Finding a lost species in the 'Lost World': predicted habitat occupancy by an endemic butterfly in a Neotropical sky-island archipelago

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Abstract. 1. Pantepui is a Neotropical archipelago of remote sky islands (tepuis) that harbours a unique and poorly known biota, such as the endemic butterfly *Antirrhea ulei*. The Vicariance-Migration hypothesis argues that Pantepui biota originated from a complex succession of climatic shifts, causing up-and-down migrations of cool-adapted species from the last glacial maximum (LGM) to the present.

2. We evaluated how environmental gradients affect *A. ulei* habitat occupancy and predict its distribution across the Eastern Pantepui. We also test whether the species had a broader distribution during the LGM, following the Vicariance-Migration hypothesis.

3. We surveyed for butterflies across 14 plots at Uei tepui, following an elevational gradient. We used Bayesian occupancy modelling to evaluate how environmental gradients affect *A. ulei* occurrence and to predict the current and past species distribution.

4. Species habitat occupancy was strongly associated with environmental gradients. Our model correctly predicted the species occurrence at all localities previously reported to be occupied by the species, and also predicted the potential species occurrence on other tepuis. Our historical prediction of species distribution showed that the species likely had a broader distribution during the LGM, in comparison with its current restricted distribution.

5. Our historical predictions suggest that the species may have spread across the Eastern Pantepui during LGM and migrated up the tepuis during the Holocene warming, in accordance with the Vicariance-Migration hypothesis. Our study shows how data from local standardised surveys can be useful to estimate the distribution pattern of other little-studied species of the Pantepui biota.

Key words. *Antirrhea*, Bayesian occupancy model, detectability, endemism, last glacial maximum, Pantepui, species distribution modelling, Vicariance-Migration hypothesis.

Introduction

The Guayana Highlands hold one of the most impressive and pristine scenic landscapes on Earth – the Pantepui. It is an archipelago of sky islands, located between the Orinoco and Amazon rivers, formed by remote table mountains (locally called

tepuis) of 1500–3000 m in elevation, with flat and nearly inaccessible summits that vary from 1 to approximately 1000 km² (Rull & Vegas-Vilarrúbia, 2020). The tepui summits are remnants of Precambrian surfaces (sandstones and quartzites), which have undergone successive erosions until the Pleistocene, creating table-top mountains (Briceño & Schubert, 1990).

Palaeoecological records have shown that the Pantepui biota originated from a complex succession of climatic shifts, which caused up-and-down migrations of species from the last glacial maximum (LGM; ~21 000 years ago) to the present

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(Rull, 2005; Rull *et al*., 2019). In this context, Pantepui cool-adapted species could have migrated downwards during glacials, seeking their particular climatic requirements and tolerances. Once spread across lowlands and uplands, these species would have had the possibility of climbing several tepuis during the Holocene warming (the last 11 700 years). Therefore, Quaternary climatic fluctuations probably triggered the Pantepui biota to disassemble during glacials and reassemble during inter-glacials, playing a significant role in Pantepui biogeography (Rull & Vegas-Vilarrúbia, 2019). However, it is worth noting that these up-and-down migrations are a complex process, which depends on the topography of each tepui and idiosyncrasies of each species (Rull & Vegas-Vilarrúbia, 2020).

The biogeographical context of Pantepui gave rise to its astonishing biodiversity with a high number of endemic species of flora and fauna (Rull & Vegas-Vilarrúbia, 2019). It was the uniqueness of these plant and animal species, discovered during the first expeditions to this hitherto new and strange environment in the late 19th century that likely inspired Sir Arthur Conan Doyle to write the famous novel entitled 'The Lost World'. One example of such a unique species is *Antirrhea ulei* (Strand, 1912) – a butterfly species considered to be endemic to the tepuis (Fig. 1). This species was described based on a female specimen collected by the botanist Ernst Ule during an expedition to Roraima Tepui in the early 20th century (Strand, 1912). However, a large amount of biological material from the Berlin museum, where the specimen was deposited, was destroyed during the Second World War, and the type of *A. ulei* was considered lost (Orellana, 2004). Thus, a new specimen of the same sex from Sierra de Lema was chosen to designate the neotype (Orellana, 2004).

