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Doré, Maël, Willmott, Keith, Leroy, Boris et al. (8 more authors) (2021) Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group. Diversity and Distributions. ISSN: 1472-4642

https://doi.org/10.1111/ddi.13455

Received: 23 April 2021 | Revised: 26 October 2021 | Accepted: 18 November 2021

DOI: 10.1111/ddi.13455

RESEARCH ARTICLE

Diversity and Distributions WILEY

Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group

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Funding information

FLMNH Museum Associates; Brazilian CNPq, Grant/Award Number: 563332/2010-7 and 303834/2015-3; Darwin Initiative; National Geographic Society, Grant/Award Number: 5751-96; National Science Foundation, Grant/Award Number: 0103746, 0639977, 0639861 and 0847582; U.S. National Academy of Sciences; Agence Nationale de la Recherche, Grant/Award Number: ANR-16-CE02-0012 (CLEARWING); United States Agency for International Development; Human Frontier Science Program, Grant/Award Number: RGP0014/2016; Fundação Amazônia Paraense de Amparo à Pesquisa, Grant/Award Number: 2011/50225-3 and

Abstract

Aim: The biodiversity crisis has highlighted the need to assess and map biodiversity in order to prioritize conservation efforts. Clearwing butterflies (tribe Ithomiini) have been proposed as biological indicators for habitat quality in Neotropical forests, which contain the world's richest biological communities. Here, we provide maps of different facets of Ithomiini diversity across the Neotropics to identify areas of evolutionary and ecological importance for conservation and evaluate their overlap with current anthropogenic threats.

Location: Neotropics.

Methods: We ran species distribution models on a data set based on 28,986 georeferenced occurrences representing 388 ithomiine species to generate maps of geographic rarity, taxonomic, phylogenetic and Müllerian mimetic wing pattern diversity. We quantified and mapped the overlap of diversity hotspots with areas threatened by or providing refuge from current anthropogenic pressures.

Results: The eastern slopes of the Andes formed the primary hotspot of taxonomic, phylogenetic and mimetic diversity, with secondary hotspots in Central America and the Atlantic Forest. Most diversity indices were strongly spatially correlated.

2012/50260-6; French Ministry of Research (MENSR); Leverhulme Trust

Editor: Deyan (HOTSP) Ge

Nevertheless, species-poor communities on the Pacific slopes of the Andes also sheltered some of the geographically rarest species. Overall, tropical montane forests that host high species and mimetic diversity as well as rare species and mimicry rings appeared particularly under threat.

Main conclusions: Remote parts of the Upper Amazon may act as refuges against current anthropogenic pressures for a limited portion of Ithomiini diversity. Furthermore, it is likely that the current threat status may worsen with ongoing climate change and deforestation. In this context, the tropical Andes occupy a crucial position as the primary hotspot for multiple facets of biodiversity for ithomiine butterflies, as they do for angiosperms, tetrapods and other insect taxa. Our results support the role of ithomiine butterflies as a suitable flagship indicator group for Neotropical butterfly diversity and reinforce the position of the tropical Andes as a flagship region for biodiversity conservation in general, and insect and butterfly conservation in particular.

KEYWORDS
anthropogenic pressures, biodiversity hotspots, geographic rarity, Human Footprint, human impacts, Ithomiini butterflies, Müllerian mimicry, phylogenetic diversity, species richness

1 | INTRODUCTION

The global biodiversity crisis is a critical environmental issue (IPBES, 2019) with unprecedented rates of species loss across multiple taxonomic groups, now referred to as the sixth mass extinction (Barnosky et al., 2011; Ceballos et al., 2015). Such species loss significantly alters biodiversity patterns and affects ecosystem functions worldwide. In particular, there is growing evidence for recent massive declines in insects (Cardoso et al., 2020; Eggleton, 2020; Montgomery et al., 2020), which represent the bulk of current biodiversity (Mora et al., 2011; Stork, 2018). This loss is concomitant with the global increase in human pressures on ecosystems, with currently 75% of the planet's non-frozen land surface impacted (Venter et al., 2016b). These alarming trends are compelling scientists to better assess and map biodiversity in order to prioritize conservation efforts given limited time and resources (Brooks et al., 2006).

One early approach towards identifying global priority areas for conservation was the delimitation of biodiversity hotspots (Myers et al., 2000): areas with high levels of vascular plant species richness and endemism, and significant loss of primary natural habitats. The Neotropics encompass seven of these biodiversity hotspots, including the richest of them: the Tropical Andes (Myers et al., 2000). However, it is not known how well such hotspots, identified on the basis of vascular plant diversity and confirmed for vertebrates, provide adequate surrogates for the diversity of other taxa, especially insects (Stork & Habel, 2014). Indeed, georeferenced primary biodiversity data for insects, particularly in the Neotropics, are very scarce due to the challenges of collecting, digitalizing and verifying taxonomic identifications for records covering often inaccessible, remote regions (Short et al., 2018; Stork, 2018). Moreover, whether species richness and endemism adequately reflect other facets of biodiversity such as phylogenetic and functional diversity may depend on the group considered (Albouy et al., 2017; Allouche et al., 2006; Devictor et al., 2010; Mazel et al., 2014; Prendergast et al., 1993; Williams et al., 1996; Zupan et al., 2014). There is therefore an urgent need to explore to what extent existing hotspots identified for well-studied taxa coincide with those of other less well-known groups, and how well those hotspots represent facets of biodiversity beyond species richness and endemism. Here, we tackle this issue by investigating the spatial distribution of different metrics of biodiversity in an integrative assessment that covers its multifaceted nature (Pollock et al., 2017, 2020). We focus our assessment on a diverse insect group, the butterfly tribe Ithomiini Godman & Salvin, 1879 (Nymphalidae: Danainae), in the world's biologically richest region, the Neotropics.

The tribe Ithomiini comprises 396 described species distributed among 42 genera and 10 subtribes (Chazot et al., 2019). These butterflies form diverse communities in humid forests from sea level to 3000 m, throughout the Neotropics. Their habitats are threatened by high rates of deforestation associated with cattle ranches, soybean and oil palm plantations, as well as industrial logging, mining and road building (Armenteras et al., 2017; Fearnside, 2017; Rajão et al., 2020; Sonter et al., 2017). In this context, ithomiine butterflies have been proposed as indicator species for habitat quality and local butterfly diversity (Beccaloni & Gaston, 1995; Brown Jr, 1997; Uehara-Prado & Freitas, 2009 but see Brown & Freitas, 2000). Ithomiini also represent the most diverse radiation of aposematic and Müllerian mimetic butterflies, whereby co-occurring unpalatable species display similar wing colour patterns that advertise their distastefulness to predators. Müllerian co-mimetic species interact mutualistically, because they share the cost incurred during the learning process of predators (Joron & Mallet, 1998; Müller, 1879; Sherratt, 2008). All Ithomiini species engage in Müllerian mimicry and drive mimicry in other distantly related groups of Lepidoptera (Beccaloni, 1997; Brown Jr. &

Benson, 1974). Remarkably, many ithomiines have partly transparent wings (McClure et al., 2019; Papageorgis, 1975; Figure 1a), which has inspired their common name of 'clearwing' butterflies. Overall, ithomiine butterflies combine their potential role as biological indicators with positive public image (e.g. Barua et al., 2012; Sumner et al., 2018), making them candidate flagship species for conservation in the Neotropics. Previous studies have already investigated the historical biogeography of the tribe. Ithomiini likely originated in the eastern Andean foothills and a major clade, composed of the five most species-rich subtribes and comprising 80% of species, diversified in Central Andes 20–10 My ago (Chazot et al., 2019). Those areas, which harbour heterogeneous landscapes favouring speciation, also coincide with known hotspots of species richness for three diverse ithomiine genera (*Ithomia*, *Napeogenes*, and *Oleria*; Chazot, Willmott, Freitas, et al., 2016). However, patterns of species diversity remain to be documented at the level of the entire tribe, across the Neotropics. Similarly, patterns of phylogenetic diversity, geographic rarity and mimicry richness remain largely uncharacterized at such scales.

Phylogenetic diversity has become a fundamental component of biodiversity assessments that addresses the evolutionary distinctiveness of species assemblages (Faith, 1992). It is recognized by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) as a key indicator for the maintenance of options in nature's contribution for people (IPBES, 2019) and is included in conservation tools such as the EDGE index for Evolutionarily Distinct and Globally Endangered species (Isaac et al., 2007). High phylogenetic diversity reflects the presence of species with distinctive evolutionary pathways, which provide a proxy for evolutionary novelties of high value for conservation (Faith, 2018).

Geographic rarity is another component of biodiversity that relates to the spatial dimension of rarity, with species with restricted distributions being considered rare compared to species with wider ranges (Rabinowitz, 1981). Species with small geographic ranges can support original functions in ecosystems (Mouillot et al., 2013), while they often face higher risks of extinction (Böhm et al., 2016; Cardillo et al., 2008; Purvis et al., 2000). Species range size is therefore commonly incorporated into diversity indices (Gumbs et al., 2020; Jetz et al., 2014; Maritz et al., 2016). Mapping species geographic rarity provides an additional tool for conservation prioritization (Cadotte & Davies, 2010), as another complementary facet of diversity patterns linked to species vulnerability and areas of endemism.

Biotic interactions, although rarely integrated in biodiversity assessments, represent the architecture of life that reflects the interdependence of all units of biodiversity (Bascompte, 2009). For example, mutualistic interactions can shape species distributions and community composition (Duffy & Johnson, 2017; Sherratt, 2006), affecting ecosystem stability (Hale et al., 2020; Pascual-García & Bastolla, 2017) and supporting ecosystem services such as pollination function or seed dispersal (Millennium Ecosystem Assessment,

