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Influence of Quaternary climate change on the potential distribution of Atlantic Forest dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae)

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ABSTRACT

Influence of Quaternary climate change on the potencial distribution of Atlantic Forest dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). The role of Cenozoic paleoclimatic changes in the distribution of dung beetles species from the Atlantic Forest (AF) remains poorly understood. We used ecological niche modeling under different scenarios (present, 6 ka, 21 ka, and 120 ka) to investigate how climatic oscillations during the Quaternary might have influenced the distribution of species endemic to this region. Models were built for five of the nine dung beetle species of the *Dichotomius sericeus* group: *D. iannuzziae*, *D. irinus*, *D. laevicollis*, *D. schiffleri*, and *D. sericeus*. The models of climatic suitability for *D. irinus* and *D. laevicollis* show a similar historical pattern in response to climate change but were divergent from *D. iannuzziae*, *D. schiffleri*, and *D. sericeus*. *Dichotomius schiffleri* is the species with the smallest area of potencial occurrence. Over time, the species probably remained limited to lowland AF areas on the Brazilian coast and, it is currently found preferentially in Restinga ecosystems along the coast. Regarding the potential distribution models at the present, *D. iannuzziae*, *D. schiffleri*, and *D. sericeus* have potential distributions similar to their realized distribution. This study shows that the historical distribution of the *D. sericeus* species group has been influenced by paleoclimatic changes that occurred in the AF over the last 120 ka.

Introduction

The Atlantic Forest (AF) domain is dated to approximately 60 million years ago, when there was an area climatically suitable for the formation and expansion of a tropical forest (Por, 1992). In the last thousands of years, oscillations in global climate and sea levels resulted in drastic changes in biodiversity distribution (Vanzolini and Williams, 1981; Carnaval and Moritz, 2008).

Climate changes along the Last Glacial Maximum (LGM, around 21 thousand years ago) have been reflected in the evolutionary history of many taxa (Mustrangi and Patton, 1997; Costa et al., 2003; Pellegrino et al., 2005; Grazziotin et al., 2006; Cabanne et al., 2007; Thomé et al., 2014). The species comprising the AF, therefore, result from a dynamic evolutionary history, though many of the details of the processes involved remain unsolved (Mustrangi and Patton, 1997; Pellegrino et al., 2005). Two are the hypotheses most widely discussed about drivers of diversification in South American tropical forests (Moritz et al., 2000): (i) Pleistocene refugia (Haffer, 1969; Vanzolini and Williams, 1970; Prance, 1982; Graham et al., 2006; Rocha and Kaefer, 2019), and (ii) rivers as geographic barriers (Wallace, 1852; Campbell Junior et al., 2006, Latrubesse et al., 2010; Fernandes et al., 2012; Ribas et al., 2012; Maldonado-Coelho et al., 2013). The diversification process would occur through the reduction of gene flow between populations caused by geographic isolation (Dantas et al., 2011).

The effects of different paleoclimatic events on AF-endemic invertebrate taxa are still poorly explored, especially concerning megadiverse groups such as insects of the order Coleoptera (Erwin, 1985; Lü et al., 2020; Baird et al., 2021). Understanding the space-time dynamics of the ecological niche occupied by these groups can provide valuable insights into the drivers of diversification along habitat transitions in the AF, and about the future of species under global climate change scenarios (Hoffmann and Sgrò, 2011; D'Amen et al., 2012). For example,

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there is evidence that paleoclimate differentiation in the northern and southern AF portions resulted in biogeographic histories divergences (Ledru et al., 2005; Carnaval and Moritz, 2008).

Ecological niche modeling (ENM) is a technique used to predict environmental suitability for the occurrence of a particular species in a spatial area. For this purpose, data from the current distribution of the species and a set of environmental variables are used. This routine is widely employed as a way of predicting the potential distribution of species with diverse goals, including biological invasions (Peterson, 2011), evolutionary patterns (Graham et al., 2004; Paul et al., 2009), phylogeography (Carnaval et al., 2014; Peres et al., 2015), historical biogeography (Sobral-Souza et al., 2015), among other purposes that demonstrate the potential of using the modeling technique for past or future temporal scenarios (Hijmans and Graham, 2006).

These models have contributed to diminishing the gaps in the knowledge of species distribution, assisting projects for conservation, such as identifying hotspots of biological diversity (Lehmann et al., 2002; Arcos et al., 2012), establishing conservation strategies for species in the current or future scenario (Guisan and Theurillat, 2001; Moritz, 2002; Mawdsley et al., 2009; Algar et al., 2009; Guisan et al., 2013; Morato et al., 2014; Porfirio et al., 2014; Hoffmann, 2021), and understanding patterns of species distribution and community establishment processes (Thuiller et al., 2006; Guisan and Rahbek, 2011).

In a nutshell, species niche reconstruction has as main objectives: (i) to reconstruct the potential historical distribution (Yesson and Culham, 2006), (ii) to find areas in the past where the environmental tolerance of the species acted as corridors of dispersal and are currently climatically inadequate (Weaver et al., 2006), (iii) understand how the climatic niche (environmental factors) and species divergence can relate (Gorel et al., 2019).