Information on the distribution of *A. ulei* is scarce and species records are limited to few tepuis. To the best of our knowledge, the species has been found at only the following tepuis: Roraima Tepui (type – Strand, 1912), Sierra de Lema (neotype) and Auyán Tepui (Orellana, 2004), Mount Wokomung (Fratello, 1996) and Mount Ayanganna (Fratello, 1999). The species occurs in the cloud forests of these tepuis at elevations above 1200 m and its larvae probably feed on *Prestoea* palms (Orellana, 2004), which are commonly found at elevations above 1000 m in the Guayana Highlands (Henderson & Galeano, 1996). It is difficult to draw conclusions about the ecology or evolutionary processes that may have affected these species with limited empirical knowledge. In such cases, species-distribution modelling can help to explain how environmental factors affect the species habitat occupancy, to predict the current pattern of species distribution, identifying potential tepuis for species occupancy, as well as reconstructing its historical distribution. Understanding historical patterns of species distribution, especially those strongly associated with specific habitats, such as butterflies, can help to understand the origin of Pantepui biota.

Here we use an occupancy-modelling approach to predict the current and historical pattern of *A. ulei* distribution across the Eastern Pantepui. Specifically, we (i) evaluate how environmental gradients affect the species' habitat occupancy at Uei Tepui, (ii) map the current species distribution based on its ecological requirements across the Eastern Pantepui, and (iii) test whether the species had a broader distribution during the LGM, when the climate now found on the Pantepui likely had a wider extent, following the Vicariance-Migration hypothesis (Rull, 2005). We expect that *A. ulei* environmental requirements are restricted to highlands, and that our model may be validated by the previous records of the species in other tepuis, as well as help to identify potential non-surveyed tepuis for species occurrence. We also expect to find that the species had a broader range during the LGM, which represents the typical Quaternary glaciation, suggesting that the species may have spread across the eastern Pantepui during glacials, and migrated upwards to the current tepuis during the Holocene warming.

Materials and methods

Study area

Our study region comprises the Eastern portion of Pantepui. Sampling was undertaken at Uei Tepui (5°5′N, 60°35′W), in
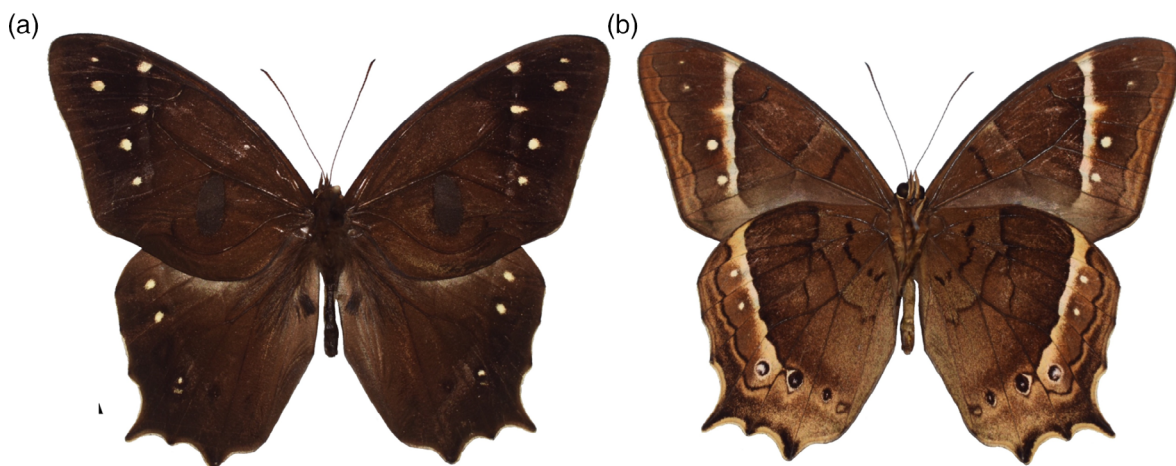

Fig 1. Dorsal (a) and ventral (b) view of a male specimen of *Antirrhea ulei* collected at Uei Tepui, Roraima State, Brazil.

