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Persisting while changing over time: modelling the historical biogeographic of cave crickets (Orthoptera, Grylloidea) in Neotropics

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Abstract

Using species distribution modelling (SDMs) techniques, we predicted the biogeographic history of crickets commonly found in Neotropical caves as a way to detect potential long-term environmental refuges in South America. Our models were built based on a thorough investigation of existing database regarding the genus *Endecous* Saussure, 1878 (Ensifera: Phalangopsidae) occurrences. The predictions of their distribution were obtained for two paleoclimate scenarios (LGM — 21 ka and Mid-Holocene — 6 ka), the current climate scenario (0 ka) and one future global warming climate scenario (RCP8.5, 2080–2100). Our findings suggest that in the past, the potential distribution of the crickets was wider, with potential forest corridors connecting different karst areas with caves within their occupancy area. The future prediction indicates a drastic reduction in their spatial distribution with an increased potential for isolation in subterranean ecosystems. Atlantic humid forest patches and caves represent the main environmental refuges for these crickets. Considering the ongoing impacts on surface environments and future climate change, the conservation of caves and karst landscapes has become one of the main strategies for the maintenance of these crickets and all the correlated subterranean communities.

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Introduction

Caves comprise natural cavities associated with different types of lithologies, that allow the colonization of different organisms (Moldovan *et al.* 2018, White & Culver 2012). In South America, caves are formed in geological groups dating from the Precambrian (Bolivia and Paraguay), Jurassic, Tertiary (Venezuela) and Cretaceous (areas along the Andes Mountain range, e.g., Bolivia, Colombia, Ecuador, Peru) (Auler 2004). In Brazil, caves are associated with rocks of different ages, since Paleoproterozoic to Quaternary (Auler *et al.* 2019), which means that current caves were already present in rock formations at least a few hundred thousand years ago.

Since the Lower Palaeocene (66 Mya) until today, many climate changes cycles (glacial and interglacial periods) occurred that initiated the genesis of vegetation adapted to the dry climate in South America (Cox *et al.* 2016), possibly influencing cave environments along these ranges, considering that most organic resources that supply caves come from the surrounding landscape (Kováč 2018). These climate changes cycles resulted in dry forests (e.g., Chaco, Savanas, Cerrado and Caatinga) and humid forests (Amazon and Atlantic Rain Forest) (Ledo & Coli 2017, Olson *et al.* 2001, Werneck *et al.* 2011). However, during the glaciation and interglaciation periods, several connections were established/lost between humid and dry forests (Cox *et al.* 2016). These events are widely known to have led to the isolation and connection of different taxonomic groups in different ecosystems (Sobral-Souza *et al.* 2015, Vitorino *et al.* 2018, Vivo 1997, Werneck *et al.* 2011), including hypogean environments (Pérez-González *et al.* 2017, Polhemus & Ferreira 2018).

Forests and caves can be environmental "refuges" for organisms that evolved or transited in many of these paleoenvironments (Bryson *et al.* 2014, Pointing *et al.* 2014). Consequently, the combined study of epigean (forests) and hypogean habitats (caves) may allow a better understanding of the biogeographic history of cave-dependent taxonomic groups (Pérez-González *et al.* 2017). This combined assessment allows the establishment of the relictual species and trace possible connections, routes and reservoir used by previous lineages in response to large-scale climate change, e.g., glaciations and interglaciations (Bryson *et al.* 2014, Pointing *et al.* 2014).

Cave crickets belong to the suborder Ensifera (Insecta: Orthoptera) and are omnivorous or scavengers (Deharveng & Bedos 2018). In the Neotropical region, the most diverse family of cave crickets is Phalangopsidae (Ensifera: Grylloidea) (Deharveng & Bedos 2018, Desutter-Grandcolas 1995). These crickets are active at night while remaining sheltered during the day, refuging in hollow trees, crevices, burrows or under dead branches (Desutter-Grandcolas 1993). Hence, their nocturnal habit favoured the use of caves as shelters, and a large number of species can be found in such subterranean environments, using caves as diary refuge ("cavicolous" *sensu* Desutter-Grandcolas 1995) or living strictly inside the caves due to isolation processes (troglobitic *sensu* Desutter-Grandcolas 1995).

In particular, the genus *Endecous* (Orthoptera: Grylloidea: Phalangopsidae) could be a good model group for large-scale studies as they present species occurring in both epigean and hypogean environments (Bolfarini & Bichuette 2015, Castro-Souza et al. 2020a, 2020b, Souza-Dias et al. 2014). In addition, resources derived from cave crickets, such as dung, bodies, carcases and eggs, can directly be consumed by several other cave invertebrate species, thus contributing to the structuring of subterranean communities (Lavoie et al. 2007, Mammola et al. 2019a, Taylor 2003, Taylor et al. 2005). This shows their biological relevance as a key group for ecological and evolutionary studies in caves (Bento et al. 2021, Fagan et al. 2007, Lavoie et al. 2007). The maintenance of key groups in caves is essential for subterranean communities' conservation and a better understanding of the temporal dynamics in these environments.

However, the true spatial distribution of *Endecous* (Wallacean shortfall) as well as many caves are unknown (Racovitzan shortfall) (see Ficetola et al. 2019, Hortal et al. 2015). Considering that current global warming affects in both epigean and hypogean habitats (Mammola et al. 2019b), it is expected that *Endecous* crickets can present changes in their spatial distribution over time as adaptive response (see Bellard et al. 2012). Therefore, the use of *species distribution models* (SDMs) (Guisan & Thuiller 2005, Peterson et al. 2011) provides a better understanding of temporal dynamics (past, present and future) and detects historically stable areas (stability consensus), when different scenarios of these models overlap (Carnaval et al. 2009, Sobral-Souza et al. 2018, Terribile et al. 2012). Such models allow to infer the potential impacts of climate change on *Endecous* ecology and conservation in the face of its potential distribution.

