areas that still remain for the species, which is likely to be highly dependent on floral resources to move across the landscape. Thus, we recommend creating more strictly protected areas (IUCN categories Ia, II, and III) to cover a higher percentage of the potential distribution of *L. dekeyseri* and the caves it might be using as a roost. Additionally, we urge the government to reinforce the legislation and fiscalization to protect Brazilian caves, and preserve and restore the vegetation across the Cerrado biome. We hope our findings stimulate governance and bat researchers to promote more research studies and conservation initiatives about *Lonchophylla dekeyseri*. We also hope the maps provided here generate discussions that will improve the knowledge regarding the distribution and ecology of endangered bats. 🐉

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