Roraima, the northernmost state of Brazil. Uei Tepui is located on the border of Brazil and Venezuela, has a maximum elevation of 2150 m, with a summit area of 2.5 km^2 and a slope area of 20 km^2 (Rull & Vegas-Vilarrúbia, 2020). Uei Tepui is protected by the Raposa Serra do Sol Indigenous Land and by the Monte Roraima National Park (ICMBio, FUNAI).

Meteorological data for Pantepui are scarce, but available data from three weather stations over a period of 12 years (1997–2009) allow some generalisation to be made (Rull & Vegas-Vilarrúbia, 2020). Annual average temperature ranges between 11.4 °C and 16.5 °C with a general elevational decrease of approximately 0.6 °C/100 m. Annual precipitation ranges from 280 to 5300 mm, and increases with elevation at a rate of 30 mm/100 m. Moisture is also provided by common dense mists. Precipitation may vary throughout the year, with rainfall being less common from December to March.

Sampling design and data collection

We surveyed butterflies in 14 plots at the beginning of the dry season (November–December 2019). Plots (sample units) consisted of 200-m long transects. Most plots were separated by at least 1 km from one another, but some higher elevation plots were separated by only 400 m due to logistical constraints.

Butterfly surveys were conducted via passive sampling, by placing eight baited butterfly traps along the centreline of each plot. At each 50 m, we hung two traps on tree branches, one in the forest understory (1–1.5 m high) and one in the canopy (15–25 m high). We baited the traps with a mixture of sugar-cane juice and bananas fermented for 48 h (Freitas *et al.*, 2014) and visited them every 48 h to check for captures and replace the bait. We left the traps active for 6–12 consecutive days (Supporting Information Table S1). All captured individuals were collected for posterior species identification and the specimens were deposited in the Entomological Collection of the National Institute for Amazon Research, Manaus, Brazil.

We gathered topographic, vegetation and climate data from GIS databases (Supporting Information Table S2). We obtained current climate data from WorlClim v.2 (Fick & Hijmans, 2017) and the LGM simulation of climate scenario from the Community Climate System Model (CCSM), developed by the Coupled Modeling Intercomparison Projects (CMIP5) and Paleoclimate Modeling Intercomparison Projects (PMIP3) available from the ecoClimate database (Lima-Ribeiro *et al.*, 2015). As most of these variables were highly correlated with each other, we summarised the environmental data with a principal component analysis (PCA). The first axis derived from this ordination was highly correlated ($r > |0.5|$) with most of the environmental variables (Supporting Information Table S2), so we used this axis (PCA 1) to represent the environmental variables in our model.

Data analysis

We assessed the pattern of *A. ulei* occurrence across our sample sites using an occupancy-modelling approach. This approach estimates the probability of a site being occupied/used (ψ) by a

given species when its detection probability is less than 1 (Mackenzie *et al.*, 2006). Given that the non-detection of a species at a sample site results from either its true absence or the failure to detect it, repeated surveys (occasions) on multiple sample sites are used to estimate the detection probability (P) of a species conditional on occupancy. In our model, *A. ulei* occurrence at a given site 'i' is denoted as O_i (i.e., the true occupancy state: 1 if present, 0 otherwise), and is the outcome of a Bernoulli trial with probability of occupancy ψ_i,

$$O_i \sim \text{Bernoulli}\,(\psi_i)$$

Similarly, the binomial detection/non-detection (1 = present; 0 = not detected) of the species (D) during a given occasion 'j' and in a given sample site 'i' are input in the form of an array D_{ij}. Therefore, whether the species is detected during a given occasion in a given site is conditional on the occupancy state O_i, as follows:

$$D_{ij} \sim \text{Bernoulli}\,(P_{ij}*O_i)$$

where P_{ij} is the probability of species detection during an occasion (survey) in a site. We substituted time for space and considered each of the four pairs of traps (understory and canopy) in each sampling plot as a sampling occasion (Supporting Information Table S1).