The dung beetles of the subfamily Scarabaeinae comprise 6.891 valid species grouped into 282 genera (Schoolmeesters, 2024). In Brazil, 786 species have been recorded in 69 genera (Vaz-de-Mello, 2024). Scarab beetles have been used for environmental conservation assessment, reserve planning, and global warming studies (Favila and Halffter, 1997; Barbero et al., 1999; Davis, 2002; Spector, 2006; Nichols et al., 2007; Nichols and Gardner, 2011). The restricted ecological niches of many species enable the use of dung beetles as environmental bioindicators or in ecological biogeographic studies. Cupello et al. (2023) stated that dung beetles have been one of the major taxa used as bioindicators during the past decades by ecologists. Despite being considered one of the major taxa for ecological studies in tropical biomes, only a couple of recent studies have been performed using ecological niche modeling to investigate how environmental and climatic suitability influence the distribution of Neotropical species (Moctezuma et al., 2021; Cupello et al., 2022; Lizardo et al., 2022; Vieira et al., 2022a; Moctezuma et al., 2024).

The *Dichotomius sericeus* species group comprises nine known species distributed in Brazil, Paraguay, and Argentina (Vaz-de-Mello et al., 2001; Valois et al., 2017; Silva et al., 2020). Its species live in AF and associated ecosystems such as Caatinga and Restinga (Vieira et al., 2008; Vieira et al., 2011; Valois et al., 2017; Silva et al., 2020). Many of these ecosystems are threatened by fragmentation, defaunation, logging, and agricultural expansion (Halffter and Favila, 1993; Audino et al., 2014; Dirzo et al., 2014; Vieira et al., 2008, 2011, 2022a). Some species of the *D. sericeus* group are, therefore, at imminent risk of extinction. For example, *Dichotomius schiffleri* Vaz-de-Mello, Gavino & Louzada, 2001 has its current geographic distribution limited to a narrow strip of Restinga on the Brazilian coast between the states of Pernambuco and Espírito Santo (Vieira et al., 2011) and, recently, *D. valoisae* Silva et al., 2020 was described from a small area of AF (Silva et al., 2020).

The species of these group are a dominant component in their communities, in addition, they are susceptible to being delimited by geographic or ecological barriers (Vieira et al., 2022b), rendering them a good model to test biogeographic hypotheses.

In this study, we built ecological niche models for species of the *Dichotomius sericeus* group in different climate periods of the present and past to verify how the climatic oscillations in the AF domain during the Quaternary influenced the species distribution. In addition, these ecological niche models can be used to verify sampling gaps along regions with high climatic suitability, something useful not only for basic sciences like biogeography and systematics but also applied ones such as conservation (Chefaoui et al., 2005; Lawler et al., 2011).

Material and methods

Study area

All species studied here are limited to areas of the AF domain. This biogeographical unit encompasses different vegetation types, namely ombrophilous, deciduous, semi-deciduous, and Araucaria forests, as well as the Restinga and the high altitude fields. The AF domain extends from the eastern coast of South America to portions further inland, following the main courses of rivers and tributaries, and mountainous regions. Morrone et al. (2022) named this biogeographic unit “Parana dominion”.

Occurrence records

The records for each species analyzed were obtained from Valois et al. (2017) (Figs. 1a-e). Each occurrence was obtained through label data from individuals examined during the taxonomic revision of the *D. sericeus* species group. The occurrence data were included individually (not transformed into presence cells). We built individual models only for species with more than ten known occurrence records: *D. iannuzziae* Valois, Vaz-de-Mello & Silva, 2017 (23 records), *D. schiffleri* (34), *D. laevicollis* (Felsche, 1901) (11), *D. sericeus* (Harold, 1867) (62), and *D. irinus* (Harold, 1867) (29).

Setting the current and paleoclimatic variables

For the prediction of the historical distribution of the species, 19 current and paleobioclimatic variables available at the WorldClim website (Fick and Hijmans, 2017) were selected. The selected historical clipping corresponds to four climate scenarios: present, mid-Holocene (6 ka), last glacial maximum – LGM (21 ka), and last interglacial maximum – LIG (120 ka). Paleoclimatic data were based on Atmosphere-Ocean-Global-Circulation-Models (AOGCM) Community Climate System Model v.3 (CCSM3) simulations. Paleoclimatic data from the LIG were based on Otto-Bliesner et al. (2006). All variables were in the WGS84 datum and were cut to the extent of Chacoan and Parana dominions (Morrone et al., 2022), with 2.5’ Arc-resolution (~5 x 5 Km, in the Equator region). This extension was chosen as the background as it encompasses all known occurrences of the species and this is considered a potential area for the historical dispersal of the species, two background selection criteria discussed by Barve et al. (2011).

The 19 bioclimatic (current climate scenario) and paleoclimatic (past climate scenario) variables available in WorldClim are correlated with each other. Therefore, a variable selection process becomes necessary as a way to reduce the collinearity of environmental data (Peterson et al., 2011; Varela et al., 2015). For that, we performed factor analysis using current bioclimatic variables through VariMax Rotation of the orthogonal axes (details in Sobral-Souza et al., 2015). In sequence, the following variables were selected: Mean Temperature of Warmest Quarter (BIO 10), Temperature Seasonality (BIO 04), Precipitation of Driest Quarter (BIO 17), and Mean Diurnal Range (BIO 02), which explain 87% of the climate variance in the spatial area of the study.