Here, we aimed to predict the biogeographic history and future distribution pattern of the crickets *Endecous* in South America, as well as to understand the spatio-temporal rearrangements of the genus to detect possible refuges. We hypothesized that (i) in the past (LGM 21 ka) the potential distribution of the genus *Endecous* was geographically wider, highlighting potential links between cave environments as result of forest vegetation expansion (Sobral-Souza et al. 2015) and (ii) in the future, the potential distribution of the genus *Endecous* will be reduced and restrict to caves from South America, as a direct result of restriction of forest habitats.

Materials and methods

Dataset compilation for *Endecous* Saussure (1878) occurrences

Niche models are based on environmental attributes suitable for species occurrence (Smith et al. 2019). Since most of the species

known for the genus *Endecous* are not formally described (Castro-Souza et al. 2020a), and some of them only have a single occurrence (Cigliano et al. 2022), we considered here the genus taxonomic level, since the genus monophyly is well supported in the cladistic literature for Phalangopsidae (Souza-Dias et al. 2015). Furthermore, most species in this genus exhibit a strong association with cave environments, unlike groups found in the same monophyletic clade of *Endecous* (genera *Luzarida*, *Melanotes* and *Palpigera*, sensu Souza-Dias (2015)), that have never been found inhabiting caves (hypogean environment), but leaf litter, tree trunks and holes or interstices up in tree (Cigliano et al. 2022; Desutter-Grandcolas 1995). In particular, *Endecous* species present apparently similar ecological niches in such subterranean habitats (e.g., similar dietary requirements, distribution inside caves), which justifies the use of the genus in such analysis.

Data occurrences of the genus *Endecous* were obtained from different sources. (i) Taxonomic Literature: references available in Orthoptera Species File Online (Cigliano et al. 2022);9 (ii) Photographs that allowed identifying the presence of the genus in online platforms: Platform iNaturalist (research from family Phalangopsidae, genus *Endecous*; available at https://www.inaturalist.org/); Blog (available in http://www.blog.gpme.org.br/); Personal files of specialists in subterranean biology (Ferreira, R.L.; Souza-Silva, M.; Cardoso, R.C., Rabelo, L.R.); (iii) Bioespeleological Studies and Orthoptera Ecological Studies: papers, dissertations, thesis and academic abstracts; (iv) Expert Observation: mentioned in the literature of studies with *Endecous* species (e.g., Mello, F.A.G.; Zefa, E.; Souza-Dias P.G.B; Bolfarini M.P.; Acosta, R.C.).; (v) ISLA Collection: specimens cataloged in the "Collection of Subterranean Invertebrates of Lavras" (ISLA), Center of Studies on Subterranean Biology, Department of Ecology and Conservation, Federal University of Lavras, Brazil.; (vi) Technical Reports: studies required by the Brazilian legislation to carry out projects in areas with caves or to regulate cave visitation. In this case, some of these studies presented locations with photos of fauna that enabled the identification and confirmation of the genus on site.

A total of 516 occurrences were registered (Figure 1, Supplementary Table 1). The georeferencing of the occurrences was obtained with the geographic coordinate system WGS84 and clustered in two categories: (I) "Records" (data with exact coordinates) and (II) "Approximate record" (data lacking exact coordinates and based on descriptive reference, e.g., municipality, city, etc.). For the Approximate Record data, we obtained the geographic coordinate by analysing satellite images of habitat and forest patches nearest the centroid described in the bibliography. Since the model's building was carried out with a 0.5º resolution grid cell, the approximate records do not jeopardize it. Data from sources whose taxonomic identification was not conclusive or confirmed were excluded. Then, with the georeferenced occurrences, we made a grid of cells with a resolution of 0.5° (~55 × 55 km) in the South American region. We filtered only one point of occurrence within each cell, thus totalling 124 cells with *Endecous* records (Figure 1b). This procedure made it possible to reduce the sampling bias, as the occurrence data tend to be concentrated in more studied areas.