We estimated both ψ and P parameters as linear responses to predictor variables using a logit link function in a regular logistic model. As the sampling effort differed across plots, we added the sampling effort on each sampling plot (values were standardised before running the model) into the model as a detection covariate; that is, we expected that the longer the sampling period, the higher the likelihood of detecting *A. ulei* in traps. We modelled the logit transformation of detection probability as follows:

$$\text{logit}(P_{ij}) = \alpha_0 + \alpha_1 * \text{sampling effort}_{ij}$$

We then considered that the occupancy probability ψ_i depended on the combination of environmental factors on site 'i' (i.e., PCA 1 scores for each site), in a logit transformation of a linear model as follows:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 * \text{PCA1}_i$$

The full hierarchical model formulation is given in Supporting Information Fig. S1. We implemented the model in a Bayesian framework using JAGS accessed via the software R, version 3.4.4 (R Development Core Team, 2018) using the package 'rjags' (Plummer, 2016) (see the R code available in Appendix S1 in Supporting Information). We used vague priors for all model parameters. We used logistic priors for intercepts [α_0 and $\beta_0 \sim$ Logistic($\mu = 0$, $\sigma = 1$)], which imply a Uniform(0, 1) prior for P and ψ in the probability scale, when covariates are equal to zero (Northrup & Gerber, 2018). We used normal priors with mean = 0 and variance = 10 for the regression coefficients [α_1 and $\beta_1 \sim$ Normal ($\mu = 0$, $\sigma = 3.16$)] describing the effects of covariates detection and occupancy probabilities in the logit scale. We conducted a prior sensitivity analysis, using

sequentially smaller values of σ, and found no differences in posterior estimates of model coefficients, nor in detection and occupancy probabilities (Supporting Information Fig. S2). We estimated posterior parameters with the Markov Chain Monte Carlo (MCMC) method using three parallel MCMC chains of 100 000 in length after discarding the first 10 000 steps of each as burn-in, and with a thinning rate of 100 steps. This combination of values ensured that all chains converged, that is, essentially oscillated around the same mean parameter value (see Supporting Information Fig. S3). We report the posterior distribution of all estimated parameters as means and standard errors (SEs), as well as the medians and the 2.5 and 97.5 percentiles, which are the Bayesian equivalent to the 95% confidence interval [highest posterior density in 95% (HPD95)].

Results

We obtained a total of 12 *A. ulei* independent detections at four (29%) of the 14 sample sites during four sampling occasions. The mean detection probability across sites was $P = 0.56$ (HPD95: 0.3–0.83), and it was not influenced by differences in sampling effort (Table 1). The mean probability of site occupancy was $\psi = 0.41$ (HPD95: 0.24–0.75), and it was affected by the environmental gradients summarised by the first PCA axis (Table 1; Fig. 2). Higher values of PCA 1 axis were associated with higher elevation, tree cover and canopy height, but also with lower temperatures and seasonal variation in temperature and precipitation (Supporting Information Table S2). PCA 1 axis captured 56% of the variation in environmental variables.

According to our model predictions, the species has a high probability of habitat occupancy on several Eastern tepuis (Fig. 3). Our model correctly predicted the species occurrence at all five localities previously reported to be occupied by the species: Roraima Tepui (type locality), Sierra de Lema (neotype), Auyán Tepui, Mount Ayanganna and Mount Wokomong. Our model also predicted the potential species occurrence at other tepuis of the Eastern chain, at Northwest of Roraima Tepui (e.g., Kukenán and Karaurín tepuis), at Chimantá massif, in Venezuela, and at Merume Mountain, in Guyana.

Table 1. Parameter estimates (link scale) from the hierarchical occupancy model for *Antirrhea ulei* occurrence at Uei Tepui in Raposa Serra do Sol Indigenous Territory.