Modeling techniques

Currently, there are several algorithms available in the literature (Qiao et al., 2019), such as presence-only, presence and background, and presence and absence algorithms. Each tends to estimate a different distribution based on different niche assumptions (Jiménez-Valverde et al., 2008). Therefore, there is no 100% efficient algorithm (Qiao et al., 2015) and it becomes necessary to use several algorithms simultaneously.

Four algorithms were selected to construct the models: two that deal only with presence data, Bioclim (Nix, 1986) and Gower (Carpenter et al., 1993), and two of pseudoabsence, Maximum Entropy – Maxent (Phillips and Dudík, 2008) and Support Vector Machines – SVM (Tax and Duin, 2004). We did not use presence-absence algorithms as true absence points are not known for the studied species. Species occurrence data were randomly divided into 70% for training and 30% for testing. The bootstrap technique was used to reduce the autocorrelation between these data (Peterson et al., 2011), opting for 10 sets of data randomization for each species within each climate scenario. The models were built for four climate scenarios: present, 6 ka, 21 ka, and 120 ka. In total, 160 models were generated (10 randomizations; 4 algorithms; 4 climate scenarios) for each species. In sequence, we established cut-off thresholds for each model to transform them into presence-absence data. The models were evaluated using True Skill Statistic (TSS, Allouche et al., 2006). The TSS values vary from -1 to 1, where negative values or close to 0 correspond to models with low accuracy, indicating that they do not differ statistically from randomly generated models. Values close to 1 correspond to excellent models. However, values above 0.5 are still considered suitable (Allouche et al., 2006).

The suitability maps of each species were obtained using the ensembles forecasting technique (Araújo and New, 2007). This technique enabled the concatenation of the 10 maps produced by each of the 4 algorithms. In sequence, it gathered the 4 maps produced by each algorithm. The 40 maps resulting from this procedure have suitability values ranging from 0–40. These values demonstrate the frequency with which the species was predicted for each cell.

Results

The niche models provided reliable predictions in all used algorithms (Table 1), except for the mean TSS value for the models generated in

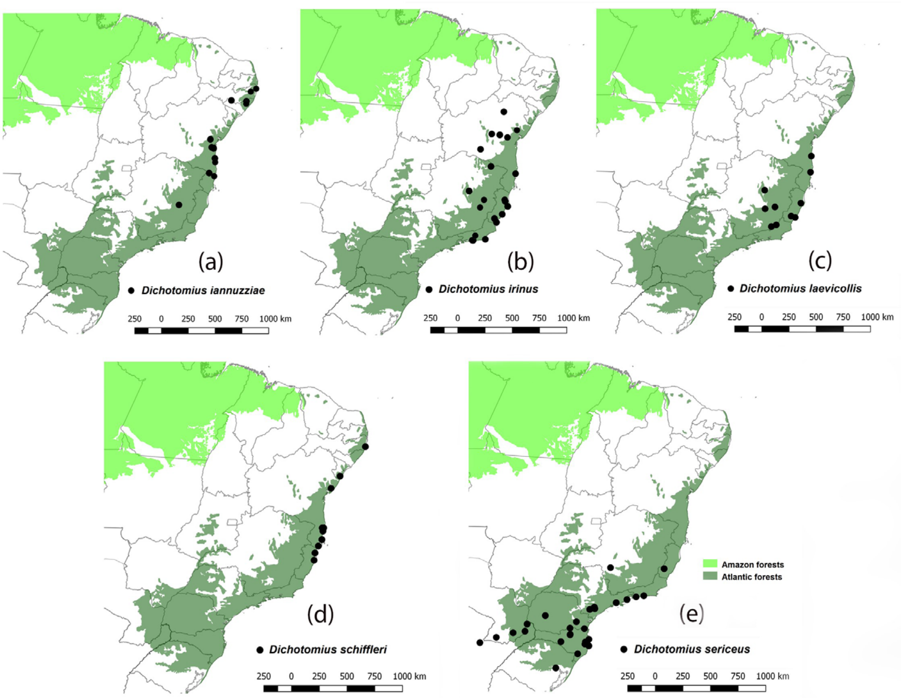

Figure 1 Known distribution of five species of the *D. sericeus* group: (a) *Dichotomius iannuzziae* Valois, Vaz-de-Mello & Silva, 2017. (b) *Dichotomius irinus* (Harold, 1867). (c) *Dichotomius laevicollis* (Felsche, 1901). (d) *Dichotomius schiffleri* Vaz-de-Mello, Gavino & Louzada, 2001. (e) *Dichotomius sericeus* (Harold, 1867).

Table 1
Mean and Standart deviation (SD) values of True Skill Statistic (TSS) for all combinations of algorithms for each generated model.