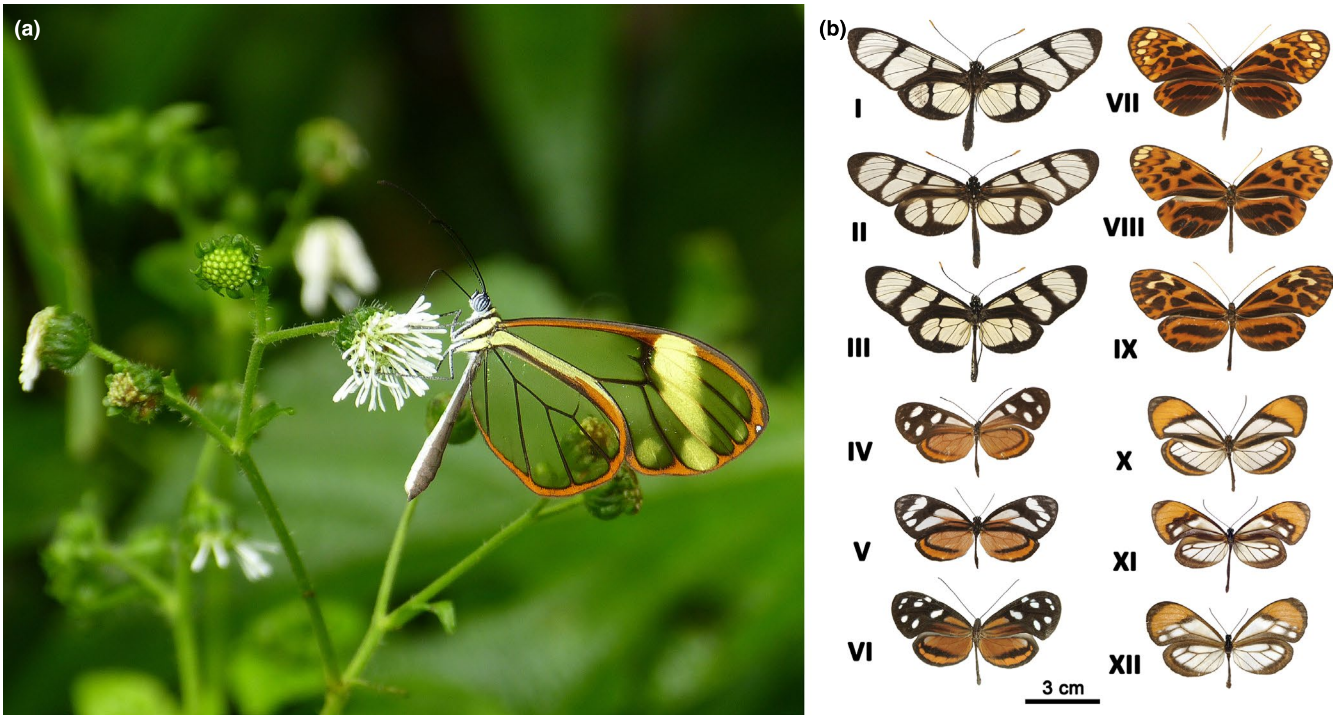

FIGURE 1 Wing patterns in ithomiine butterflies. (a) Specimen of *Hypomenitis libethris* harbouring the wing pattern LIBETHRIS with transparent areas. Photo credits: Andrew Neild, 2016. (b) Illustration of the convergence of wing patterns across Ithomiini. Mimicry ring CONFUSA: *Methona confusa psamathe* (I), *Thyridia psidii ino* (II), *Methona themisto* (III). Mimicry ring ILLINISSA: *Oleria ilerdina priscilla* (IV), *Napeogenes sylphis ercilla* (V), *Hyposcada illinissa illinissa* (VI). Mimicry ring MAELUS: *Melinaea satevis cydon* (VII), *Hypothyris anastasia anastasina* (VIII), *Hypothyris fluonia pardalina* (IX). Mimicry ring AURELIANA: *Napeogenes sylphis corena* (X), *Hypoleria aureliana* (XI), *Pseudoscada fluora aureola* (XII). Photo credits: Nicolas Chazot, 2015

2005). Müllerian mimicry systems, such as ithomiine butterflies, provide an excellent opportunity to study mutualistic interactions, because interacting species can be identified through their similarity in warning patterns. Müllerian mimicry is known to affect individual fitness and constrain species distribution (Aubier et al., 2017; Chazot et al., 2014; Kapan, 2001; Langham, 2004; Mallet & Barton, 1989; Sherratt, 2006). Additionally, mimetic species form adaptively assembled mutualistic communities that are predicted to suffer more from community disassembly due to the loss of those mutualistic interactions (Toby Kiers et al., 2010) and to be more sensitive to co-extinction cascades (Dunn et al., 2009). Therefore, Müllerian mimicry systems provide opportunities to map patterns of mimicry richness and geographic rarity, which reflect the distribution of mutualistic interactions in space, a component of functional diversity that is particularly relevant for conservation.

In this study, (1) we provide modelled distribution maps of taxonomic, phylogenetic and mimetic diversity as well as geographic rarity, for the entire tribe Ithomiini across the Neotropics, in order to identify biodiversity hotspots as areas of both evolutionary and ecological importance for conservation; (2) we evaluate the spatial relationships among those facets of Ithomiini diversity; and (3) we assess current anthropogenic threats to Ithomiini biodiversity hotspots, highlighting risk areas with high anthropogenic pressures, and potential refuges with currently low levels of human influence.

2 | METHODS

2.1 | Data sources

We compiled from multiple sources an initial data set of 28,986 georeferenced occurrences for 388 ithomiine butterfly species in their natural habitats, out of the 396 known species, spanning 25 countries across the Neotropics (see maps of occurrences, sampling effort, sampling completeness and bioregions in Figure S1.1, S1.2, S1.3 & S1.4). This data set provided 19,271 species-grid-cell records for distribution modelling at a 0.25° × 0.25° spatial resolution after removing duplicate records from single grid cells, which are available from Zenodo at https://doi.org/10.5281/zenodo.4696055. The data come from fieldwork by the authors over the past five decades, and records from over 60 museums and private collections detailed in the online archive metadata. Each record is associated with its location, its taxonomic identity and its mimicry ring membership (i.e. a wing colour pattern shared by individuals reflecting mutualistic interactions). The current classification of wing patterns presents 44 mimicry rings (Figure S2.5) updated from previous works (Beccaloni, 1997; Chazot et al., 2014, 2019; Elias et al., 2008; Jiggins et al., 2006; Willmott & Mallet, 2004).

Sets of co-mimetic species (i.e. sharing a wing pattern) form mimicry rings (Figure 1b). Most Ithomiini species comprise several to many subspecies that may belong to distinct Müllerian mimicry rings. Additionally, some subspecies show a sexual dimorphism with males and females belonging to different mimicry rings. Since we intended to map mimicry ring distribution as well as species distribution, we defined Operational Mimicry Units (OMUs) as the set of individuals within the same species that shared the same mimicry pattern. An OMU may either be equivalent to an entire species, if all individuals of all subspecies of that species share the same pattern, or it may represent individuals from a smaller group of subspecies that share a common mimicry pattern, in which case a single species may be represented by multiple OMUs. A total of 783 OMUs were used as modelling units for distribution models (complete list in Appendix 4). The mimicry classification of all 1511 subspecies is available from Zenodo at https://doi.org/10.5281/zenodo.5497876.

To compute indices of phylogenetic diversity, we used a recently published time-calibrated phylogeny of the Ithomiini (Chazot et al., 2019; Figure S3.6), which represents 339 out of the 388 species with georeferenced records.

2.2 | Data analyses

2.2.1 | Species distribution modelling (SDM)

In order to map the current distributions of ithomiines, we developed species distribution models (SDMs) relating occurrence data with a set of environmental variables. We describe our SDM methods following the ODMAP (Overview, Data, Model, Assessment, Prediction) protocol for species distribution models (Zurell et al., 2020). Here, we provide the overview of the distribution models while the remaining ODMAP sections, providing details in modelling steps, justifications for modelling choices and a more in-depth discussion about potential caveats and limits, are detailed in Appendix 5.

We aimed to model the current distribution of species and mimicry rings, as well as to infer the current patterns of geographic rarity and taxonomic, phylogenetic and mimicry ring diversity (as described further below) for the whole Ithomiini tribe. We proceeded as follows: (1) we retrieved environmental predictors of Ithomiini distribution, (2) we obtained multiple environmental suitability maps for each OMU employing a set of SDM algorithms, (3) we derived for each OMU a median ensemble model depicting its modelled distribution, (4) we stacked these modelled distribution maps in order to obtain in each pixel the predicted occurrence of OMUs, while observed binary maps of OMU with less than six occurrences were included directly at this step, then we (5) derived species and mimicry ring distribution maps and compute various taxonomic, phylogenetic and mimicry diversity and geographic rarity indices (Figure 2).

Our models encompassed the entire distribution of the tribe in the Neotropics (Longitude 120°E–30°E, Latitude 37°S–28°N) at a 0.25° × 0.25° spatial resolution. Thus, each quarter-degree grid cell (hereafter, pixel) represents a virtual community of ca. 27.8 km × 27.8 km. This resolution is appropriate for niche models based on large-scale predictors such as climate (McGill, 2010), limits commission errors (Di Marco et al., 2017) and appears sufficient to identify broad geographic patterns of diversity at a scale relevant

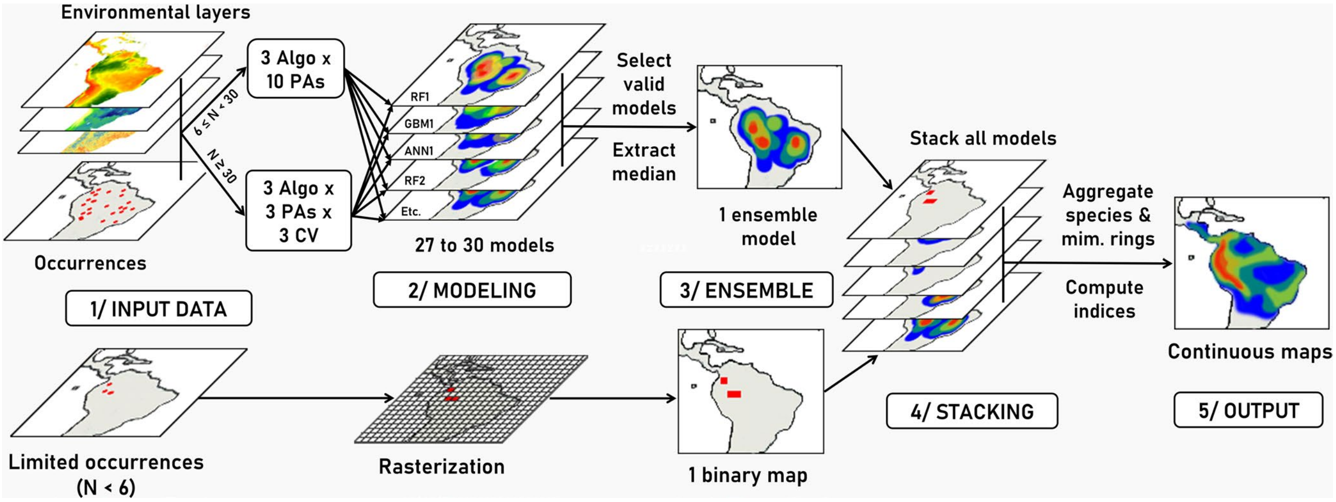

FIGURE 2 Species Distribution Model (SDM) workflow depicting the different analytical steps performed. Distribution models are computed for each OMU. Depending on sample size, modelling steps and settings differed. Clipping step to constrain SDM projections to plausible distribution ranges is not shown on the chart. Algo = algorithms used in the study, namely random forest (RF), gradient boosting models (GBM) and artificial neural networks (ANN); PAs = sets of pseudo-absences; CV = cross-validation folds; mim. rings = mimicry rings

to biodiversity conservation (e.g. Abreu-Jardim et al., 2021; Gumbs et al., 2020; Robuchon et al., 2021; Roll et al., 2017). We selected climate, represented by annual temperature and humidity levels and seasonality (MERRAclim v.2.0; Vega et al., 2017), elevation (SRTM Dataset v.4.1; Farr et al., 2007) and vegetation cover (GLCF; Sexton et al., 2013), as environmental predictor variables for distribution modelling. Indeed, these environmental dimensions have been regarded as important in determining large-scale distribution patterns and structuring ithomiine communities (Beccaloni, 1997; Chazot et al., 2014).

We fitted SDMs for 563 OMUs for which we had at least six occurrences available (71.9% of OMUs, encompassing 335 species, i.e. 86.3% of species with known occurrences). We included the remaining 220 OMUs (28.1%) in stacks as binary rasters of presences–absences. We fitted SDMs in *biomod2* v.3.4.6 (Thuiller et al., 2020) using three machine learning algorithms to cope with small sample sizes: random forest, generalized boosted models and artificial neural networks. We drew pseudo-absences from those occurrences in a target group strategy (Mateo et al., 2010), a procedure to increase the likelihood that sampled pseudo-absences were effectively located in sites where OMUs were absent. We evaluated model performance with maximized Jaccard indices. For 361 OMUs with small sample sizes ($N < 30$; 46.1%), models were evaluated upon the calibration data set. For 202 OMUs with large sample sizes ($N \geq 30$; 25.8%), we ran an additional 3-fold spatial block cross-validation step (Roberts et al., 2017; Valavi et al., 2019) to improve model evaluation. We discarded models with a poor performance (Jaccard index < 0.95 without cross-validation; Jaccard index < 0.6 with cross-validation) and produced an ensemble model based on the median of predictions. We clipped final outputs with OMU-specific buffered alpha-hulls and, where relevant, we constrained outputs to the east or west of the Andean continental divide, to limit the extent of possible distributions to reasonable areas.

We derived species and mimicry ring distribution maps from the modelled distribution maps of OMUs as the likelihood of finding at least one of the OMUs belonging to the species/mimicry ring in the community (i.e. in the pixel). In the final post-processing step, we computed six diversity and geographic rarity indices based directly on the stack of species and mimicry ring maps. Additionally, we present in Appendix 9 four additional indices evaluating similar facets of diversity with alternative methods to explore the robustness of our analyses to index selection.