In order to determine the paleo and the current distribution, as well as the future genus distribution in South America, we used the bioclimatic quantitative data obtained from five Atmospheric-Ocean Global Circulation Models (AOGCMs) adapted from Lima-Ribeiro et al. (2015): (1) CCSM4; (2) CNRM-CM5;
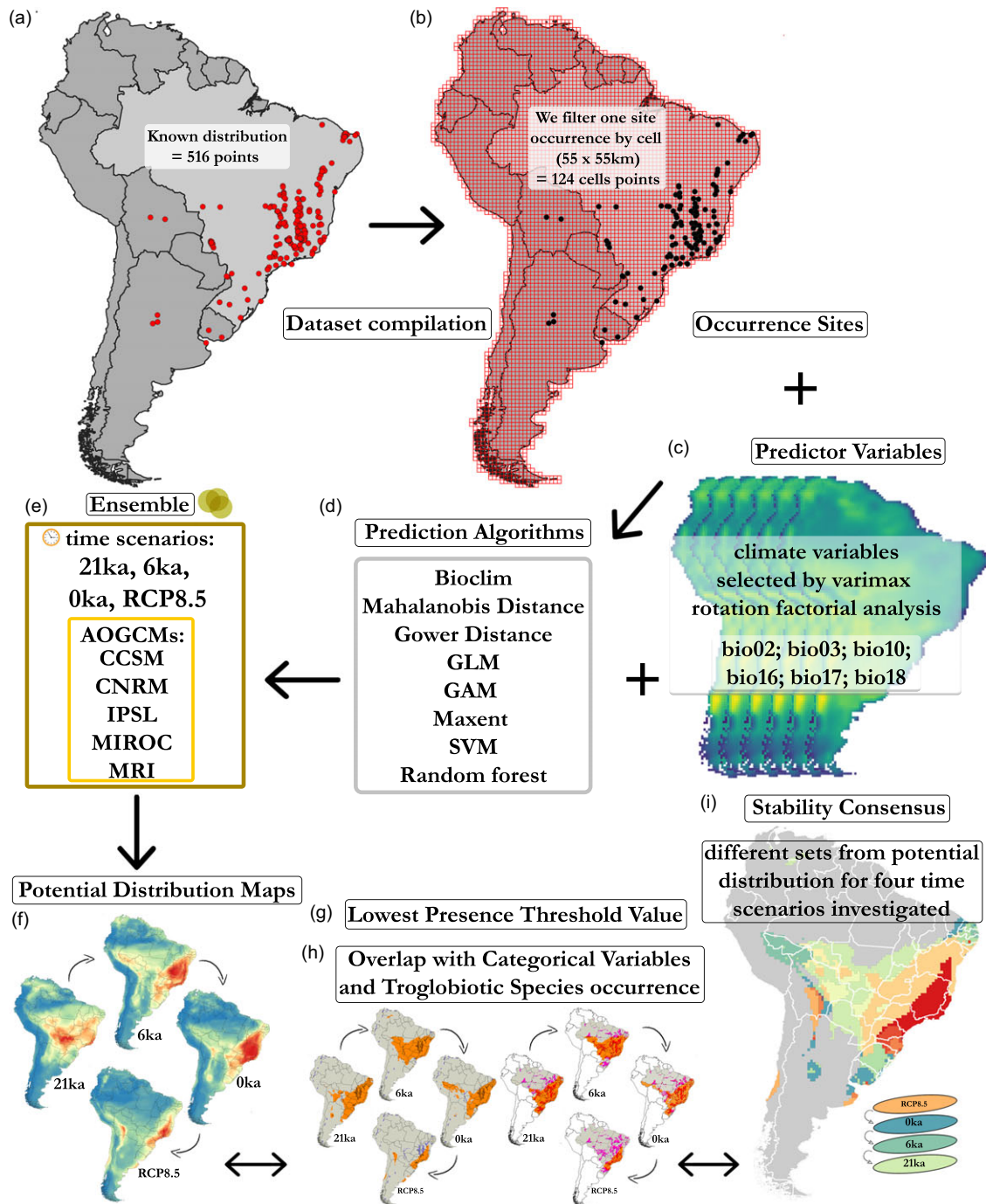
Figure 1. Outline summarizing our methodological and analytical steps to predict the potential distribution of the genus *Endecous* Saussure, 1878. The first step consisted in compiling as much data as known for the distribution of the genus (a). Next, we filter the occurrence data, leaving only one presence point per grid (b). The third step consists of associating the occurrence sites (b), predictor environmental variables (c), and algorithms (d), to building models. For this, we use the method of Ensemble (e), which consists of superimposing the models for each algorithm, inside each AOGCM, for each time scenario investigated (e). Then consensus maps are built for the genus (f). Next, we use the *Lowest Predicted Value* Threshold *(lpt)* to create binary presence maps, as of the lowest predicted value on environmental suitability according to the occurrence sites. Finally, binary maps overlapped with categorical variables and occurrence sites of troglobitic species. In addition, we also overlap the binary maps in the four-scenario investigated to check possible areas climatically stable of the niche potential of *Endecous*.

(3) IPSL-CM5ALR; (4) MIROC-ESM; (5) MRI-CGCM3. Since these models represent the temporal dynamics and climate conditions of the planet, they enable us to simulate the past, present and future climate conditions. The use of multiple AOGCMs simulations is strongly suggested in SDMs studies (Zurrell *et al.* 2020).

Since there might be distinct patterns presented by the AOGCMs, we used different climate projections (see Varela *et al.* 2015). For each AOGCMs, six bioclimatic variables from the EcoClimate database (http://www.ecoclimate.org) were used: Bio02 = Mean Diurnal Temperature Range (mean of monthly (max temp – min temp)); Bio03 = Isothermality; Bio10 = Mean

Table 1. Results of varimax rotation factorial analysis, used for the selection of more explanatory variables among the 19 bioclimatic variables (Nix 1986, Hijmans et al. 2005) for the construction of SDMs

Bioclimatic Variables/Vectorial Axes (I—VI)	I	II	III	IV	V	VI
BIO1	0.94	0.12	0.16	0.27	0.05	0.01
BIO2	0.06	0.13	0.32	0.16	**0.91**	0.15
BIO3	0.35	0.23	0.01	**0.78**	0.02	0.17
BIO4	0.34	0.34	0.03	0.79	0.28	0.02
BIO5	0.94	0.07	0.2	0	0.2	0.16
BIO6	0.83	0.2	0.06	0.44	0.24	0.11
BIO7	0.16	0.24	0.15	0.7	0.64	0.02
BIO8	0.92	0.01	0.15	0.07	0.03	0.19
BIO9	0.8	0.19	0.11	0.42	0.12	0.26
BIO10	**0.98**	0.02	0.16	0.01	0.05	0.05
BIO11	0.86	0.2	0.13	0.43	0.11	0.03
BIO12	0.11	0.89	0.25	0.24	0.04	0.24
BIO13	0.16	0.93	0.13	0.22	0.09	0.1
BIO14	0.25	0.08	0.91	0	0.17	0.08
BIO15	0.25	0.18	0.78	0.18	0.06	0.03
BIO16	0.12	**0.93**	0.13	0.18	0.06	0.21
BIO17	0.11	0.2	**0.92**	0.16	**0.13**	0.09
BIO18	0.17	0.39	0.19	0.16	0.15	**0.71**
BIO19	0.09	0.6	0.18	0.04	0.12	0.31
S.S.L	6.135	3.507	2.716	2.598	1.547	0.917
Proportion	0.323	0.185	0.143	0.137	0.081	0.048
Cumulative	0.323	0.507	0.650	0.787	0.869	0.917

Temperature of Warmest Quarter; Bio16, Bio17, Bio18 (precipitation of Wettest, Driest and Warmest Quarter, respectively). These variables were selected from a total of 19 available (Lima-Ribeiro et al. 2015), through Varimax rotation factorial analysis (Fávero et al. 2009) (Figure 1c, Table 1). The six selected variables showed low correlation with each other and high representativeness in the explanation of orthogonal axes.