Algorithm	Bioclim	Gower	Maxent	SVM
Dichotomius laevicollis	0.33 ± 0.22	0.73 ± 0.21	0.57 ± 0.22	0.67 ± 0.27
Dichotomius schiffleri	0.86 ± 0.11	0.97 ± 0.06	1.00 ± 0.00	1.00 ± 0.00
Dichotomius iannuzziae	0.65 ± 0.17	0.80 ± 0.11	0.90 ± 0.09	0.93 ± 0.09
Dichotomius irinus	0.75 ± 0.18	0.89 ± 0.09	0.94 ± 0.07	0.90 ± 0.10
Dichotomius sericeus	0.68 ± 0.08	0.78 ± 0.08	0.75 ± 0.13	0.83 ± 0.12

SVM sector vector machine

Bioclim for *D. laevicollis* (0.33 ± 0.22). All other models generated for each species reached mean values above 0.5 for all algorithms.

The models generated for *D. iannuzziae* in the LIG (120 ka) indicate continuous areas of climate suitability along the northeastern coast of Brazil (Fig. 2a). This species had the potential distribution areas retracted and fragmented during the LGM (21 ka). The climate suitability areas were restricted to small and isolated portions along the northeastern coastline that would have behaved as refuges (Fig. 2b). In the Holocene (6 ka), the climate suitability areas for the species would expand again, potentially reconnecting disjunct populations (Fig. 2c). At present, the species has a broad potential distribution (Fig. 2d). These supposed recently colonized areas and the areas that would have been permanently inhabited can be validated in future molecular studies. However, the climate suitability areas for *D. iannuzziae* were always restricted to northeastern Brazil within the entire time frame analyzed (Figs. 2a-d).

In general, *D. irinus* presents a historical pattern of climate suitability areas different from *D. iannuzziae*. At 120 ka, the species had disjunct climate suitability areas (i - one in northeastern Brazil, from the coast to inland portions; ii - one on the southeastern coast; iii - four disjunct areas inland along a northeastern/southwestern axis) (Fig. 3a). During the LGM, the potential climate areas were concentrated in northeastern Brazil, both on the coast and inland (Fig. 3b). Since then, the potential areas have expanded along the southeastern coast and inland areas of AF (Figs. 3c-d).

The historical patterns of the potential areas of *D. laevicollis* are similar to those of *D. irinus*. These two species presented a higher climate suitability in isolated refuges in the northeastern, southeastern coast, and inland AF in 120 ka (Figs. 3a, 4a). *Dichotomius laevicollis* also showed the same pattern of displacement to the northeastern during the LGM, and had its potential climatically favorable areas expanded into the AF from 6 ka to the present (Figs. 4c-d). However, concerning the previous species, *D. laevicollis* presents more extensive and continuous areas, besides a few changes in its climate suitability areas over time, showing greater tolerance to historical climate changes (Figs. 4a-d).

Dichotomius schiffleri has the smallest area of climate suitability (Figs. 5a-d). Over time, the species probably remained limited to lowland AF areas on the Brazilian coast. It is currently found preferentially in Restinga ecosystems along the coast. At 21 ka, the climate suitability areas became greatly reduced (Fig. 5b).

Dichotomius sericeus has the most extensive areas of climatic suitability (Figs. 6a-d). The species is currently recorded in the southeastern portion of the continent, from the interior highland forests to the coastal areas (Valois et al., 2017) (Fig. 1e). Climate changes during the LGM would have reduced its areas of climatic suitability and at the same time promoted an expansion along a narrow strip across the Atlantic coast towards the northeastern region of Brazil (Fig. 6b). Over the last 6 ka, suitable areas became mainly concentrated in southern and southeastern Brazilian AF, reaching Argentina, Paraguay, and portions of the Bolivian Chaco through AF incursions (Figs. 6c-d).

Discussion

Herein, we studied how climatic oscillations throughout the Quaternary have influenced the potential distribution based on climate for dung beetles endemic to the AF. The *Dichotomius sericeus* species group currently has a wide occurrence in areas of the AF Domain (Valois et al., 2017) (Figs. 1a-e). However, the historical distribution models built for the analyzed species indicate that climatic oscillations during the Quaternary influenced the distribution patterns differently over time, with some retractions and/or expansions in areas of climatic suitability (Figs. 2-6).