2.2.2 | Diversity and geographic rarity indices

We computed species and mimicry richness as the expected number of species and mimicry rings found in our communities (i.e. in each pixel), by summing the continuous outputs from models as recommended by Calabrese et al. (2014). To estimate phylogenetic diversity, we computed Faith's phylogenetic diversity index (Faith, 1992) based on the phylogeny of the Ithomiini tribe (Chazot et al., 2019) encompassing 339 species and 719 OMUs. This index estimates the total length of branches connecting all the species within a community, capturing the quantity of evolutionary history they represent.

We assigned geographic rarity weights for each species and mimicry ring based on their relative geographic ranges following the threshold-dependent exponentially decaying weighting scheme of Leroy et al. (2013). This method assigns weights that exponentially increase below the chosen rarity threshold and rapidly decay to zero above the threshold, thereby limiting the impact of common species on community indices. We chose the rarity threshold at which the average proportion of rare species in communities was 25%, as detailed in Leroy et al. (2012). Next, we used these rarity weights to calculate an index of rarity for each community, which was the average rarity weight for all species or mimicry rings. These indices can be seen as proxies for relative levels of endemism since they quantify the relative importance of species or mimicry ring with small ranges in communities.

To quantify the importance of mutualistic interactions, we estimated the mean size (i.e. number of species) for mimicry rings within each community. Communities with high mean mimicry ring size correspond to greater frequencies of mutualistic interactions, while communities with low mean mimicry ring size host in average species engaged in fewer mutualistic interactions. Assuming that the richest mimicry rings also tend to be the most abundant, species belonging to smaller mimicry rings, thus harbouring locally rare patterns, are likely more vulnerable to predation by naïve predators, and thereby to local extinctions (Müller, 1879). As such, a low mean mimicry ring size may relate to higher vulnerability on average in the mimicry community.

Additionally, we computed indices of effective richness based on Shannon's diversity indices and an index of evolutionary distinctiveness based on Fair-Proportions (Redding, 2003), and we mapped the size of the main mimicry ring in each community (see Figure S9.22). A flow chart and additional details on index computation based on our modelled distribution maps are provided in Appendix 8. The robustness of indices was tested with several sensitivity analyses as described in the ODMAP protocol. Results showed no qualitative difference with the results presented in the main text (see Figure S5.12–S5.16).

2.2.3 | Estimation of index correlation

We computed pairwise Spearman's rho coefficients (ρ) to estimate the spatial congruence among our indices. We tested for the significance of these relationships with corrected degrees of freedom accounting for the positive spatial autocorrelation among observations (Clifford et al., 1989; Haining, 1991). Then, we built a heatmap of spatial congruence among indices based on the absolute Spearman's rho coefficients. Additionally, we ran a hierarchical clustering analysis based on those same absolute coefficients as distances from perfect correlation (*i.e.* $d = 1 - |\rho|$) with a complete linkage method to produce a dendrogram revealing classes of indices showing highly similar patterns. We distinguished four classes of indices that represented the main facets of biodiversity while grouping indices that were highly correlated and revealed virtually similar hotspots. This resulted in applying a threshold of $|\rho|$ equal to 0.94 (see details in Results). Then, we selected one index per class for subsequent analyses of anthropogenic threats on diversity hotspots.

2.2.4 | Spatial overlap between biodiversity hotspots and anthropogenic threats

We used the 2009 Human Footprint index (Venter et al., 2016a) as a measure of anthropogenic threats to our communities of ithomiine butterflies. Despite representing anthropogenic pressures from a decade ago, Human Footprint remains the most comprehensive and recent map available for worldwide cumulative human pressures on terrestrial ecosystems (see Figure S6.17). It is still widely used in similar large-scale conservation assessments, which allows for standardization and comparative analyses (e.g. Allan et al., 2019; Di Marco et al., 2018; Elsen et al., 2020; Maron et al., 2020; Tucker et al., 2018). The index combines eight variables that measure direct human impacts on the environment, namely (1) human population density, (2) night-time light pollution, (3) extent of built environments, (4) crop land cover, (5) pasture land cover, and (6) proximity to railways, (7) to major roadways and (8) to navigable waterways.

We defined two levels of hotspots as the top 5% and 25% of communities showing the highest values for each of our indices. Similarly, we defined areas of very high (top 5%), high (top 25%), low (bottom 25%) and very low (bottom 5%) threats based on the Human Footprint scores of communities. Then, we characterized as risk areas communities showing the highest values in a facet of Ithomiini diversity (*i.e.* hotspots), and the highest levels of anthropogenic pressures. Risk areas should be considered as priorities for reactive conservation with the goal of reducing high anthropogenic impact on threatened biodiversity (Brooks et al., 2006). Conversely, we characterized refuge areas as communities within hotspots with the lowest levels of pressures. Refuges should be prioritized for proactive conservation, with the goal of preserving these diverse areas from future anthropogenic threats (Brooks et al., 2006), providing shelter for a portion of ithomiine biodiversity. Finally, we mapped risk areas and refuge areas for four indices selected to represent our classes of highly correlated indices, namely (1) species richness, (2) mean species geographic rarity, (3) mimicry richness and (4) mean mimicry geographic rarity.

2.3 | Reproducibility and data availability

We conducted all analyses using R 3.6.2 (R Core Team, 2019) with packages ‘raster’ 3.0–12 (Hijmans, 2020), ‘biomod2’ 3.4.6 (Thuiller et al., 2020), ‘sf’ 0.9–0 (Pebesma, 2018), ‘blockCV’ 2.1.1 (Valavi et al., 2019), ‘alphahull’ 2.2 (Pateiro-Lopez & Rodriguez-Casal, 2019), ‘ape’ 5.3 (Paradis & Schliep, 2019), ‘geiger’ 2.0.6.1 (Harmon et al., 2008), ‘Rarity’ 1.6.3 (Leroy, 2016) and others. All R scripts are available on GitHub at https://github.com/MaelDore/ithomiini_diversity. Species-grid-cell records and the mimicry classification used for modelling are available from Zenodo at https://doi.org/10.5281/zenodo.4696055 and https://doi.org/10.5281/zenodo.5497876.

3 | RESULTS

We inferred the distribution for each of the 388 species and 44 mimicry rings based on the 783 OMUs. All OMU/species/mimicry ring modelled distribution maps can be found at https://doi.org/10.5281/zenodo.4673446. Examples are provided in Appendix 7.

3.1 | Index maps

The Eastern slopes of the Andes appeared as the primary hotspot of Ithomiini taxonomic, phylogenetic and mimetic diversity, especially between 500 and 2500 m (Figure 3a, c, d, g). We estimated that some quarter-degree grid cells (hereafter referred to as communities) may harbour as many as 120 species, representing up to 28 mimicry rings, especially in Ecuador and Peru. These species totals partly represent alpha-diversity and partly different habitats contained within single quarter-degree grid cells. The Atlantic Forest and the highlands of Central America appeared as secondary hotspots but fall far behind in terms of numbers of species, mimicry richness and phylogenetic diversity. Conversely, we estimated species and mimicry richness, and phylogenetic diversity,

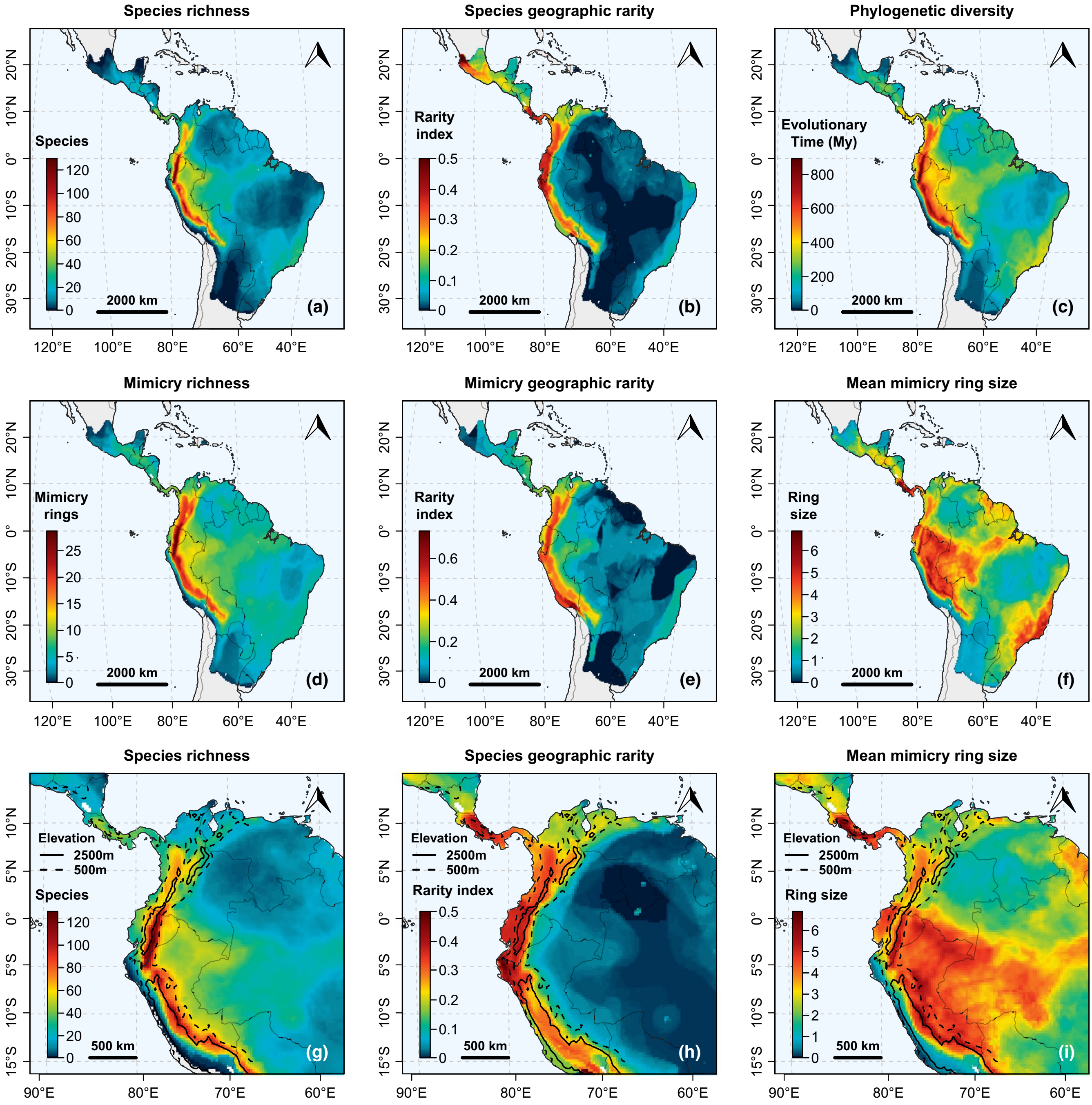

FIGURE 3 Heatmaps of the different facets of Ithomiini diversity in the Neotropics for quarter-degree grid cells. (a) Species richness. (b) Mean species geographic rarity based on species range. (c) Faith's phylogenetic diversity (Faith, 1992). (d) Mimicry richness (*i.e.* number of mimicry rings). (e) Mean mimicry geographic rarity based on mimicry ring range. (f) Mean mimicry ring size as mean number of species per mimicry ring. Maps g, h and i: Zoom on the northwestern Andes region for species richness (g), species geographic rarity (h) and mean mimicry ring size (i). Contour lines represent elevation for 500 m (dashed lines) and 2500 m (solid lines). Political boundaries are displayed in light grey. All maps are projected under Mollweide's projection, centred on the meridian 75°E

to be relatively low in regions with low forest cover such as in the Llanos, in the semi-arid Caatinga, in the seasonal Cerrado savannas, and the Pantanal wetlands (see map of bioregions in Figure S1.4). Regions around the outer margin of the Ithomiini distribution such as the north of Central America, the Chaco region and the Pampas grasslands from Northwest Argentina to Uruguay (see map of bioregions in Figure S1.4), also show relatively low levels of richness and phylogenetic diversity.