Niche modelling of the genus *Endecous* Saussure 1878

Different mathematical algorithms that have been currently used for niche models building aimed to infer species spatial distribution patterns (Barry & Elith 2006, Diniz-Filho et al. 2009, Zurrell et al. 2020). We used eight algorithms to test the potential spatial distribution of the genus *Endecous* in four temporal predicted scenarios: 21 ka (Last Glacial Maximum), 6 ka (mid-Holocene), 0 ka (1950–1999, current) and RCP 8.5 (mean of simulations for 2080–2100, with increasing CO_2 emissions towards the end of the 21st century) (Figure 1d). Such algorithms can be categorized as: *i*—algorithms of presence: Bioclim (Nix 1986); Mahalanobis Distance (Farber & Kadmon 2003) and Domain – Gower distance (Carpenter et al. 1993); *ii*— algorithms of presence/absence: General Linear Model (GLMz) (Guisan et al. 2002) and General Additive Model (GAM) (Guisan et al. 2002); *iii*—Machine Learning Algorithms: Support Vector Machines (SVM)

(Tax & Duin 2004), Maximum Entropy (Phillips & Dudik 2008) and Random Forest (RDNFOR) (Guisan et al. 2002).

For each algorithm, 10 randomly repetitions were performed using the bootstrapping partition, with double partitioning for occurrence sites (70% training and 30% test), in order to evaluate the model predictive power (true skill statistic (TSS)) (Allouche et al. 2006). TSS values close to one (1) were classified as good, zero (0) values were classified as random and negative values (close to −1) were classified as poor models.

The ensemble method was used to concatenate all built models in a single map (Araújo & New 2007): first, the models obtained in each algorithm (10 replicates), then between the algorithms (8 algorithms), and finally the AOGCM (5AGCMs) (Figure 1e). A total of 400 models were built (10 models × 8 algorithms × 5 AOGCMS) for each temporal period (21 ka, 6 ka, 0 ka and 2100). Thus, each cell on the map has a prediction value ranging from 0 to 400, which, divided by 400, represents the prediction frequency of *Endecous* occurrence within the grid (Figure 1f; Supplementary Figure 1). Then, we used the *Lowest Predicted Value Threshold (lpt)* to create binary maps of presence (Pearson et al. 2007) (Figure 1g).

The temporal binary maps were compared with the South American karstic areas (shapefile available at: https://www.fos.auckland.ac.nz/our_research/karst/. Accessed March 21, 2021), and the records of troglobitic *Endecous* species (only occurring in caves) (Figure 1h). The records of cave-restricted species were not used for the niche models building since it was assumed they were not being influenced directly by external climatic variables used on the models, as the remaining species (which are troglophilic, thus, presenting external populations). Furthermore, we also contrasted the binary maps with the Cave Occurrence Areas in Brazil, data provided by the National Center for Cave Research and Conservation (CECAV) (shapefile available at: https://www.icmbio.gov.br/cecav/projetos-e-atividades/provincias-espeleologicas.html. Accessed March 21, 2021) (Figure 1h). Finally, we ensembled the temporal binary potential distribution maps to obtain consensus on areas of climatic stability within the possible potential niche of *Endecous* (representing potential refuges for the genus) (Figure 1i).

All analyses mentioned above were performed in R (R Development Core Team, 2021). Species distribution models were built using *dismo* package (Hijmans et al. 2022). Maps were made through QGIS 3.4 (Free 2021) and Inkscape (Inkscape Team 2004–2021) software.

Results

The niche models showed great adjustments, with TSS values greater than 0.5 for each algorithm analysed (Table 2). The six bioclimatic variables selected explained approximately 91% of the environmental variation in South America climate conditions.

The temporal predictions showed that *Endecous* had a wide spatial distribution 21 ka ago (LGM), extending along central and western South America, with additional small patches in northwestern South America, between Colombia and Venezuela. During the LGM, the *Endecous* distribution coincided with the main existing Brazilian karstic areas (e.g., Araras, Corumbá, Açungui, Bambuí and Una geological groups) and with two karstic areas of Bolivia and Paraguay (Figure 2, 21 ka).

The spatial paleodistribution was fragmented in the middle Holocene (6 ka) with occupancy losses in central South America, in the Araras and Corumbá carbonatic groups, respectively,

Table 2. True Skill Statistic (TSS) values for each combination of algorithms and AOGCM for SDMs of the genus *Endecous* Saussure, 1878