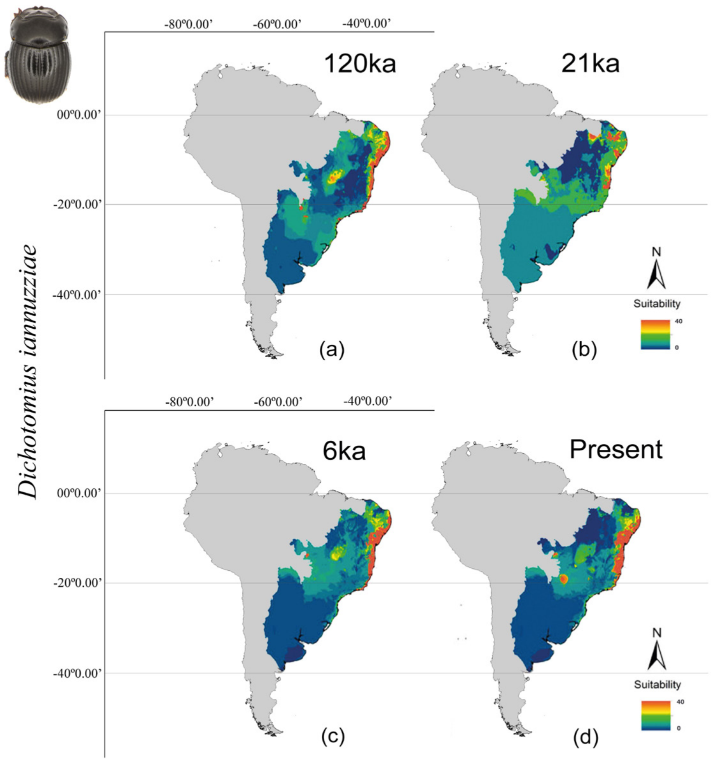

Figure 2 Ensembles Forecasting Models for *Dichotomius iannuzziae* in four historical climate scenarios: (a) 120ka. (b) 21ka. (c) 6ka. (d) Present. Colors represent different degrees of climatic suitability (red: high suitability, blue: low suitability).

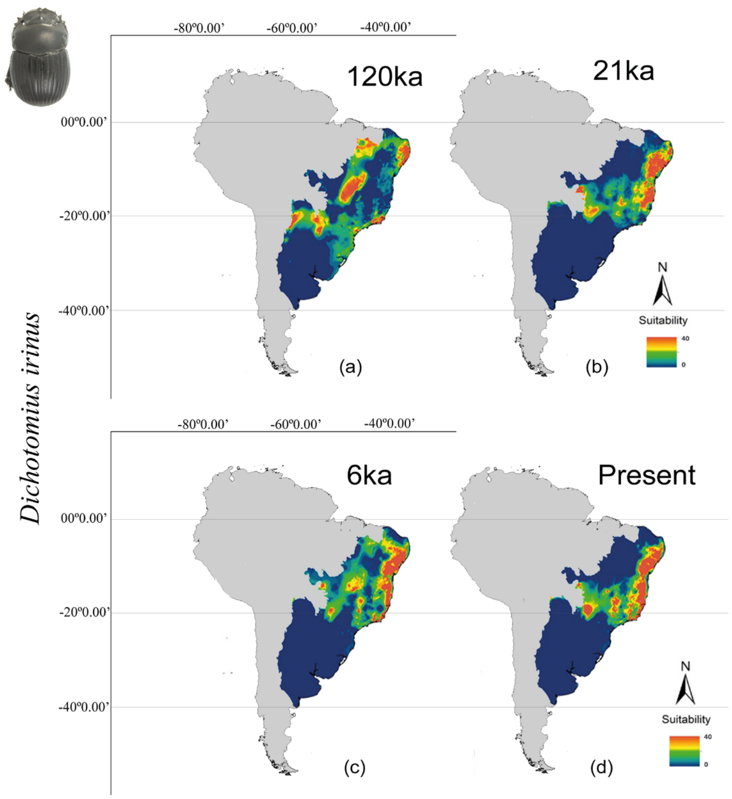

Figure 3 Ensembles Forecasting Models for *Dichotomius irinus* in four historical climate scenarios: (a) 120ka. (b) 21ka. (c) 6ka. (d) Present. Colors represent different degrees of climatic suitability (red: high suitability, blue: low suitability).

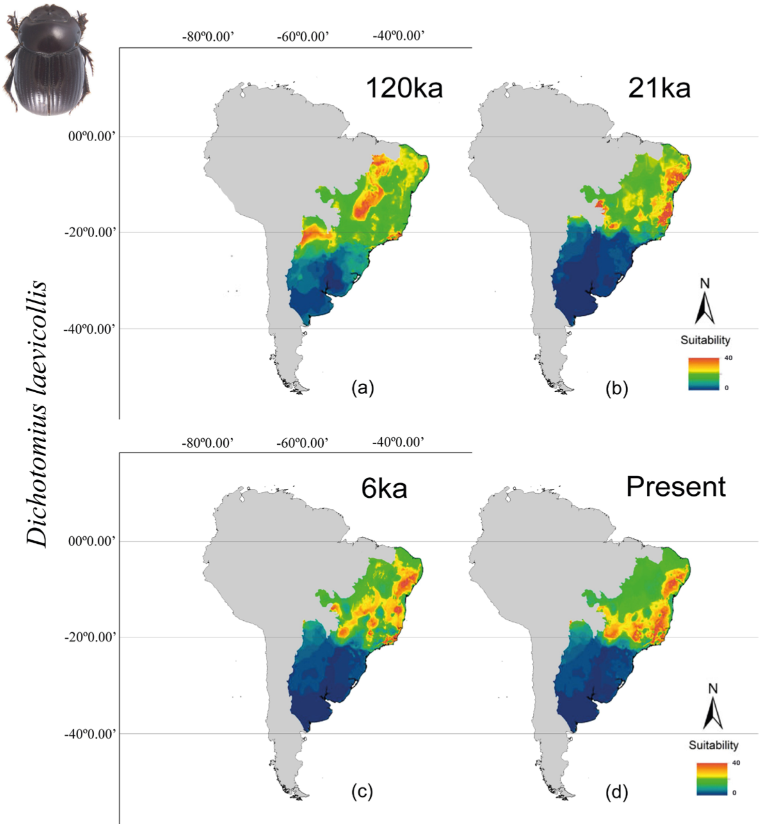

Figure 4 Ensembles Forecasting Models for *Dichotomius laevicollis* in four historical climate scenarios: (a) 120ka. (b) 21ka. (c) 6ka. (d) Present. Colors represent different degrees of climatic suitability (red: high suitability, blue: low suitability).