Parameter	Estimate (SE)	2.5%	Median	97.5%
α_0	0.30 (0.02)	−1.71	0.30	2.01
α_1	0.89 (0.02)	−1.43	0.89	3.12
β_0	−2.81 (0.03)	−6.82	−2.71	0.55
β_1	0.84 (0.01)	−0.22	0.79	2.18

α_0 and α_1 are the coefficients (intercept and slope, respectively) of a logistic model of *A. ulei* detection probability P; β_0 and β_1 are the coefficients (intercept and slope, respectively) of a logistic model of *A. ulei* probability of occurrence ψ. See full model formulation in Supporting Information Fig. S1.
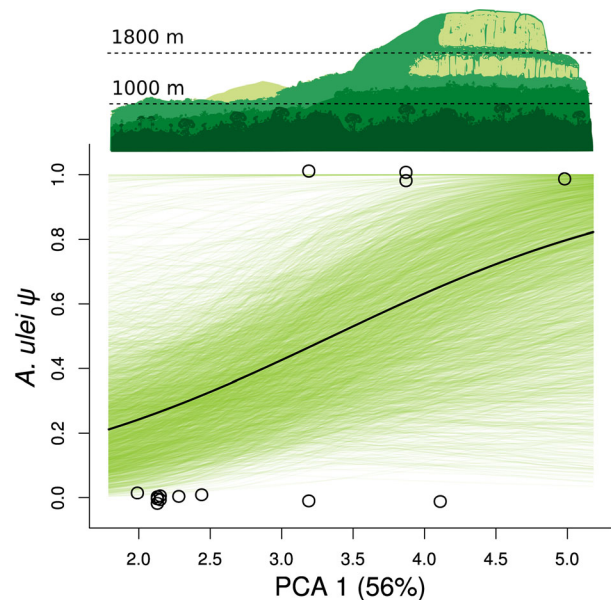

Fig 2. Predicted habitat occupancy by *Antirrhea ulei* across sample sites at Uei Tepui, according to a Bayesian hierarchical occupancy model. The logit transformation of *A. ulei* probability of habitat occupancy (y-axis; *A. ulei* ψ) was modelled as a linear function of several environmental gradients summarised by the first axis of a PCA ordination (x-axis; PCA 1). The species mean probability of occurrence (black line) increases markedly with increasing values of the PCA 1 axis. Light green lines represent all models fitted according to posterior estimates and the higher density of lines indicates the area with higher model confidence.

Our prediction of the historical change in the distribution of the species is shown in Fig. 4. According to our model, the species likely had a wider distribution during the LGM and populations were probably more connected to each other, even though the species already had a patchy pattern of occurrence, restricted to the highlands of the Eastern Pantepui. As the climate started to warm during the Holocene, the species lost part of its suitable habitat at lower elevations, being restricted to the higher areas, where the tepuis are currently found.