ALGORITHM/ AOGCMs	BIOCLIM	GAM	GLM	GOWER	MAHALANOBIS	MAXENT	RANDOMFOREST	SVM	Mean	Standard Deviation
CCSM	0,5405	0,6757	0,5216	0,5162	0,6378	0,6757	0,6568	0,6595	0,6105	0,0712
CNRM	0,4703	0,6405	0,4351	0,4811	0,6054	0,5919	0,6243	0,6649	0,5642	0,0882
IPSL	0,5892	0,6946	0,5189	0,6243	0,6892	0,7000	0,7027	0,7108	0,6537	0,0696
MIROC	0,4081	0,6892	0,4297	0,3568	0,7270	0,6622	0,7108	0,7162	0,5875	0,1592
MRI	0,5189	0,6405	0,5108	0,5324	0,7216	0,6405	0,6784	0,6432	0,6108	0,0795
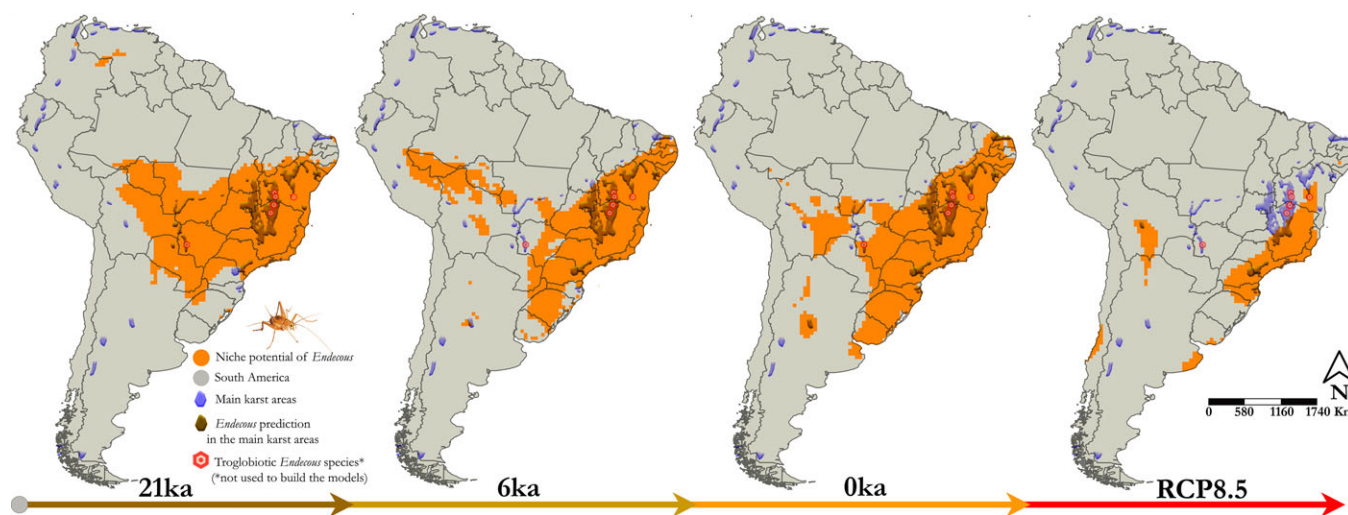
Figure 2. Potential distribution for genus *Endecous* Saussure, 1878 during Last Glacial Maximum (21 ka), Mid-Holocene (6 ka), Current (0 ka) and Future (RCP8.5, 2080–2100). The models were overlapping with the main karst areas in South America, since most of the genus is facultative in caves. The colouring of the arrows represents the temperature rise in each scenario (cold ⇒ hot).

located in the States of Mato Grosso and Mato Grosso do Sul (Brazil). However, a slight geographical expansion occurred in southern and northeastern Brazil, including part of the Apodi carbonatic group. Distribution patches may also be verified bordering Peru and Bolivia, southern Argentina and Andean regions during the mid-holocene (Figure 2, 6 ka).

The current *Endecous* potential spatial distribution is broader than the known occurrence data (Figure 1a), incorporating areas of central and northeastern South America. The predictions showed a distribution pattern similar to 6 ka ago and presented spatial losses and rearrangements along the distribution patches, mainly in the Andean region. In Brazil, there is an area gain in the central region, covering again some karst regions that had been lost in the middle Holocene (Araras and Corumbá groups). Furthermore, the distribution of *Endecous* has expanded towards northeastern and southern Brazil, with southward expansions to other countries, such as Uruguay and part of eastern Argentina (Figure 2, 0 ka).

The spatial predictions to future climate scenarios (RCP8.5, 2080–2100) showed a potential decrease in spatial occupancy and occurrence of *Endecous* in karstic areas of northeastern and southeastern South America. Its distribution will mainly occur in a continuous area in eastern and southeastern Brazil. Smaller occupancy patches are expected in southern Uruguay and eastern Argentina and throughout the central and southern Andean region, comprising the borders with Bolivia, Argentina and Chile, respectively. Such distributional retractions exclude possible

occurrences of the genus in all karstic areas of Argentina and the entire territory of Paraguay (Figure 2, RCP8.5).

Regarding the analysis of *Endecous* distribution in cave occurrence areas in Brazil, the models showed that 21,000 years ago all *Endecous* populations were established throughout all biomes and occupied large karstic areas, likely inhabiting caves that already exist in these regions (Figure 3, 21 ka). However, it also showed that there was a reduction in *Endecous* distribution in central Brazil approximately 6,000 years ago, and the same pattern has been observed for the current scenario (Figure 3, 6 ka and 0 ka). The predictions for future distribution patterns (2080–2100) show that a rearrangement could occur with an intensive decrease in the genus distribution in areas of cave occurrence in central, southeastern and northeastern Brazil (Figure 3, RCP8.5).