Mean geographic rarity of species and mimicry peaked on the western slopes of the Andes facing the Pacific coast and appeared generally high in the Andes (Figure 3b, e, h). Mean species geographic rarity was also estimated to reach high levels in Central America. Conversely, few species and mimicry rings with restricted ranges occurred in the species-poor Cerrado savannas, in the Chaco region and in the semi-arid Caatinga (Figure 3b, e). The Amazon basin also hosted few rare species and mimicry rings, with the notable exception of the regions around the course of the Amazon River in the Upper Amazon (Figure 3b, e, h).

Communities with the largest mimicry rings on average, that host the highest proportion of mutualistic interactions, were estimated to occur in Central America in Panama and Costa Rica, on the eastern slopes of the Andes in Ecuador and Peru, along the Amazon River, and in the Atlantic Forest (Figure 3f, i). Conversely, communities in the species-poor Llanos, Caatinga, Cerrado and Chaco regions contained the most vulnerable mimicry rings with the fewest species on average (Figure 3f).

3.2 | Correlation among indices

All indices were significantly positively correlated (Table S10.26: Clifford's correction for Spearman's rank test, all pairwise *p*-values < 0.001). We distinguished four classes of indices based on their levels of correlation (Figure 4). The dendrogram and correlation heatmap for the full set of ten indices are presented in Figure S9.23.

The first class represented a set of indices strongly correlated with species richness (Figure 4; Table S10.27). Species richness appeared to be a very strong predictor of Faith's phylogenetic diversity (Tables S10.26 and S10.27: $\rho = 0.996$, $t = 84.0$, Clifford's $df = 56.7$, $p < 0.001$), and mean mimicry ring size (Tables S10.26 and S10.27: $\rho = 0.941$, $t = 21.2$, Clifford's $df = 57.9$, $p < 0.001$).

Mimicry richness also correlated strongly with species richness (Tables S10.26 and S10.27: $\rho = 0.934$, $t = 19.7$, Clifford's $df = 56.6$, $p < 0.001$), but it was less strongly correlated with the other indices of the first group (Table S10.26: $\rho = 0.854$ in average). Moreover, the relationship between species richness and mimicry richness was not strictly linear: some communities with the highest number of mimicry rings are not the most speciose (Figure S10.24c). Since this pattern can lead to differences in hotspot identification, we attributed mimicry richness to a second class of indices on its own (Figure 4).

Geographic rarity indices (species and mimicry) were more closely correlated with each other (Tables S10.26 and S10.27: $\rho = 0.657$, $t = 7.05$, Clifford's $df = 65.5$, $p < 0.001$) than with any other indices. However, they were less correlated with each other than the first group of indices. As such, they formed a third and fourth class of indices (Figure 4). They were nonetheless moderately correlated with species richness (Tables S10.26 and S10.27: $\rho = 0.473$, $t = 4.34$, Clifford's $df = 65.4$, $p < 0.001$ for mean species geographic rarity; $\rho = 0.606$, $t = 5.98$, Clifford's $df = 61.5$, $p < 0.001$ for mean mimicry ring geographic rarity). Indeed, species-rich communities tended to present high mean geographic rarity values, while species-poor communities exhibited the entire range of relative levels of species endemism (Figure S10.24a and S10.24b). Similarly, communities with high mimicry richness showed high mean mimicry geographic rarity, while communities with few mimicry rings could exhibit the entire range of relative levels of mimicry endemism (Figure S10.24d).

Correlations including the four additional indices computed (namely species Shannon's diversity, mimicry Shannon's diversity, Evolutionary Distinctiveness and the maximum mimicry ring size) supported the classification in four classes of indices and can be found in Appendices 9 and 10.

3.3 | Threat and refuge maps

Our assessment of current anthropogenic threats on Ithomiini diversity hotspots showed that the northern Andean cordilleras combine high taxonomic and mimetic diversity with high levels of human impact, making them a region of focus for conservation. Meanwhile, remote portions of the Upper Amazon rainforest may act to some extent as refuges for the different facets of Ithomiini diversity (Figure 5). However, the top 5% hotspots consistently demonstrated very limited to no overlap with potential refuge areas for all indices (Figures 5b, d, f, h and 6b).

We estimated hotspots of species richness to be under relatively high anthropogenic pressures in the Andes, with most of the mountainous areas below 2500 m coinciding with species-rich communities and high human impact levels (Figure 5a). The Atlantic Forest, as the secondary hotspot for Ithomiini species richness, appeared to be the most threatened with a large portion of its range falling under high levels of threats, including the top 5% of the most threatened communities (Figure 5a). The Upper Amazon encompassed a significant part of potential refuge areas with low levels of threats (Figures 5a and 6a; 33.3% of hotspots compared to the expected 25% overlap), but these areas showed limited overlap with the top 5% of the richest communities (Figures 5b and 6b; 13% of hotspots compared to the expected 25% overlap).

We estimated mean species geographic rarity hotspots to be relatively more threatened than the other facets of Ithomiini diversity, and also to deviate positively from that expected from a random distribution of anthropogenic threats (Figures 5c–d and 6). This trend remained detectable when exploring other thresholds to define the hotspots (Figure S11.28). Hotspots in the Andes, the coastal part of the Atlantic Forest, and the mountainous spine of Central America showed high to very high levels of threats

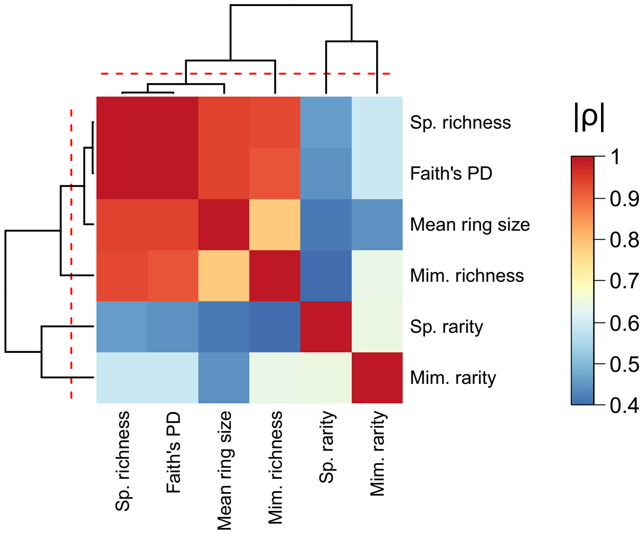

FIGURE 4 Heatmap of spatial correlations across Ithomiini biodiversity indices with associated dendrogram depicting the hierarchical clustering of the indices. Correlations are estimated as the absolute values of Spearman's rho statistics (ρ). Dendrogram built with a complete link method. Red dashed lines represent the threshold used to regroup indices with strong correlation ($|\rho| = 0.94$). Sp. = Species. Mim. = Mimicry. PD = Phylogenetic Diversity. Rarity as mean geographic rarity

(Figure 5e; 42.9% of overlap compared to the expected 25%, and 10.3% compared to the expected 5% for the highest levels of threats). Meanwhile, only a small portion of the Upper Amazon was estimated as a potential refuge area for communities with high levels of endemism (Figures 5c and 6a; 4.5% compared to the expected 25% overlap), and virtually none encompassed the top 5% of the communities with the rarest species on average (Figures 5d and 6b).

Hotspots of mimicry richness showed similar patterns to species richness due to the relatively high spatial congruence between the two indices (Figures 4 and 5). The main difference was that the Atlantic Forest did not rank as a hotspot for mimicry diversity and therefore reduced perceived threat levels on mimicry richness hotspots compared to species richness hotspots (Figures 5a, e and 6a; 15.8% for mimicry richness and 23.9% for species richness vs. 25% expected overlap).

Likewise, we estimated hotspots for mean mimicry ring geographic rarity to face high levels of threats in the Andes, Central America and the coastal part of the Atlantic Forest. They also extend moderately to the relatively less threatened part of the Upper Amazon, along the course of the Amazon River (Figure 5g–h). However, the top 5% hotspots found in the Andes and on the Pacific coast coincided with very few potential refuge areas (Figures 5h and 6b; 1.5% and 0% vs. 25% and 5% expected overlaps, respectively, for the low and very low levels of threats) while being more threatened than expected from a random distribution of anthropogenic threats (Figure 6b; 34.4% and 6.7% vs. 25% and 5% expected overlaps).

4 | DISCUSSION

4.1 | Spatial congruence of the facets of Ithomiini diversity

In our integrative approach to mapping Ithomiini diversity, we found that estimated species, mimicry and phylogenetic diversity indices are strongly correlated across the Neotropics. All indices peaked on the eastern slopes of the Peruvian and Ecuadorian Andes, and in the Upper Amazon region, while the Atlantic Forest and Central American mountains appeared as secondary richness hotspots (Figure 3a, c, d). We also uncovered relatively low levels of biodiversity in the Llanos, the Guyana Shield and the Cerrado savannas. As is common in stack-SDM procedures, these predictions likely overestimate richness and diversity within individual grid cells because species are likely absent in at least some environmentally suitable grid cells where they are predicted to occur (see ODMAP in Appendix 5). However, this potential bias affects all cells evenly and therefore does not prevent the generation of meaningful insights into the relative patterns of biodiversity and the identification of hotspots.

Spatial patterns of ithomiine biodiversity likely result from the combined effects of historical, ecological and topographical factors. The tribe likely originated in the eastern Andean foothills, about 26 My ago and diversified in the Andes throughout the Miocene (Chazot et al., 2019). The demise of the Pebas, a large wetland system that occupied the lowlands on the eastern side of the Andes, led to the expansion of the modern Amazonian forest (Hoorn & Wesselingh, 2010), allowing multiple colonizations and diversification in the Upper Amazon during the last 10 My (Chazot et al., 2018, 2019; Chazot, Willmott, Condamine, et al., 2016; De-Silva et al., 2016, 2017; Elias et al., 2009). Ithomiini are strongly specialized on their larval hostplants, and hostplants are likely a limiting resource (Drummond III & Brown Jr, 1987; Willmott & Mallet, 2004). The diversity of Solanaceae, on which most Ithomiini feed as larvae, also peaks in the Andes and the Upper Amazon (Knapp, 2002; Ulloa Ulloa et al., 2017), thereby potentially enabling greater local Ithomiini diversity. This apparent spatial correlation between species diversity in ithomiines and their hostplants is consistent with a hostplant-mediated adaptive radiation scenario (Willmott & Freitas, 2006). Finally, the topological complexity of the Andes and adjacent foothills creates high variability in abiotic conditions, habitat and vegetation types (Osborne, 2012), which generates species turn-over, mimicry shifts and fosters vicariant speciation (Chazot et al., 2014; Elias et al., 2009; Jiggins et al., 2006). Therefore, the tropical Andes represent the primary hotspot of alpha-diversity (Figure 3a), but also beta-diversity with high local endemicity (Figure 3b and h) and turnover across communities, both of high interest for conservation. The Upper Amazon, because of its proximity and historical exchanges with the Andes, its soil enriched with orogenic sediments, as well as a more variable climate and heterogeneous forest structure hosting numerous microhabitats, tends to host more diverse communities