Discussion

We found that *A. ulei* has higher probability of occurrence at higher values of our environmental gradients (PCA 1), that is, in habitats at higher elevations (above ~1400 m), with a high percent of tree cover and with taller forests, but also with lower temperatures and less seasonal variation in temperature and precipitation. A higher probability of occurrence of the species at the forested habitats of tepuis is expected, since this is a forest-dwelling species that occurs in the lower strata of the forest (Orellana, 2004). Besides, the common host plants for *Antirrhea* butterflies are mainly palms from the genus *Prestoea*, *Euterpe*, *Oenocarpus*, *Geonoma* and *Calyptrogyne* (Heredia & Alvarez-lopez, 2004; Beccaloni *et al.*, 2008), which can be abundant in forested habitats in tepuis (Henderson & Galeano, 1996); but
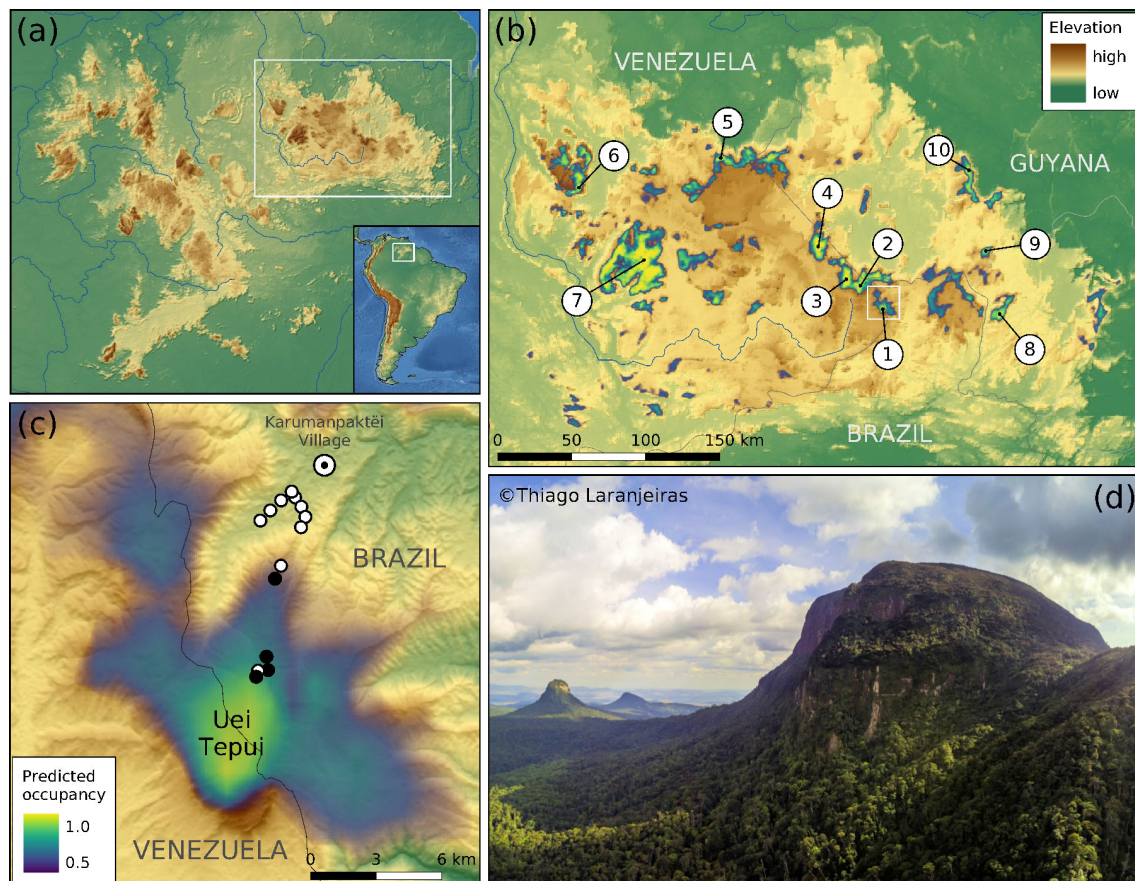
Fig 3. Predicted habitat occupancy by *Antirrhea ulei* in Eastern Tepuis, according to a Bayesian hierarchical-occupancy model. (a) Map of Pantepui and its location within South America (inset); white rectangle enlarged in (b). (b) Map of Eastern Pantepui showing the predicted habitat occupancy by the species and localities mentioned in the text; white rectangle enlarged in (c). (c) Map of Uei Tepui showing the predicted habitat occupancy by the species and sampling plots location. Black points show plots where the species was present, whereas white points show plots where the species was not detected. (d) Aerial view of the northern face of Uei Tepui, showing tepui summit and lower forested slopes. The model was fitted to data collected in Uei Tepui (c) and then extrapolated to the extent of the Eastern tepuis (b). 1. Uei Tepui; 2. Roraima Tepui; 3. Kukenán Tepui; 4. Karaurin Tepui; 5. Sierra de Lema; 6. Auyán Tepui; 7. Chimantá Massif; 8. Mount Wokomong; 9. Mount Ayanganna; 10. Merume Mountains. Photo: Thiago Laranjeiras.

are rare or nearly absent in the shrub and herbaceous vegetation of tepui summits (pers. observ.). Butterfly distribution is strongly associated with vegetation; therefore, the presence of the host plant is one (and perhaps the most) important biotic factor limiting the species occurrence (DeVries, 1986; Koh *et al.*, 2004). In fact, butterfly endemism appears gradually from the middle elevations (~1000 m), at the montane level, and increases notably with altitude, especially above 1500 m, when vegetation switches to upper montane with high degree of endemism in plants (Viloria & Costa, 2019).