The models revealed possible refuges for *Endecous* in the four scenarios analyzed (21 ka ∩ 6 ka ∩ 0 ka ∩ RCP8.5), including epigean and hypogean environments in Brazil (Figure 4a and b – karst areas in red color). On the epigean regions, its distribution remained stable mainly in Atlantic rainforest regions, although it also comprised two smaller regions of the Caatinga (semi-arid) and Cerrado (savanna) biomes (Figure 4). In the hypogean environment, the most stable regions (21 ka ∩ 6 ka ∩ 0 ka ∩ RCP8.5) comprised part of the Açungui group and the southernmost Bambuí and Una groups. In addition, in at least one of the temporal scenarios, the distribution encompasses karstic areas of South America (Figure 4b – karstic areas in orange).
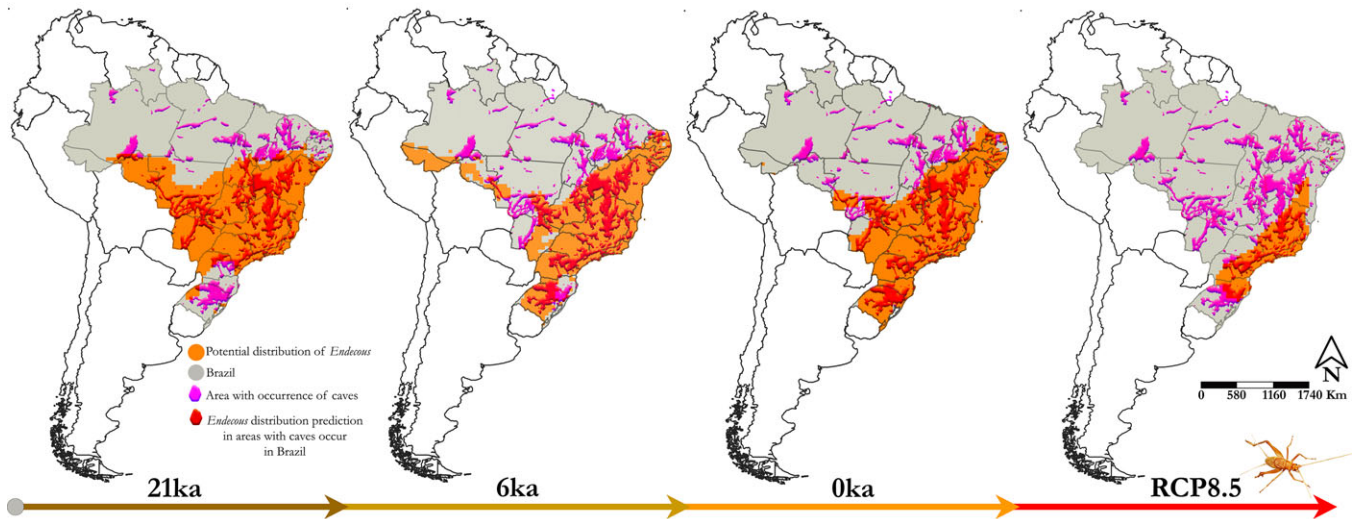
Figure 3. Potential distribution for genus *Endecous* Saussure, 1878 during Last Glacial Maximum (21 ka), Mid-Holocene (6 ka), Current (0 ka) and Future (RCP8.5, 2080–2100). The models were overlapping the main areas with the occurrence of caves from Brazil, since most known data in this study come from these environments. The colouring of the arrows represents the temperature rise in each scenario (cold ⇨ hot).
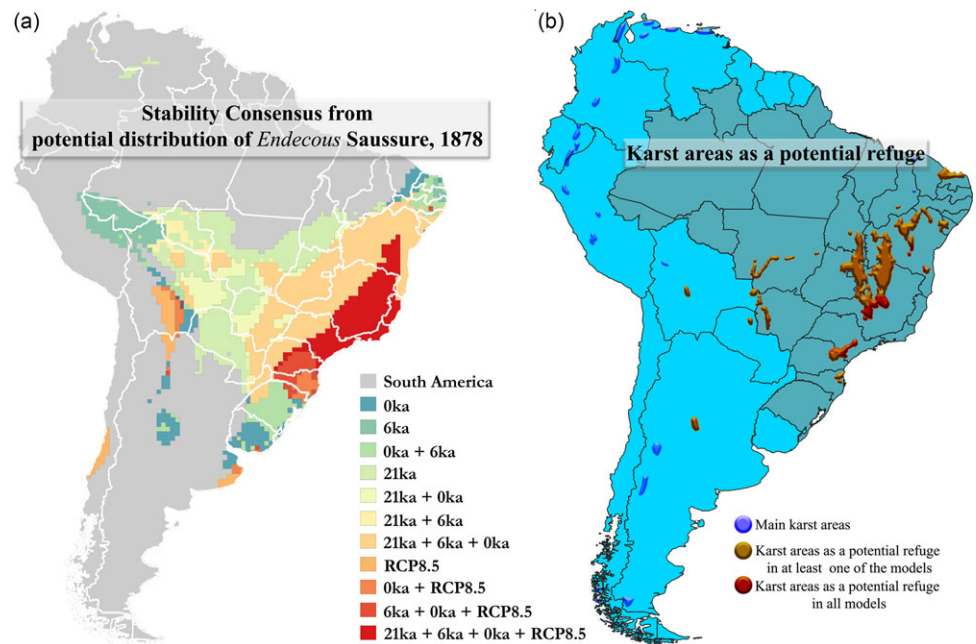

Figure 4. (a) Stability Consensus comparing different combinations between the four scenarios the potential distribution for genus *Endecous* Saussure, 1878. Legend: Last Glacial Maximum (21 ka), Mid-Holocene (6 ka), Current (0 ka) and Future (RCP8.5, 2080–2100); (b) Karst areas as a potential refuge from Species distribution models (SDMs) of the *Endecous* Saussure, 1878.