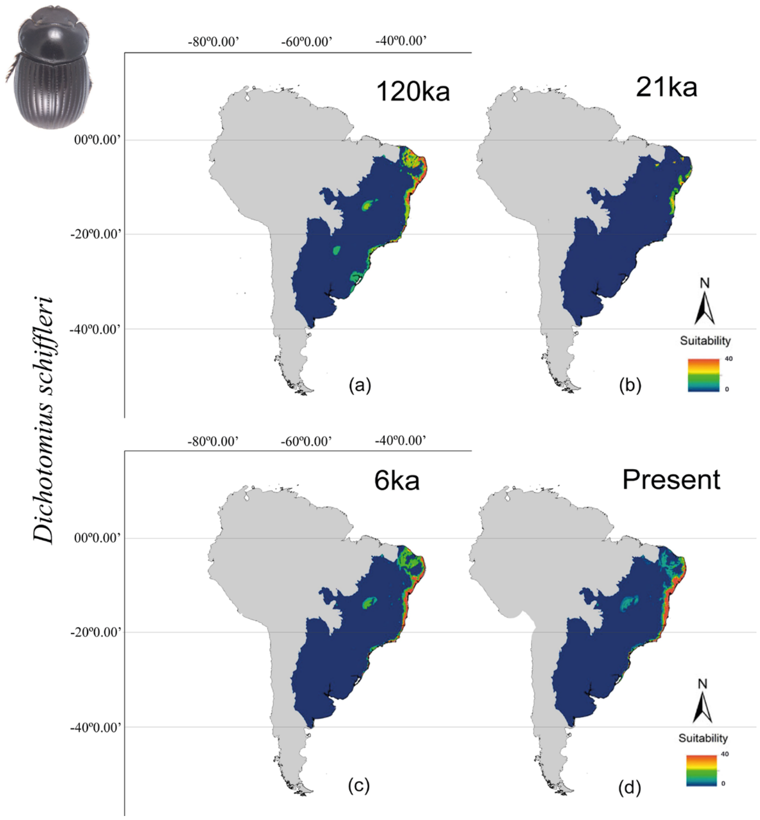

Figure 5 Ensembles Forecasting Models for *Dichotomius schiffleri* in four historical climate scenarios: (a) 120ka. (b) 21ka. (c) 6ka. (d) Present. Colors represent different degrees of climatic suitability (red: high suitability, blue: low suitability).

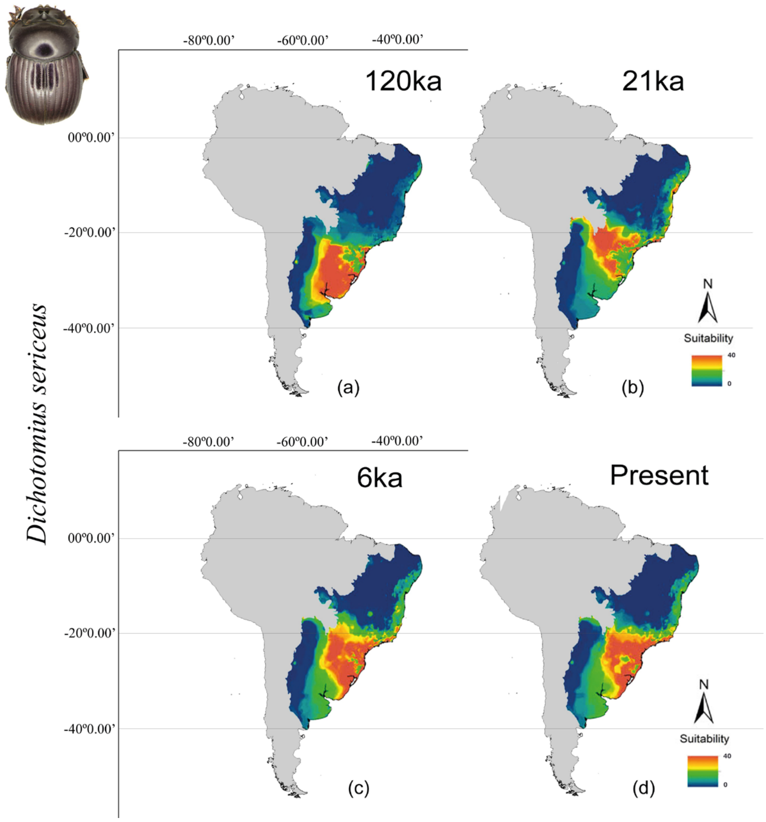

Figure 6 Ensembles Forecasting Models for *Dichotomius sericeus* in four historical climate scenarios: (a) 120ka. (b) 21ka. (c) 6ka. (d) Present. Colors represent different degrees of climatic suitability (red: high suitability, blue: low suitability).