Our sampling at Uei Tepui did not cover the whole range of tepui environmental variation. As we moved from 1000 to 1800 m (the approximate elevation range our sampling covered), vegetation structure changed from submontane-to-montane dense forests to ~7-m tall cloud forests with gnarled tree trunks covered with mosses and a dense, nearly impenetrable understory. At the highest elevation we established a plot (1820 m), forest canopy was very short, so we were only able to install traps

in the understory. Above this elevation, at Uei Tepui summit, the vegetation changed drastically to a mosaic of shrub and herbaceous vegetation on a bare rock substrate, with very sparse small trees, on which we could not hang traps. We have opportunistically surveyed the Uei Tepui summit with insect nets, but we did not detect any *A. ulei* individuals, nor palm species (i.e., their host plants), in these habitats. Therefore, although our model predicts that the species has the highest probability of occurrence at elevations above 1800 m and on tepui summits, our sampling did not cover the environmental variation above this elevation, so we recommend that the predicted presence of species on tepui summits be regarded with caution. We believe that tepui summits are likely not suitable habitats for the species due to their vegetation structure and floristic composition.

Our model correctly predicted the presence of the species in all locations previously described to be occupied by the species and also predicted potential areas for species occurrence on several other tepuis (e.g., Chimantá massif). Although the butterfly
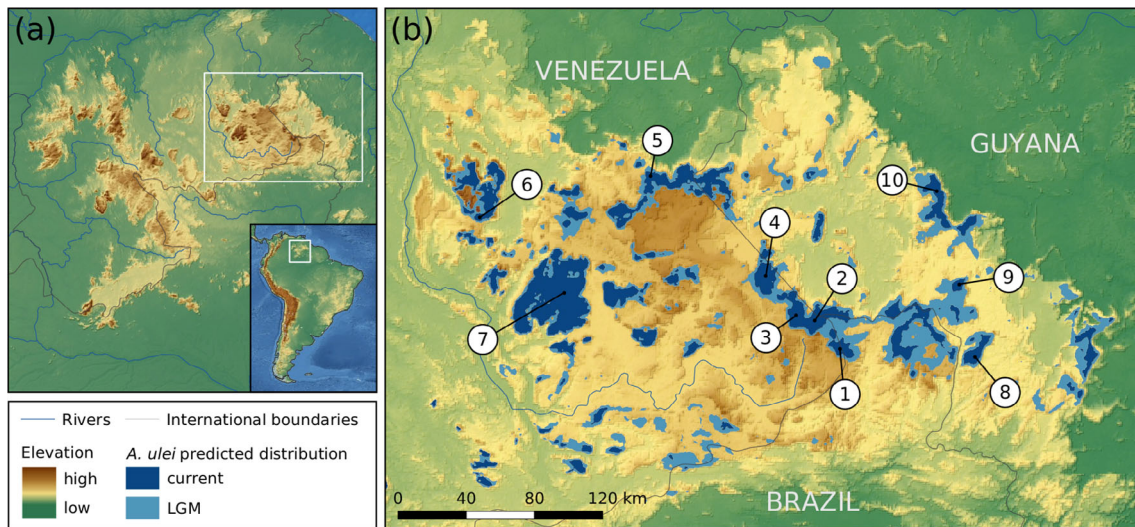
Fig 4. Current and historical predicted distribution of *Antirrhea ulei*. (a) Map of Pantepui and its location within South America (inset); white rectangle enlarged in (b). (b) Map of Eastern Pantepui showing the current and past predicted distribution of the species and localities mentioned in the text. Binary prediction of habitat occupancy was set at threshold of 0.5 of probability of occupancy. Historical prediction was based on climatic conditions during the last glacial maximum (LGM) according to the Community Climate System Model (CCSM; Lima-Ribeiro *et al*., 2015). 1. Uei Tepui; 2. Roraima Tepui; 3. Kukenán Tepui; 4. Karaurin Tepui; 5. Sierra de Lema; 6. Auyán Tepui; 7. Chimantá Massif; 8. Mount Wokomong; 9. Mount Ayanganna; 10. Merume Mountains.