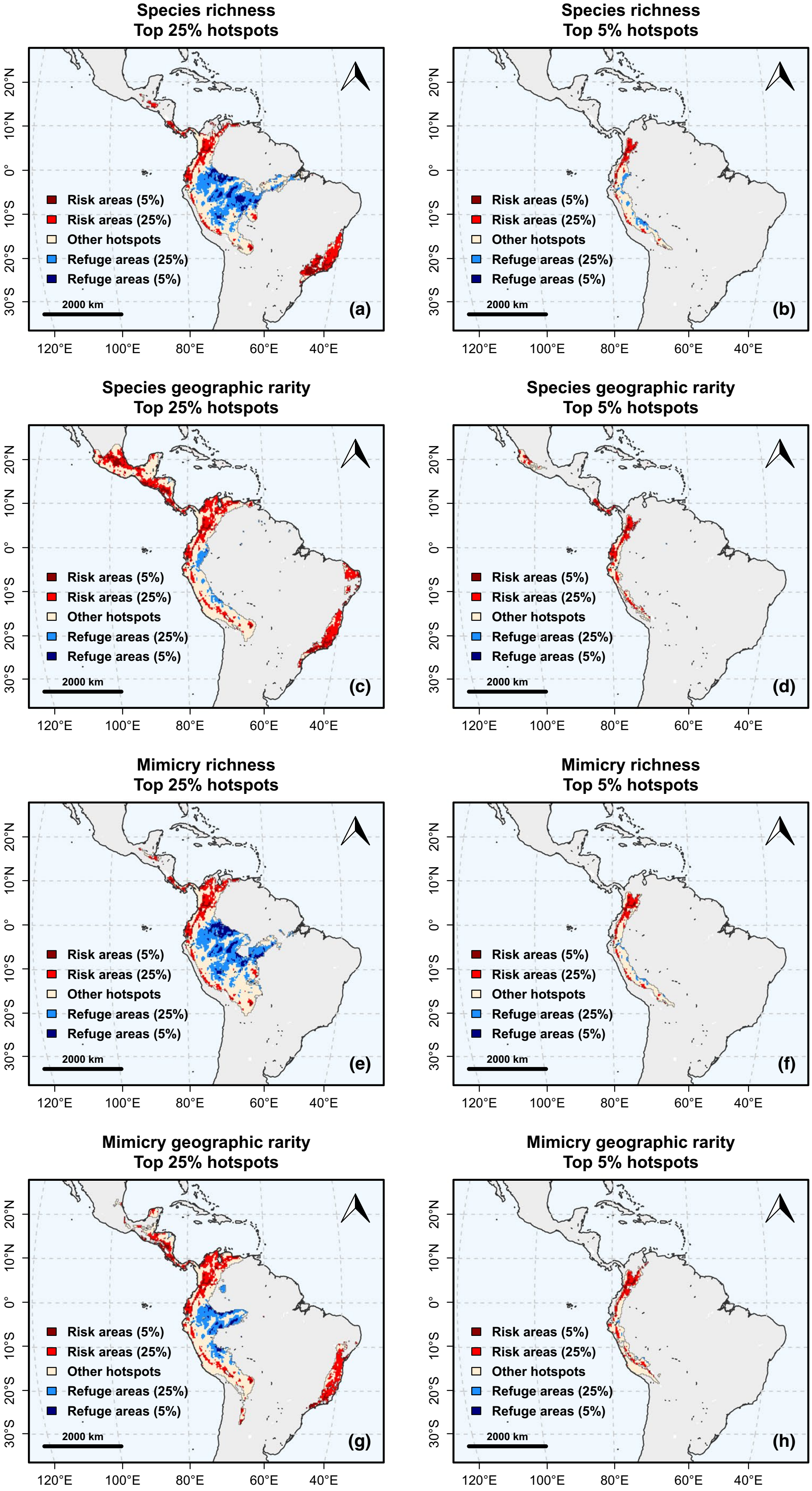

FIGURE 5 Legend on next page

FIGURE 5 Maps of risk and refuge areas for four predicted Ithomiini diversity hotspots. Only hotspots are displayed, defined as the top 25% (Panels a, c, e, g, on the left) or top 5% (Panels b, d, f, h, on the right) of highest-ranking communities for each index. Anthropogenic threat levels are based on the Human Footprint index, classified within quantiles 5% and 25% for lower and upper end of the distribution. Risk areas (in red) represent areas of overlap between high threat zones and hotspots. Refuge areas (in blue) represent areas of overlap between low threat zones and hotspots. Hotspots not falling into areas of high or low threat levels are displayed in light colour. (a) and (b): Species richness. (c) and (d): Mean species geographic rarity based on species range. (e) and (f): Mimicry richness (*i.e.* number of mimicry rings). (g) and (h): Mean mimicry geographic rarity based on mimicry ring range

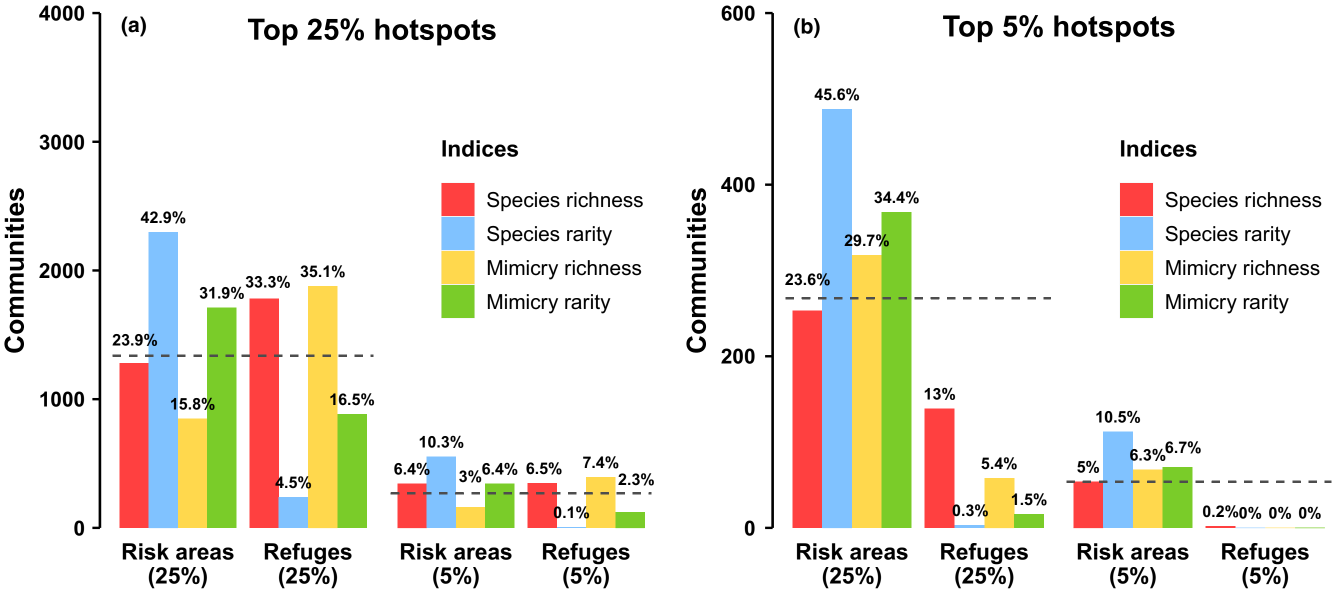

FIGURE 6 Comparison of extent of risk and refuge areas between indices. Risk areas represent areas of overlap between high anthropogenic pressures and biodiversity hotspots. Refuge areas represent areas of overlap between low anthropogenic levels and biodiversity hotspots. Y-axis represents the number of communities (i.e. grid cells) within risk and refuge areas for each biodiversity hotspots. Species rarity describes mean geographic rarity based on species range. Horizontal dashed lines represent the expected size of the overlap for a random distribution of anthropogenic threats. Percentages displayed on bars represent the proportion of the hotspot overlapping with the threat area. (a) For the top 25% hotspots. (b) For the top 5% hotspots

than the more stable forests found in the Lower Amazon (Figure 3a; Brown Jr., 2005; Brown Jr. & Freitas, 2002; Sombroek, 2000).

Conservation efforts focused on hotspots of taxonomic diversity alone may not necessarily be effective for conserving a large fraction of species, or other aspects of biodiversity (Devictor et al., 2010; Godoy-Bürki et al., 2014; Williams et al., 1996; Williams & Humphries, 1994; Zupan et al., 2014). As such, areas that host rare and endangered biological features should also be considered (Prendergast et al., 1993; Lawler et al., 2003; e.g. Alliance for Zero Extinction: Parr et al., 2009; Key Biodiversity Areas: KBA Standards & Appeals Committee, 2020). Our mean geographic rarity indices provide a useful tool to predict areas of high endemicity that may differ from diversity hotspots. Still, geographic rarity indices appeared positively correlated with species and mimicry richness at the continental scale (Figure S10.24a and S10.24d). Species-rich communities that host mostly species with small ranges were found in the Andean and Central American mountains (Figure 3b). These regions harbour steep environmental gradients (Osborne, 2012) enabling strong hostplant turn-over (Knapp, 2002), which may limit ithomiine species ranges. Yet, some species-poor communities also coincide with high levels of species and mimicry rarity. Such communities are found in the outer edges of the global distribution of Ithomiini, especially on the Pacific slopes of the Andes (Figure 3b, e, h). There, a strong environmental gradient and geographic barriers such as the Pacific Ocean, the Peruvian coastal desert and the Central Andes could explain the restricted ranges of the few resident species and mimicry rings. Moreover, unusual environmental conditions found at the outer edges of the Ithomiini range may select for specific lineages and mimicry patterns due to environmental filtering.

Overall, Ithomiini biodiversity hotspots appear fairly congruent with biodiversity hotspots based on vascular plant species richness and endemism (Myers et al., 2000). As such, the tropical Andes stand out as the primary hotspot for the multiple facets of Ithomiini biodiversity. Secondary hotspots of Ithomiini diversity, namely the Atlantic Forest, Central American mountains and the Pacific slopes of the Andes, also coincide with areas previously recognized as biodiversity hotspots (Myers et al., 2000). Moreover, our inferred patterns of diversity and endemism are in line with the trends observed for other taxa in the Neotropics. Angiosperms and tetrapods show a peak of diversity and endemism in the western part of Amazonia and in the Andean foothills (Gumbs et al., 2020; Jenkins et al., 2013; Kier et al., 2009; Morawetz & Raedig, 2007; Roll et al., 2017; Ter

Steege et al., 2003). Among insect taxa, the overall biodiversity patterns of Ithomiini are consistent with those of Cicindelinae beetles (Pearson & Carroll, 2001), *Adelpha* butterflies (Mullen et al., 2011), Nymphidiina butterflies (Hall, 2018) and Heliconiini butterflies (Rosser et al., 2012). Conversely, the distribution of bees in the Neotropics presents an opposite trend, with higher richness per area reached in the Chaco regions, Caatinga, dry Southern Andes and Atlantic forest, reflecting the great success of this group in xeric and seasonal habitats (Orr et al., 2021). Overall, these results support the role of ithomiine butterflies as suitable flagship indicator group for Neotropical butterfly diversity and reinforce the position of the tropical Andes as the flagship region for biodiversity conservation in general and insect and butterfly conservation in particular.

4.2 | Distribution patterns of mimetic interactions

Mimicry rings displayed strong distinctive geographic patterns, suggesting different underlying biogeographical trajectories (see examples in Figure S7.20; names are provided in capital letters hereafter). Central America and the Atlantic Forest are secondary hotspots for Ithomiini species richness and host relatively large mimicry rings (Figure 3a, f and i), but few of those rings are endemic to these regions (Figure 3e). Only two mimicry rings are endemic to the Atlantic Forest (HEMIXANTHE and LYSIMNIA), while in Central America, some mimicry rings extend south to the northern Cordilleras of the Andes (DILUCIDA, EXCELSA, PARALLELIS), and others span a large part of the entire distribution of Ithomiini (e.g. AGNOSIA, EURIMEDIA, MAMERCUS). By contrast, the Amazon forest harbours about ten endemic mimicry rings, whose centres of species richness are located in the Upper Amazon (e.g. AURELIANA, MAELUS, SINILIA) close to the predicted centre of origin of the tribe, and along the Amazon River (i.e. DOTO, EGRA). Most narrow-ranging and species-poor mimicry rings are found in the Andes (Figure 3e), where mimicry rings are strongly segregated along the altitudinal gradients (Chazot et al., 2014). Lowland communities shelter mostly wide-ranging rings (e.g. CONFUSA, HERMIAS, LERIDA) while highland communities host rare, narrow-ranging rings (e.g. DERCYLLIDAS, HEWITSONI, THEUDELINDA) comprising species adapted to higher altitudes. Paradoxically, mimicry rings with transparent patterns tend to be found in higher proportions at high elevations (e.g. THABENA-F, PANTHYALE, OZIA), in contrast to predictions of the thermal melanism hypothesis that opaque patterns should be under positive selection under colder climates (Clusella Trullas et al., 2007; Dufour et al., 2018). As such, further research is still needed to better understand the selective advantages of these transparent wings that shape the biogeography of mimicry patterns in ithomiines.