Discussion

Our findings suggest that the *Endecous* spatial distribution occupied a broad region in central and western South America, covering and linking groups of areas where caves were present (Figures 2 and 3, scenarios 21 ka and 6 ka). The current distribution scenario (0 ka) was similar to 6 ka, showing rearrangements and expansions to the northeast and south of South America (Figures 2 and 3, scenario 0 ka). For the future scenario, the predictions are worrying, as there is a retraction of almost two-thirds of the potential areas for the genus occurrence, isolating several regions with caves that were previously connected, which may indicate a reduction of suitable climatic areas and the isolation of *Endecous* in epigean and hypogean environments (Figures 2 and 3, scenario RCP8.5, 2080–2100).

By overlaying all models, it is possible to detect potential refuges for the genus in eastern and southeastern South America, mainly in the Atlantic Rainforests (Figures 2 and 3, overlapping scenarios 21 ka, 6 ka, 0 ka, RCP8.5). Furthermore, considering the current impacts on epigean environments, the conservation of karst landscapes can represent a vital action to preserve several *Endecous* lineages.

The Atlantic Rainforests as a source and temporal refuge of *Endecous* crickets

The current distribution and paleodistribution of *Endecous* encompass the late Pleistocene expansion and retraction cycles of humid forests in South America (see Ledo & Colli 2017, Sobral-Souza *et al.* 2015). Furthermore, their distribution in areas currently known as dry forest diagonal (Dinerstein *et al.* 2017, Olson *et al.* 2001), similarly to 6,000 and 21,000 years ago (e.g., Werneck *et al.* 2011, 2012), indicates that these areas could

have been transitional and expansion zones, where the *Endecous* could have colonized and established in caves. In addition, the presence of small refuges, such as hypogean habitats and/or vestiges of humid forests and riparian forests, or even certain preference for more shaded phytophysiognomies (e.g., Cerrado and Riparian Forests) in arid locations, may explain the occurrence of *Endecous* along dry forests, and in turn the constant presence of *Endecous* inhabiting caves in arid biomes (Castro-Souza *et al.* 2017, Souza-Dias *et al.* 2014, Zefa *et al.* 2014).

The abovementioned explanations corroborate many studies indicating that the dry diagonal was a permeable barrier (due to several persistent patches of wet vegetation) that split the South American humid forests into the Amazon and Atlantic Forest (Johnson *et al.* 1999, Redford & Fonseca 1986, Weisenberg & Mori 2020). The current distribution of many taxonomic groups, such as arachnids (Peres *et al.* 2017), small mammals (Costa 2003, Redford & Fonseca 1986), birds (Silva 1996, Willis 1992), reptiles (Weisenberg & Mori 2020), anurans (Vasconcelos & Doro 2016), butterflies (Cabette *et al.* 2017, Matos-Maraví *et al.* 2021) and crickets (De Campos *et al.* 2021) inside remnant humid forests along the dry diagonal is explained by this past separation of humid forests.

The spatial rearrangements (21 ka, 6 ka, 0 ka and RCP8.5) indicated that the most stable occurrence areas of *Endecous* are associated with the Atlantic Forest. This highlights moisture as a threshold condition for these crickets, since they depend on substrate moisture for oviposition (De Farias-Martins *et al.* 2017). Considering that caves frequently present high moisture content and climatic stability (Mejía-Ortíz *et al.* 2021, Moldovan *et al.* 2018, Sánchez-Fernández *et al.* 2018), the frequent observations of the genus associated with climatically stable regions within caves also coincide to what is exposed by the models. Furthermore, cave crickets may have sensitivity to desiccation (Lavoie *et al.* 2007) what favours their association to hypogean environments.

It is plausible to assume that humid forests have played an important role as population reservoirs for the genus *Endecous*. Furthermore, since the genus was continuously distributed over a vast geographic region, connections between caves were established, along with colonization events in such environments, supporting our first hypothesis.

Analysis in different temporal scenarios (21 ka, 6 ka, 0 ka and RCP8.5) based on the current *Endecous* distribution showed that these crickets almost did not reach the north of the Amazon biome. The same pattern was observed for the sympatric genus *Eidmanacris* Chopard, 1956 (Castro-Souza *et al.* 2020b), a group that is also dependent on remnants of humid forests and cave habitats (De Campos *et al.* 2021). Although these two genera can co-occur inside caves, there is spatial segregation between their populations, with *Endecous* inhabiting deeper regions and *Eidmanacris* occurring near cave entrances, which would avoid competitive exclusion (Castro-Souza *et al.* 2020b, Paixão *et al.* 2017).

In the Amazon biome, other genera of phalangopsids have been registered inside caves, as *Uvaroviella* Chopard, 1923 and *Phalangopsis* Serville, 1831. Additionally, studies in 844 caves in this region have never reported *Endecous* or *Eidmanacris* (supplementary material, Jaffe *et al.* 2016). Accordingly, it is plausible to infer that its dispersion is limited to the dry diagonal and Atlantic rainforests during the glacial and interglacial cycles. It is also possible that if there had been populations of *Endecous* in the Amazon biome in the past, interspecific competition might have occurred between *Endecous* and other crickets of similar habitat preference, as the genus *Phalangopsis*. This could have led to the exclusion of *Endecous* from the Amazon biome.

Another factor to be considered is that the *Endecous* species cannot fly because they are micropterous or apterous, which limits their dispersion through migration corridors with suitable habitats (e.g., forest habitats or caves, according to what we know). This also helps to explain the current and paleodistribution of the genus along the forests and caves inside of the Cerrado biome, since there is a greater floristic and climatic similarity between the Cerrado and the Atlantic Forest, than the Cerrado and the Amazon forest (Méio *et al.* 2003, Nimer 1989).

The future predictions (2080–2100) showed that the potential distribution of *Endecous* crickets would become restricted on epigean habitats, with its potential isolation in caves in South America, corroborating our second hypothesis. This habitat reduction or restriction can be intensified because favourable epigean habitats, such as the Cerrado and Atlantic Rainforests, have been strongly threatened by agricultural expansion, urbanization and mining (Dinerstein *et al.* 2017, MapBiomas Project 2021, Mittermeier *et al.* 2004, Myers *et al.* 2000, Souza *et al.* 2020, Sugai *et al.* 2015).