surveys in the Pantepui began in the middle of the 19th century (Viloria & Costa, 2019), most of them were opportunistic surveys or surveys that did not follow a standardised sampling protocol. All previous records of species occurrence were opportunistic (Strand, 1912; Fratello, 1996, 1999; Orellana, 2004) and, although there have been butterfly surveys on other tepuis (Viloria & Costa, 2019), they probably failed to detect the species at these locations because they were also opportunistic surveys. To the best of our knowledge, our study represents the first systematic survey of the species, following a standardised sampling protocol and with estimation of detection probability of the species. According to our estimated detection probability ($P = 0.56$), it is expected that opportunistic surveys, or even systematic ones, will often not find the species in a given tepui that it occupies. Future systematic surveys in tepuis we predicted to be occupied by the species would help to understand whether those areas are truly occupied by the species and were not detected in previous surveys, or they represent false positive locations.

Our results suggest that the species likely had a wider distribution during the LGM. With a broader area of suitable habitat available and open migration pathways among tepuis, populations were probably more connected. The current pattern of species distribution suggests that, when the climate warmed during inter-glacials in the Holocene, the suitable habitat at lower elevations became unsuitable and populations may have migrated upwards, becoming isolated on the current tepuis. Therefore, our findings are in accordance with the Vicariance-Migration hypothesis (Rull, 2005), which proposes that glaciations were characterised by the biotic spread of Pantepui sensitive species and inter-glacial upward migration would have favoured vicariance and extinction by habitat loss. We call for studies with

molecular data and/or wing-colour patterns, assessing the differentiation between populations from different tepuis, to confirm such hypothesis, by evaluating whether the divergence time among populations is congruent with LGM. Additionally, we highlight that *A. ulei* distribution may be more strongly associated with its host-plant than with the environmental variables we evaluated, and that its host-plant may not have migrated as fast as the butterfly during glaciations.

Traditionally, Pantepui endemism has been explained by two major speciation processes: ancient vicariance versus recent dispersals, and various hypotheses have been proposed to explain the current distribution of Pantepui biota (Rull, 2019). *Antirrhea* diverged from other species in the *Morpho* and *Caerois* genera during the Eocene (~38 mya; Wahlberg *et al*., 2009). It is not known yet whether *A. ulei* originated in the Pantepui or dispersed from somewhere else (e.g., proto-Andes), due to the lack of phylogeographic studies of the genus. In any case, our findings support the idea that Holocene climatic oscillations played an important role in population isolation by vicariance and habitat loss, and may also have had an important role in the diversification of the genus, although genetic data would confirm this hypothesis. A similar model of diversification would have happened with the anurans *Oreophrynella* and *Atelopus*, whose divergence occurred ~40 mya (Eocene) in the proto-Andes and after they dispersed to Pantepui, they diversified there by vicariance (Kok *et al*., 2018).

This study illustrates how data from local standard surveys can be useful to estimate species ecological requirements and help to understand the distribution pattern of little-studied species. Our model correctly predicted the species occurrence at all localities previously reported to be occupied by the species, and further predicted other potential tepui localities for species

occurrence. Further systematic surveys may help to validate our model predictions. We also found that the species likely had a broader extent of suitable habitat during the LGM and may have spread across the eastern Pantepui, migrating upwards to the current tepuis as its suitable habitat was being lost during the Holocene warming, in accordance with the Vicariance-Migration hypothesis. The framework used in this study can be replicated to other endemics and/or poorly known species to help to understand the evolution of Pantepui biota.

Acknowledgements

Data Availability Statement

All data that support the findings of this study are available in the Supporting Information of this article.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Detection history of *Antirrhea ulei* across sample sites.
Table S2. Variables used in the model.
Figure S1. Model formulation.
Figure S2. Prior sensitivity analysis on posterior estimates.
Appendix S1. R code for model implementation.
Figure S3. Chains convergence.

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