The disjunct climatically suitable areas observed in some models, mainly in the 120 ka (Figs. 3a, 4a) and 21 ka models (Figs. 2b, 5b), suggests that climate oscillations may have contributed to diversification processes within the group through geographic isolation of lineages. According to the refugia hypothesis (Haffer, 1969; Haffer and Prance, 2002, cyclical climate changes in the Pleistocene drove speciation processes by promoting contraction, fragmentation, expansion, and reconnection of tropical forests.

The combination of distribution data and phylogenetic information can provide robust hypotheses to understand diversification processes and biogeographic patterns in tropical forests (Batalha-Filho et al., 2013; Mascarenhas et al., 2019; Silveira et al., 2019; Sheu et al., 2020). Unfortunately, there are still no molecular dating or phylogenetic analysis published for the *D. sericeus* species group. These information may be helpful to understand whether the Quaternary climate changes had influenced the species ranges and their respective populational sizes, or if were also responsible for speciation processes within the group.

During the Quaternary period, some species exhibited distinct responses to climate changes. *Dichotomius irinus* and *D. laevicollis* had a similar historical pattern (Figs. 3a-d, 4a-d). At the same time, they were distinct from *D. iannuzziae*, *D. schiffleri*, and *D. sericeus* (Figs. 2a-d, 5a-d, 6a-d). In 120 ka, the climatically suitable areas of those two species were quite fragmented, with a high suitability in isolated refuges in northeastern Brazil, the southeastern coast, and inland AF (Figs. 3a, 4a). Meanwhile, the other three species had a more continuous suitable areas in this period (Figs. 2a, 5a, 6a). During the LGM, the areas of climate suitability of *D. irinus* and *D. laevicolis* also exhibited the same pattern of displacement into northeastern Brazil, and expansion to inland AF from 6 ka to the present (Figs. 3b, 4b). On the other hand, other species showed retraction and fragmentation into their range (Figs. 2b, 5b, 6b) instead of changing their areas of climatic suitability as mentioned for *D. irinus* and *D. laevicollis*.

The regional response to climate change among the studied species may be associated with differences in their altitudinal ranges. According to Batalha-Filho et al. (2014), the lowlands and upland regions of the AF seem to have been differently affected by the Quaternary climate change. In general, species from lowland forests were strongly influenced by the effect of the Last Glacial Maximum (Carnaval et al., 2009), while some highland species were not (Amaro et al., 2012; Batalha-Filho et al., 2012). Individuals of *D. irinus* and *D. laevicollis* are generally found in moderate elevations and inland plateau regions, while *D. schiffleri*, for instance, is currently found at low elevations close to sea level (Valois et al., 2017) (Figs. 1b-d). This latter species might have suffered a drastic reduction in areas of climatic suitability during the LGM (Fig. 5b).

Except for *D. sericeus*, which exhibits climatically suitable areas in the southern and southeastern AF (Figs. 6a-d), all other species have climatically suitable areas along lower latitudes. *D. sericeus* is a habitat generalist species, and its geographic distribution comprises intermediate latitudes of AF from Argentina and Paraguay to southern and southeastern Brazil (Fig. 1e) (Valois et al., 2017). The species may have expanded its distribution northwards in the LGM through a narrow strip along the coast of Brazil to the northeastern region (Fig. 6b). The climate during this period would have provided milder temperatures and favorable conditions for its establishment in that region.

The potential distribution models at the present exhibits similar potential distributions for *D. iannuzziae*, *D. schiffleri*, and *D. sericeus* (Figs. 2d, 5d, 6d) compared to their current known ranges (Figs. 1a, d, e). *D. iannuzziae* occurrence goes from northern Pernambuco to eastern Minas Gerais (Valois et al., 2017; Araújo et al., 2020) (Fig. 1a); in *D. schiffleri* it goes from the southern coast of Pernambuco to the north coast of Espírito Santo (Valois et al., 2017) (Fig. 1d); and in *D. sericeus* it stretches along wide portions in southern and southeastern Brazil, reaching Argentina and Paraguay by the AF incursions through main rivers and tributaries (Valois et al., 2017) (Fig. 1e).

The models for *D. irinus* and *D. laevicollis* indicate that the inland AF in northeastern Brazil has favorable climatic conditions for these species maintenance, as well as some isolated parts of the Brazilian central plateau (Figs. 3d, 4d). However, these species have known distributions more restricted. *Dichotomius irinus* was only recorded from northern Bahia to Rio de Janeiro (Valois et al., 2017) (Fig. 1b), and *D. laevicollis* from southern Bahia to Rio de Janeiro, through Espírito Santo and the central and eastern portions of Minas Gerais (Valois et al., 2017) (Fig. 1c). Although the models have indicated climatically suitable areas in inland northeastern Brazil, we believe the absence of records for these two species in northern Bahia is not due to sampling gaps. Several collections of dung beetles have already been carried out in different ecosystems of the northeastern region (Costa et al., 2009; Silva et al., 2010; Barretto et al., 2021). Therefore, we believe that historical and/or ecological aspects of biogeography, such as geographic or ecological barriers, can better explain these distribution patterns. For example, the greatest species richness of the group is found in northeastern Brazil; such diversity may mean that all available niches for medium-sized borrowers have already been filled there. Competitive exclusion from these native, locally adapted species might, in turn, have prevented both *D. irinus* and *D. laevicollis* from dispersing and occupying the region.