Altogether, mimicry richness is expected to follow species richness since more species provide greater opportunities to harbour different wing patterns. In parallel, mimicry fuels species richness by limiting the exclusion effect of competition among co-occurring co-mimetic species (Gross, 2008). However, aposematic signals are predicted to converge locally due to positive frequency-dependent selection incurred by predators (Müller, 1879). Therefore, mimicry richness should increase more slowly than species richness and plateau when all ecological niches are occupied and a (set of) wing pattern(s) already dominates each niche (Joron & Mallet, 1998). The relationship between Ithomiini mimicry and species richness was positive (Figure 4), but it appeared only slightly saturated (S10.24c). This suggests that even in species-rich communities, there is some free ecological space, or that the effect of selection for wing pattern convergence is weaker than thought in Müllerian mimetic communities. For instance, the high numbers of mimicry rings found in the most speciose communities in the Ecuadorian and Peruvian tropical Andes may arise because the steep environmental and altitudinal gradients in these regions create a small scale mosaic of zones within each grid cell, hosting locally adapted species and mimicry rings with fuzzy limits (Sherratt, 2006; e.g. altitudinal bands; Chazot et al., 2014). This dense spatial structuring facilitates the recurrent permeation of species and mimicry rings from adjacent zones that may not represent local adaptive peaks of the available niches. Yet, such species could persist, rescued by recurrent immigration (Brown Jr. & Freitas, 2002; Joron & Iwasa, 2005), thereby fuelling local mimicry richness. From a conservation point of view, preserving high species richness should also ensure the preservation of mimicry richness. We estimated that rich communities may not only harbour the highest number of species but also the highest proportion of mutualistic interactions in the ithomiine butterfly communities, with the largest mimicry rings on average (Figures 3a and f, 4). Thus, species in those communities might be better protected against secondary extinctions that would result from the loss of mutualistic interactions associated with the extirpation of their co-mimetic species.

4.3 | Threats and refuges for Ithomiini diversity hotspots

In this study, we highlighted areas of high risks for biodiversity loss, of priority interest for reactive conservation to reduce high anthropogenic pressures on biodiversity. In parallel, we defined refuge areas, of priority interest for proactive conservation to provide shelters for biodiversity from human pressures (Brooks et al., 2006). As such, hotspots for species and mimicry richness, and phylogenetic diversity, located in the Andes and the Upper Amazon, face contrasting situations. While the Upper Amazon has some of the most intact ecosystems in remote areas, the Andes, particularly the rich communities in the western foothills in Ecuador and the three Andean cordilleras in Colombia, are facing high levels of human impacts (Figures 5a, b, e, f and 6). The second diversity hotspot, the Atlantic Forest, is also of great concern, demonstrating the highest level of human pressures and relentless fragmentation of its forested habitats (Ribeiro et al., 2009). Communities with geographically rare species and mimicry rings are found mostly in Andean and Central American mountain ranges, coinciding with areas of high human impacts (Figure 5c, d). Their situation is of particular concern since species with small distribution ranges are known to face higher risks of extinction (Böhm et al., 2016; Cardillo et al., 2008; Purvis et al., 2000), thereby also impacting the narrowly distributed mimicry rings they represent.

The spatial location of threats and refuges for Ithomiini biodiversity uncovered here appear consistent with trends observed for vertebrates in general. The slopes of the northern and central Andes and the Atlantic Forest are the regions with the highest number of threatened and near-threatened vertebrates (along with South East Asia), while the Amazon rainforest has been suggested as the major refuge for vertebrate richness (Allan et al., 2019). Our study complements this picture by casting light on the specific situation of tropical highlands in the Neotropics. Mountains provide heterogeneous landscapes that host a high diversity of ithomiine species and mimicry rings, especially geographically rare and vulnerable ones. They act as a refuge for lowland species that become increasingly restricted to higher altitudes by climate warming (Chen et al., 2009), while species already adapted to high elevations, with narrow physiological specializations, are threatened by the extirpation of their climatic niche (Ohlemüller et al., 2008). Yet, many tropical species, with typically narrow niches and slow niche evolutionary rate, are suspected to lag behind the shift of their climatic envelope (Jezkova & Wiens, 2016). In the case of Ithomiini, which rely on local mutualistic interactions with co-mimics and host plants, the threat of community disassembly due to climate change is even more profound (Sheldon et al., 2011; Toby Kiers et al., 2010). Mountain habitats are particularly under threat from human activities, with high deforestation rates due mostly to the competition for arable lands (Armenteras et al., 2017). Even where human population density is low in remote mountain regions, natural habitats may come under threat from road-building and mining operations (Bax et al., 2019; Sonter et al., 2017).

Remote portions of the Upper Amazon forest may currently act as refuges for a fraction of Ithomiini diversity. Yet, even within protected areas, landscape-level changes can impact insect faunas (Hallmann et al., 2017, 2020; Salcido et al., 2020). The Upper Amazon remains largely exposed to climate change, notably increases in temperature and drought intensity (Malhi et al., 2008; Nobre et al., 2016), and to deforestation threats (Carvalho et al., 2019; Escobar, 2020). Thus, the potential refuge areas we have mapped represent only the currently less threatened areas of Ithomiini diversity hotspots, but do not guarantee the conservation of all the biodiversity facets they currently host, especially in the face of global changes. The next avenue for research is therefore to model the effects of climate change and future land-use changes on the patterns of Ithomiini diversity to refine conservation perspectives in a changing world.

ACKNOWLEDGEMENTS

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest, or non-financial interest in the subject matter or materials discussed in this manuscript. MD is financed by the French Ministry of Research (MENSR). We thank the museum curators who allowed us to examine the Ithomiini collections under their care and individuals who provided access to or shared information from their private collections or fieldwork, including Keith S. Brown Jr., Eric Quinter, Allan & Lesley Wolhuter, Steven Heydon, Jeff & Cathy Smith, Lynn Kimsey, John Rawlins, Olaf Mielke, Mirna Casagrande, Chris Jiggins, Fabio Vitale, Jackie Miller, Andy Warren, Andrei Sourakov, Francisco Piñas, Gerrit ten Broek, Santiago Villamarín, Jamie Radford, Jean-François Le Crom, Jean-Claude Petit, Wolfram Mey, Miguel Monné, Tomasz Pyrcz, Phil Ackery, Blanca Huertas, George McGavin, Pierre Boyer, Fernanda Checa, Sebastián Padrón, Heinz Schröder, Christoph Häuser, Bob Robbins, Don Harvey, Brian Harris, Axel Hausmann, Lisa de Silva, Melanie McClure and Paola Santacruz. We thank S. Villamarín, S. Nogales, the INABIO and Ecuadorian Ministerio del Ambiente for arranging the necessary permits for research in Ecuador, most recently under the project 'Diversity and Biology of Lepidoptera in Ecuador' (No. 006-19 IC-FLO-FAU-DNB/MA). Museum and fieldwork in Ecuador were funded in part by the Leverhulme Trust, the Darwin Initiative, the FLMNH Museum Associates, the National Geographic Society (Research and Exploration Grant # 5751-96) and NSF (# 0103746, #0639977, #0639861, #0847582, #1256742). We thank the INRENA/SERFOR for arranging the necessary permits for research in Peru. We thank the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for providing a research permit in Brazil (SISBIO no. 10802-5). Brazilian species are registered at the Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado (SisGen – AD7B279, AD23304, ACCDE4A, A33D8D7, ADF1F75, A37A48D). ME acknowledges funding by the ANR grant CLEARWING (ANR-16-CE02-0012) and a Human Frontier Science Program grant (RGP0014/2016). AVLF acknowledges the FAPESP (Biota-FAPESP grants 2011/50225-3, 2012/50260-6 and 2013/50297-0), the Brazilian CNPq (563332/2010-7 and 303834/2015-3) and United States Agency for International Development (USAID) and the U.S. National Academy of Sciences (NAS) under the PEER program (Mapping and Conserving Butterfly Biodiversity in the Brazilian Amazon—Sponsor Grant Award Number: AID-OAA-A-11-00012). For their companionship and assistance in the field, we thank Julia and Jamie Robinson Willmott, Alexandre Toporov, Raúl Aldaz, and Ismael Aldas. We thank the numerous people who contributed to databasing museum specimens, particularly Fraser Simpson. Models were run with the support of the computer cluster 'Plateforme Calcul Intensif Algorithmique' (UMS2700-PCIA) of the Muséum national d'Histoire naturelle MNHN.

CONFLICT OF INTEREST

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest, or non-financial interest in the subject matter or materials discussed in this manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13455.

DATA AVAILABILITY STATEMENT

All R scripts are available on GitHub at https://github.com/MaelDore/ithomiini_diversity. Species-grid-cell records and mimicry classification used for modelling are available from Zenodo at https://doi.org/10.5281/zenodo.4696055 and https://doi.org/10.5281/zenodo.5497876. All OMU/species/mimicry ring modelled distribution maps are available from Zenodo at https://doi.org/10.5281/zenodo.4673446.

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REFERENCES

Abreu-Jardim, T. P. F., Jardim, L., Ballesteros-Mejia, L., Maciel, N. M., & Collevatti, R. G. (2021). Predicting impacts of global climatic change on genetic and phylogeographical diversity of a Neotropical treefrog. *Diversity and Distributions*, *27*(8), 1519–1535. https://doi.org/10.1111/ddi.13299

Albouy, C., Delattre, V. L., Mérigot, B., Meynard, C. N., & Leprieur, F. (2017). Multifaceted biodiversity hotspots of marine mammals for conservation priorities. *Diversity and Distributions*, *23*(6), 615–626. https://doi.org/10.1111/ddi.12556

Allan, J. R., Watson, J. E. M., Di Marco, M., O'Bryan, C. J., Possingham, H. P., Atkinson, S. C., & Venter, O. (2019). Hotspots of human impact on threatened terrestrial vertebrates. *PLoS Biology*, *17*(3), 1–18. https://doi.org/10.1371/journal.pbio.3000158

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Armenteras, D., Espelta, J. M., Rodríguez, N., & Retana, J. (2017). Deforestation dynamics and drivers in different forest types in Latin America: Three decades of studies (1980–2010). *Global Environmental Change*, *46*, 139–147. https://doi.org/10.1016/j.gloenvcha.2017.09.002

Aubier, T. G., Elias, M., Llaurens, V., & Chazot, N. (2017). Mutualistic mimicry enhances species diversification through spatial segregation and extension of the ecological niche space. *Evolution*, *71*(4), 826–844. https://doi.org/10.1111/evo.13182

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336), 51–57. https://doi.org/10.1038/nature09678

Barua, M., Gurdak, D. J., Ahmed, R. A., & Tamuly, J. (2012). Selecting flagships for invertebrate conservation. *Biodiversity and Conservation*, *21*(6), 1457–1476. https://doi.org/10.1007/s10531-012-0257-7

Bascompte, J. (2009). Disentangling the web of life. *Science*, *325*(5939), 416–419. https://doi.org/10.1126/science.1170749

Bax, V., Francesconi, W., & Delgado, A. (2019). Land-use conflicts between biodiversity conservation and extractive industries in the Peruvian Andes. *Journal of Environmental Management*, *232*, 1028–1036. https://doi.org/10.1016/j.jenvman.2018.12.016

Beccaloni, G. W. (1997). Ecology, natural history and behaviour of Ithomiine butterflies and their mimics in ecuador. *Tropical Lepidoptera*, *8*(2), 103–124.