The continued deforestation of the Atlantic Forest has intensified in Brazil (2018–2019), especially in State of Minas Gerais (INPE 2021, SOS Mata Atlântica 2021). The Brazilian political–environmental scenario often brings bills (e.g., PL 3729/04, PL 191/20 (Brasil 2021a, 2021b)) seeking to use regions currently protected and conserved by law. This certainly represents a constant threat, which makes the effects of future climate change even more severe for the ecology of these crickets and associated subterranean biota.

Finally, although our models have indicated the genus is more intimately associated with the Atlantic Forest than with the dry diagonal, it is not possible to address any origin for the genus without an updated and broadly taxon-inclusive phylogeny. Furthermore, many of our records came from caves (hypogean environments) since it is easier to find and sample *Endecous* species in such habitats. Thus, due to the extensive sampling gaps in surface environments, further samplings along the dry diagonal and the Amazon forest are recommended, as well as a taxonomic review of the genus, accompanied by molecular phylogeny. Only then, it will be possible to understand more precisely the biogeographic pathways used by the different species of this genus.

Caves as potential refuges for the species conservation in the future

The Atlantic Rainforest and subterranean environments are the main refuges for the crickets *Endecous*. Furthermore, due to the fact that the hypogean environments are more climatically stable than epigean (Badino 2010, Brookfield *et al.* 2016, Mammola *et al.* 2019b), many *Endecous* populations distributed in caves were less vulnerable to climatic oscillations that occurred at the surface in the past and are likely to occur in the future (2080–2100). Hence, considering that caves are important refuges, and that such environments can become, in some areas, the only suitable habitat for species in the face of global warming, cave preservation is crucial for the maintenance of many populations of different species.

Brazilian's legislation on the protection of the spelaeological heritage provides for a categorization of caves into levels of relevance (maximum, high, medium or low), being the caves of 'maximum relevance' the only ones fully protected (Decree No. 6640 of November 7, 2008 and Normative Instruction No. 01/2017, Ganem 2009). However, this legislation is currently under strong political debate, due to the proposal of a retrograde decree

(nº. 10.935/2022) which allows the destruction of any cavities, even those considered as presenting maximum relevance (Ferreira *et al.* 2022). Furthermore, most *Endecous* species are 'troglophiles' (facultative in caves), and only few species are restricted to cave habitats (troglobitic). Therefore, this may be a setback for *Endecous* conservation, since their presence would not be enough to classify a cave as 'maximum relevance', reinforcing that such habitats may be crucial for many species in the future.

Although we did not use records of troglobitic *Endecous* in our dataset, when superimposing such occurrences with the models built, it is evident that the ancestors of these species colonized the caves in the past, since the potential paleodistribution of the genus was wide and encompassed regions where such species currently occur. Thus, it is important to emphasize that facultative cave ancestors have great potential to become cave specialists in the future (Chapman 1982), with *Endecous* being a living example, given that it is one of the only two genera of crickets in Brazil with troglobitic species (Bolfarini & Bichuette 2015, Castro-Souza *et al.* 2020a, Souza-Dias *et al.* 2014). Furthermore, geographically isolated refuges may have contributed to the increase in speciation within caves (e.g., Castro-Souza *et al.* 2020a), which increases the taxonomic complexity of the genus (Castro-Souza, R.A & Ferreira, R.L. unpubl. data from analysis of DNA barcoding).

In addition, a phalangopsid (Luzarinae) found in an amber from the early Miocene (around 20 million years from the Dominican Republic (Heads 2010), demonstrates the ancient history of occurrence of this group in the Americas and allows us to assume that many ancestors of phalangopsid species could already be colonizing existing caves due to their nocturnal and foraging lifestyle. In particular, many South American cave phalangopsidae (e.g. *Adelosgryllus*, *Endecous*, *Phalangopsis* and *Strinatia*) (Campos *et al.* 2017, Castro-Souza *et al.* 2020b, Cigliano *et al.* 2022, Junta *et al.* 2020, Merlo *et al.* 2022, Mesa *et al.* 1999) reveal pre-adaptations reported for other cave crickets (Desutter-Grandcolas 1993; Desutter-Grandcolas 1997; Heads 2010), such as eye size reduced, loss of ocelli, absence of auditory tympana and body discoloration. However, to confirm that the traits are pre-adaptations, it is necessary to evaluate them together with the habitat from a phylogenetic perspective (Desutter-Grandcolas 1997). Thus, the past investigated in our study (the last 21 ka) likely represents just the "tip of the iceberg" in the biogeographic history of South American cave crickets, as uncountable events of colonization, speciation and extinction may have occurred in different caves along the continent, which highlights the need for more studies of evolution and biogeography of this group.

Caves are more than a refuge to the *Endecous* species. They are natural laboratories that play an important role on the biodiversity conservation and the understanding of evolutive processes which this crickets has been undergoing. These subterranean environments are also a source of important biological information regarding the evolutive lineages of this group. Furthermore, the study of key species, hereby represented by the genus *Endecous*, will certainly aid on the conservation of subterranean ecosystems (Wynne *et al.* 2021). This information may surrogate more well-defined conservation actions, which should not only aim at troglobite species, but also at some key facultative cave-dwelling groups. Although some organisms inhabiting caves are not restricted to these environments, they may be undergoing speciation processes and may also be key species to the subterranean environment. The data presented in this study broadens the knowledge of the crickets *Endecous* and highlights the importance of cave conservation for better biodiversity conservation policies.

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