As mentioned, the current distribution of species richness is not homogeneous along the AF. The northeastern region has several regional endemics and different phytophysiognomies, such as dense ombrophylous forest, open ombrophylous forest, submontane semideciduous seasonal forest, montane semideciduous seasonal forest, and associated ecosystems, such as mangroves and restingas, which provide varied ecological niches for these species. Eight out of the nine known species of the group currently occupy the AF domain in northeastern Brazil (Vieira et al., 2008; Vieira et al., 2011; Valois et al., 2017; Araújo et al., 2020; Silva et al., 2020). Two of those species, *D. schiffleri* and *D. valoisae*, are already recognized as threatened (Vieira et al., 2008; Vieira et al., 2011; Silva et al., 2020). In addition, northeastern Brazil has the most endangered AF remnants in the country. This region has only about 2.21% of its original coverage reduced to small and isolated fragments, some smaller than 10 ha (Tabarelli et al., 2006).

Dichotomius schiffleri probably experienced populational bottlenecks that may have reduced genetic variability since at 21 ka the climate suitability areas became greatly reduced (Fig. 5b). It has its current geographic distribution limited to a narrow strip of the Brazilian coast (Vieira et al., 2011; Vieira et al., 2022a) (Fig. 1d). Individuals are found usually inhabiting restinga ecosystems between the states of Pernambuco and Espírito Santo. Restinga refers to a mosaic of different coastal vegetation types, ranging from open scrubs to forests. These ecosystems have undergone an intense transformation since European colonization (Lacerda et al., 1984). Most of restinga areas are threatened by residential development, fire, and wood exploitation (Vieira et al., 2008, 2011, 2022a). Even in the face of this ongoing habitat loss, it has not been adequately prioritized in most conservation strategies due to its low levels of faunal and flora endemism (Vieira et al., 2008). The few protected areas that have been created were established in disturbed fragments after habitat loss had already occurred. The extirpation of restinga patches brings on colonization by cerrado-adapted and generalist species of dung beetles from other ecoregions, which may lead to local species extinctions (Vieira et al., 2022a). Historical climate changes need to be investigated to better understand why forest dung beetle species are sensitive to microclimate changes and habitat modification.

The present study highlights the influence of the historical climate scenarios on forest dung beetle species in tropical forests. Climate suitability of dung beetle species is an issue not frequently addressed in research, despite the urgent need for species distribution data under a scenario of ongoing climate change (Lobo and Davis, 1999; Martín-Piera, 2001; Lobo and Martín-Piera, 2002; Chefaoui et al., 2005; Dortel et al., 2013; Vieira et al., 2022b). Some recent studies that have addressed climate suitability in Neotropical fauna of dung beetles provided new insights into the Mexican Transition Zone theory (Moctezuma et al., 2024), the effects of climate changes on the spatial distribution of endangered dung beetles (Vieira et al., 2022a), and the use of species distribution models to describe dung beetle species richness or to test their diversification patterns (Moctezuma et al., 2021; Cupello et al., 2022; Lizardo et al., 2022). Hence, we reinforce that past climate patterns must be addressed to understand the present and predict the future patterns of dung beetle species distributions to provide reliable data for conservation purposes.

The historical distribution of the *D. sericeus* dung beetles species group has been influenced by paleoclimatic changes that occurred in the AF over the last 120 ka. These species are sensitive to climate change and, due to the strong habitat restrictions of some species such as *D. schiffleri*, they may be considered endangered. The paleoclimatic models might be integrated with models of ancestral area reconstruction to test diversification hypotheses in the AF. This approach connects hypotheses of historical and ecological biogeography, providing subsidies to understanding patterns of diversification and species richness by considering the biogeographic history of species and clades that give rise to these patterns.

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Conflicts of interest

The author declares no conflicts of interest.

Author contribution statement

FS Conceptualization-Equal, Investigation-Equal, Project administration-Equal, Resources-Equal, Supervision-Equal, Writing – original draft-Lead, Writing – review & editing-Lead. LV Conceptualization-Equal, Data curation-Equal, Formal analysis-Equal, Methodology-Equal, Software-Equal, Validation-Equal. ABM Data curation-Equal, Investigation-Equal, Resources-Equal, Validation-Equal, Writing – review & editing-Equal. MV Conceptualization-Equal, Data curation-Equal, Investigation-Equal, Validation-Equal, Writing – review & editing-Equal. JL Conceptualization-Equal, Investigation-Equal, Project administration-Equal, Resources-Equal, Supervision-Equal. TSS Formal analysis-Equal, Investigation-Equal, Methodology-Equal, Software-Equal, Validation-Equal. FVM Conceptualization-Equal, Data curation-Equal, Project administration-Equal, Resources-Equal, Supervision-Equal.

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