Beccaloni, G. W., & Gaston, K. J. (1995). Predicting the species richness of neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation*, *71*(1), 77–86. https://doi.org/10.1016/0006-3207(94)00023-J

Böhm, M., Williams, R., Bramhall, H. R., Mcmillan, K. M., Davidson, A. D., Garcia, A., Bland, L. M., Bielby, J., & Collen, B. (2016). Correlates of extinction risk in squamate reptiles: The relative importance of biology, geography, threat and range size. *Global Ecology and Biogeography*, *25*(4), 391–405. https://doi.org/10.1111/geb.12419

Brooks, T. M., Mittermeier, R. A., Da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., Mittermeier, C. G., Pilgrim, J. D., & Rodrigues, A. S. L. (2006). Global biodiversity conservation priorities. *Science*, *313*(5783), 58–61. https://doi.org/10.1126/science.1127609

Brown, K. S. Jr (1997). Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. *Journal of Insect Conservation*, *1*, 25–42. https://doi.org/10.1023/A:1018422807610

Brown, K. S. (2005). Geologic, evolutionary and ecological bases of the diversification of neotropical butterflies: implications for conservation. In E. Bermingham, C. W. Dick, & C. Moritz (Ed.), *Tropical rain- forest: past, present and future* (pp. 166–201). Univ. of Chicago Press.

Brown, K. S. Jr, & Benson, W. W. (1974). Adaptive polymorphism associated with multiple müllerian mimicry in *Heliconius numata*. *Biotropica*, *6*(4), 205–228. https://www.jstor.org/stable/2989666

Brown, K. S. Jr, & Freitas, A. V. L. (2000). Atlantic forest butterflies: Indicators for landscape conservation. *Biotropica*, *32*(4, Special Issue: The Brazilian Atlantic Forest), 934–956. https://www.jstor.org/stable/2663930

Brown, K. S. Jr, & Freitas, A. V. L. (2002). Diversidade Biológica no Alto Juruá: Avaliação, Causas e Manutenção. In: M. M. Carneiro da Cunha, & M. B. Almeida (Eds.), *Enciclopédia da floresta. O Alto Juruá: Práticas e conhecimentos das populações* (p. 735). Companhia das Letras.

Cadotte, M. W., & Davies, J. T. (2010). Rarest of the rare: Advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions*, *16*(3), 376–385. https://doi.org/10.1111/j.1472-4642.2010.00650.x

Calabrese, J. M., Certain, G., Kraan, C., & Dormann, C. F. (2014). Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, *23*(1), 99–112. https://doi.org/10.1111/geb.12102

Cardillo, M., MacE, G. M., Gittleman, J. L., Jones, K. E., Bielby, J., & Purvis, A. (2008). The predictability of extinction: Biological and external correlates of decline in mammals. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1641), 1441–1448. https://doi.org/10.1098/rspb.2008.0179

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kwak, M. L., Mammola, S., Ari Noriega, J., Orfinger, A. B., Pedraza, F., Pryke, J. S., Roque, F. O., Samways, M. J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, *242*, 108426. https://doi.org/10.1016/j.biocon.2020.108426

Carvalho, W. D., Mustin, K., Hilário, R. R., Vasconcelos, I. M., Eilers, V., & Fearnside, P. M. (2019). Deforestation control in the Brazilian Amazon: A conservation struggle being lost as agreements and regulations are subverted and bypassed. *Perspectives in Ecology and Conservation*, *17*(3), 122–130. https://doi.org/10.1016/j.pecon.2019.06.002

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), 9–13. https://doi.org/10.1126/sciadv.1400253

Chazot, N., De-Silva, D. L., Willmott, K. R., Freitas, A. V. L., Lamas, G., Mallet, J., Giraldo, C. E., Uribe, S., & Elias, M. (2018). Contrasting patterns of Andean diversification among three diverse clades of Neotropical clearwing butterflies. *Ecology and Evolution*, *8*(8), 3965–3982. https://doi.org/10.1002/ece3.3622

Chazot, N., Willmott, K. R., Condamine, F. L., De-Silva, D. L., Freitas, A. V. L., Lamas, G., Morlon, H., Giraldo, C. E., Jiggins, C. D., Joron, M., Mallet, J., Uribe, S., & Elias, M. (2016). Into the Andes:

multiple independent colonizations drive montane diversity in the Neotropical clearwing butterflies Godyridina. *Molecular Ecology*, *25*(22), 5765–5784. https://doi.org/10.1111/mec.13773

Chazot, N., Willmott, K. R., Freitas, A. V. L., de Silva, D. L., Pellens, R., & Elias, M. (2016). Patterns of Species, Phylogenetic and Mimicry Diversity of Clearwing Butterflies in the Neotropics. In R. Pellens, & P. Grandcolas (Eds.), *Biodiversity Conservation and Phylogenetic Systematics* (Vol. *14*, pp. 333–354). Springer. https://doi.org/10.1007/978-3-319-22461-9_17

Chazot, N., Willmott, K. R., Lamas, G., Freitas, A. V. L., Piron-Prunier, F., Arias, C. F., Mallet, J., De-Silva, D. L., & Elias, M. (2019). Renewed diversification following Miocene landscape turnover in a Neotropical butterfly radiation. *Global Ecology and Biogeography*, *28*(8), 1118–1132. https://doi.org/10.1111/geb.12919

Chazot, N., Willmott, K. R., Santacruz Endara, P. G., Toporov, A., Hill, R. I., Jiggins, C. D., & Elias, M. (2014). Mutualistic mimicry and filtering by altitude shape the structure of andean butterfly communities. *The American Naturalist*, *183*(1), 26–39. https://doi.org/10.1086/674100

Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J. D., Chey, V. K., Barlow, H. S., Hill, J. K., & Thomas, C. D. (2009). Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences*, *106*(5), 1479–1483. https://doi.org/10.1073/pnas.0809320106

Clifford, P., Richardson, S., & Hemon, D. (1989). Assessing the significance of the correlation between two spatial processes. *Biometrics*, *45*(1), 123–134. https://www.jstor.org/stable/2532039 https://doi.org/10.2307/2532039

Clusella Trullas, S., van Wyk, J. H., & Spotila, J. R. (2007). Thermal melanism in ectotherms. *Journal of Thermal Biology*, *32*(5), 235–245. https://doi.org/10.1016/j.jtherbio.2007.01.013

De-Silva, D. L., Elias, M., Willmott, K., Mallet, J., & Day, J. J. (2016). Diversification of clearwing butterflies with the rise of the Andes. *Journal of Biogeography*, *43*(1), 44–58. https://doi.org/10.1111/jbi.12611

De-Silva, D. L., Mota, L. L., Chazot, N., Mallarino, R., Silva-Brandão, K. L., Piñerez, L. M. G., Freitas, A. V. L., Lamas, G., Joron, M., Mallet, J., Giraldo, C. E., Uribe, S., Särkinen, T., Knapp, S., Jiggins, C. D., Willmott, K. R., & Elias, M. (2017). North Andean origin and diversification of the largest ithomiine butterfly genus. *Scientific Reports*, *7*(45966). https://doi.org/10.1038/srep45966

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters*, *13*(8), 1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x

Di Marco, M., Venter, O., Possingham, H. P., & Watson, J. E. M. (2018). Changes in human footprint drive changes in species extinction risk. *Nature Communications*, *9*(1), 4621. https://doi.org/10.1038/s41467-018-07049-5

Di Marco, M., Watson, J. E. M., Possingham, H. P., & Venter, O. (2017). Limitations and trade-offs in the use of species distribution maps for protected area planning. *Journal of Applied Ecology*, *54*(2), 402–411. https://doi.org/10.1111/1365-2664.12771

Drummond, B. A. III, & Brown, K. S. Jr (1987). Ithomiinae (Lepidoptera: Nymphalidae): Summary of Known Larval Food Plants. *Annals of the Missouri Botanical Garden*, *74*(2), 341. https://doi.org/10.2307/2399405

Duffy, K. J., & Johnson, S. D. (2017). Specialized mutualisms may constrain the geographical distribution of flowering plants. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1866), 20171841. https://doi.org/10.1098/rspb.2017.1841

Dufour, P. C., Willmott, K. R., Padrón, P. S., Xing, S., Bonebrake, T. C., & Scheffers, B. R. (2018). Divergent melanism strategies in Andean butterfly communities structure diversity patterns and climate responses. *Journal of Biogeography*, *45*(11), 2471–2482. https://doi.org/10.1111/jbi.13433

Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction: Are most endangered species parasites and mutualists? *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3037–3045. https://doi.org/10.1098/rspb.2009.0413

Eggleton, P. (2020). The state of the world's insects. *Annual Review of Environment and Resources*, *45*, 61–82. https://doi.org/10.1146/annurev-environ-012420-050035

Elias, M., Gompert, Z., Jiggins, C., & Willmott, K. (2008). Mutualistic interactions drive ecological niche convergence in a diverse butterfly community. *PLoS Biology*, *6*(12), e300. https://doi.org/10.1371/journal.pbio.0060300

Elias, M., Joron, M., Willmott, K., Silva-Brandão, K. L., Kaiser, V., Arias, C. F., Piñerez, L. M. G., Uribe, S., Brower, A. V. Z., Freitas, A. V. L., & Jiggins, C. D. (2009). Out of the Andes: Patterns of diversification in clearwing butterflies. *Molecular Ecology*, *18*(8), 1716–1729. https://doi.org/10.1111/j.1365-294X.2009.04149.x

Elsen, P. R., Monahan, W. B., & Merenlender, A. M. (2020). Topography and human pressure in mountain ranges alter expected species responses to climate change. *Nature Communications*, *11*(1), 1–10. https://doi.org/10.1038/s41467-020-15881-x

Escobar, H. (2020). Deforestation in the Brazilian Amazon is still rising sharply. *Science*, *369*(6504), 613. https://doi.org/10.1126/SCIENCE.369.6504.613

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Faith, D. P. (2018). Phylogenetic Diversity and Conservation Evaluation: Perspectives on Multiple Values, Indices, and Scales of Application. In R. A. Scherson, & D. P. Faith (Eds.), *Phylogenetic Diversity: Applications and Challenges in Biodiversity Science* (pp. 1–26). Springer International Publishing. https://doi.org/10.1007/978-3-319-93145-6_1

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., & Alsdorf, D. (2007). The shuttle radar topography mission. *Reviews of Geophysics*, *45*(2), RG2004. https://doi.org/10.1029/2005RG000183

Fearnside, P. (2017). Deforestation of the Brazilian Amazon. In Oxford Research Encyclopedia of Environmental Science (Issue July). https://doi.org/10.1093/acrefore/9780199389414.013.102

Godoy-Bürki, A. C., Ortega-Baes, P., Sajama, J. M., & Aagesen, L. (2014). Conservation priorities in the Southern Central Andes: Mismatch between endemism and diversity hotspots in the regional flora. *Biodiversity and Conservation*, *23*(1), 81–107. https://doi.org/10.1007/s10531-013-0586-1

Gross, K. (2008). Positive interactions among competitors can produce species-rich communities. *Ecology Letters*, *11*(9), 929–936. https://doi.org/10.1111/j.1461-0248.2008.01204.x

Gumbs, R., Gray, C. L., Böhm, M., Hoffmann, M., Grenyer, R., Meiri, S., Roll, U., Owen, N. R., & Rosindell, J. (2020). Global priorities for conservation of reptilian phylogenetic diversity in the face of human impacts. *Nature Communications*, *11*(2016), 1–13. https://doi.org/10.1038/s41467-020-16410-6

Haining, R. (1991). Bivariate correlation with spatial data. *Geographical Analysis*, *23*(3), 210–227. https://doi.org/10.1111/j.1538-4632.1991.tb00235.x

Hale, K. R. S., Valdovinos, F. S., & Martinez, N. D. (2020). Mutualism increases diversity, stability, and function of multiplex networks that integrate pollinators into food webs. *Nature Communications*, *11*(1), 1–14. https://doi.org/10.1038/s41467-020-15688-w

Hall, J. P. W. (2018). *A Monograph of the Nymphidiina (Lepidoptera: Riodinidae: Nymphidiini): Phylogeny, Taxonomy, Biology and Biogeography*. The Entomological Society of Washington.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., &

De Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, *12*(10), e0185809. https://doi.org/10.1371/journal.pone.0185809

Hallmann, C. A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., van Deijk, J., van Steenis, W., & Jongejans, E. (2020). Declining abundance of beetles, moths and caddisflies in the Netherlands. *Insect Conservation and Diversity*, *13*(2), 127–139. https://doi.org/10.1111/icad.12377

Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. (2008). GEIGER: Investigating evolutionary radiations. *Bioinformatics*, *24*(1), 129–131. https://doi.org/10.1093/bioinformatics/btm538

Hijmans, R. J. (2020). raster: Geographic Data Analysis and Modeling. R package version 3.0-12. https://cran.r-project.org/package=raster

Hoorn, C., & Wesselingh, F. P. (Eds.). (2010). *Amazonia - Landscape and species evolution: A look into the past*. Wiley-Blackwell.

IPBES. (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. In E. S. Brondizio, J. Settele, S. Díaz, & H. T. Ngo (Eds.), Bonn, Germany: IPBES secretariat. https://doi.org/10.5281/zenodo.3831673

Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C., & Baillie, J. E. M. (2007). Mammals on the EDGE: Conservation priorities based on threat and phylogeny. *PLoS One*, *2*(3), e296. https://doi.org/10.1371/journal.pone.0000296

Jenkins, C. N., Pimm, S. L., & Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences*, *110*(28), E2602–E2610. https://doi.org/10.1073/pnas.1302251110

Jetz, W., Thomas, G. H., Joy, J. B., Redding, D. W., Hartmann, K., & Mooers, A. O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, *24*(9), 919–930. https://doi.org/10.1016/j.cub.2014.03.011

Jezkova, T., & Wiens, J. J. (2016). Rates of change in climatic niches in plant and animal populations are much slower than projected climate change. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20162104. https://doi.org/10.1098/rspb.2016.2104

Jiggins, C. D., Mallarino, R., Willmott, K. R., & Bermingham, E. (2006). The phylogenetic pattern of speciation and wing pattern change in neotropical ithomia butterflies (Lepidoptera: Nymphalidae). *Evolution*, *60*(7), 1454–1466. https://doi.org/10.1111/j.0014-3820.2006.tb01224.x

Joron, M., & Iwasa, Y. (2005). The evolution of a Müllerian mimic in a spatially distributed community. *Journal of Theoretical Biology*, *237*(1), 87–103. https://doi.org/10.1016/j.jtbi.2005.04.005

Joron, M., & Mallet, J. L. B. (1998). Diversity in mimicry: Paradox or paradigm? *Trends in Ecology and Evolution*, *13*(11), 461–466. https://doi.org/10.1016/S0169-5347(98)01483-9

Kapan, D. D. (2001). Three-butterfly system provides a field test of müllerian mimicry. *Nature*, *409*(6818), 338–340. https://doi.org/10.1038/35053066

KBA Standards and Appeals Committee (2020). Guidelines for using A Global Standard for the Identification of Key Biodiversity Areas. Version 1.1. Prepared by the KBA Standards and Appeals Committee of the IUCN Species Survival Commission and IUCN World Commission on Protected Areas.

Kier, G., Kreft, H., Tien, M. L., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(23), 9322–9327. https://doi.org/10.1073/pnas.0810306106

Knapp, S. (2002). Assessing patterns of plant endemism in neotropical uplands. *Botanical Review*, *68*(1, Plant Evolution and Endemism in Andean South America (Jan.-Mar., 2002)), 22–37. https://www.jstor.org/stable/4354409

Langham, G. M. (2004). Specialized avian predators repeatedly attack novel color morphs of Heliconius butterflies. *Evolution*, *58*(12), 2783–2787. https://doi.org/10.1111/j.0014-3820.2004.tb01629.x

Lawler, J. J., White, D., Sifneos, J. C., & Master, L. L. (2003). Rare species and the use of indicator groups for conservation planning. *Conservation Biology*, *17*(3), 875–882. https://doi.org/10.1046/j.1523-1739.2003.01638.x

Leroy, B. (2016). Rarity: Calculation of Rarity Indices for Species and Assemblages of Species. R package version 1.3-6. https://cran.r-project.org/package=Rarity

Leroy, B., Canard, A., & Ysnel, F. (2013). Integrating multiple scales in rarity assessments of invertebrate taxa. *Diversity and Distributions*, *19*(7), 794–803. https://doi.org/10.1111/ddi.12040

Leroy, B., Petillon, J., Gallon, R., Canard, A., & Ysnel, F. (2012). Improving occurrence-based rarity metrics in conservation studies by including multiple rarity cut-off points. *Insect Conservation and Diversity*, *5*(2), 159–168. https://doi.org/10.1111/j.1752-4598.2011.00148.x

Malhi, Y., Roberts, J. T., Betts, R. A., Killeen, T. J., Li, W., & Nobre, C. A. (2008). Climate change, deforestation, and the fate of the Amazon. *Science*, *319*(5860), 169–172. https://doi.org/10.1126/science.1146961

Mallet, J., & Barton, N. H. (1989). Strong natural selection in a warning-color hybrid zone. *Evolution*, *43*(2), 421. https://doi.org/10.2307/2409217

Maritz, B., Penner, J., Martins, M., Crnobrnja-Isailović, J., Spear, S., Alencar, L. R. V., Sigala-Rodriguez, J., Messenger, K., Clark, R. W., Soorae, P., Luiselli, L., Jenkins, C., & Greene, H. W. (2016). Identifying global priorities for the conservation of vipers. *Biological Conservation*, *204*, 94–102. https://doi.org/10.1016/j.biocon.2016.05.004

Maron, M., Simmonds, J. S., Watson, J. E. M., Sonter, L. J., Bennun, L., Griffiths, V. F., Quétier, F., von Hase, A., Edwards, S., Rainey, H., Bull, J. W., Savy, C. E., Victurine, R., Kiesecker, J., Puydarrieux, P., Stevens, T., Cozannet, N., & Jones, J. P. G. (2020). Global no net loss of natural ecosystems. *Nature Ecology and Evolution*, *4*(1), 46–49. https://doi.org/10.1038/s41559-019-1067-z

Mateo, R. G., Croat, T. B., Felicísimo, Á. M., & Muñoz, J. (2010). Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections. *Diversity and Distributions*, *16*(1), 84–94. https://doi.org/10.1111/j.1472-4642.2009.00617.x

Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., Cianciaruso, M. V., Loyola, R., Diniz-Filho, J. A. F., Mouillot, D., & Thuiller, W. (2014). Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Global Ecology and Biogeography*, *23*(8), 836–847. https://doi.org/10.1111/geb.12158

McClure, M., Clerc, C., Desbois, C., Meichanetzoglou, A., Cau, M., Bastin-Héline, L., Bacigalupo, J., Houssin, C., Pinna, C., Nay, B., Llaurens, V., Berthier, S., Andraud, C., Gomez, D., & Elias, M. (2019). Why has transparency evolved in aposematic butterflies? Insights from the largest radiation of aposematic butterflies, the Ithomiini. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1901), 20182769. https://doi.org/10.1098/rspb.2018.2769

McGill, B. J. (2010). Matters of scale. *Science*, *328*(5978), 575–576. https://doi.org/10.1126/science.1188528

Millennium Ecosystem Assessment (2005). *Ecosystems and Human Wellbeing: Synthesis*. Island Press. https://doi.org/10.5822/978-1-61091-484-0_1

Montgomery, G. A., Dunn, R. R., Fox, R., Jongejans, E., Leather, S. R., Saunders, M. E., Shortall, C. R., Tingley, M. W., & Wagner, D. L. (2020). Is the insect apocalypse upon us? How to find out. *Biological Conservation*, *241*, 108327. https://doi.org/10.1016/j.biocon.2019.108327

Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B., & Worm, B. (2011). How many species are there on earth and in the ocean? *PLoS Biology*, *9*(8), 1–8. https://doi.org/10.1371/journal.pbio.1001127

Morawetz, W., & Raedig, C. (2007). Angiosperm biodiversity, endemism and conservation in the neotropics. *Taxon*, *56*(4), 1245. https://doi.org/10.2307/25065916

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C. E. T., Renaud, J., & Thuiller, W. (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, *11*(5), e1001569. https://doi.org/10.1371/journal.pbio.1001569

Mullen, S. P., Savage, W. K., Wahlberg, N., & Willmott, K. R. (2011). Rapid diversification and not clade age explains high diversity in neotropical Adelpha butterflies. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1713), 1777–1785. https://doi.org/10.1098/rspb.2010.2140

Müller, F. (1879). Ituna and Thyridia; a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London*, xx–xxix.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Nobre, C. A., Sampaio, G., Borma, L. S., Castilla-Rubio, J. C., Silva, J. S., & Cardoso, M. (2016). Land-use and climate change risks in the amazon and the need of a novel sustainable development paradigm. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(39), 10759–10768. https://doi.org/10.1073/pnas.1605516113

Ohlemüller, R., Anderson, B. J., Araújo, M. B., Butchart, S. H. M., Kudrna, O., Ridgely, R. S., & Thomas, C. D. (2008). The coincidence of climatic and species rarity: High risk to small-range species from climate change. *Biology Letters*, *4*(5), 568–572. https://doi.org/10.1098/rsbl.2008.0097

Orr, M. C., Hughes, A. C., Chesters, D., Pickering, J., Zhu, C. D., & Ascher, J. S. (2021). Global patterns and drivers of bee distribution. *Current Biology*, *31*(3), 451–458.e4. https://doi.org/10.1016/j.cub.2020.10.053

Osborne, P. (2012). Mountains, zonation and community gradients. In *Tropical Ecosystems and Ecological Concepts* (2nd ed., pp. 315–333). Cambridge University Press. https://doi.org/10.1017/cbo9781139057868.010

Papageorgis, C. (1975). Mimicry in Neotropical butterflies. *American Scientist*, *63*(5), 522–532.

Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*(3), 526–528. https://doi.org/10.1093/bioinformatics/bty633

Parr, M. J., Bennun, L., Boucher, T., Brooks, T., Chutas, C. A., Dinerstein, E., Drummond, G. M., Eken, G., Fenwick, G., Foster, M., Martínez-Gómez, J. E., Mittermeier, R., & Molur, S. (2009). Why we should aim for zero extinction. *Trends in Ecology and Evolution*, *24*(4), 181. https://doi.org/10.1016/j.tree.2009.01.001

Pascual-García, A., & Bastolla, U. (2017). Mutualism supports biodiversity when the direct competition is weak. *Nature Communications*, *8*(1), 14326. https://doi.org/10.1038/ncomms14326

Pateiro-Lopez, B., & Rodriguez-Casal, A. (2019). alphahull: Generalization of the Convex Hull of a Sample of Points in the Plane. R package version 2.2. https://cran.r-project.org/package=alphahull

Pearson, D. L., & Carroll, S. S. (2001). Predicting patterns of tiger beetle (Coleoptera: Cicindelidae) species richness in northwestern south america. *Studies on Neotropical Fauna and Environment*, *36*(2), 125–136. https://doi.org/10.1076/snfe.36.2.125.2139

Pebesma, E. (2018). Simple features for R: standardized support for spatial vector data. *The R Journal*, *10*(1), 439–446. https://doi.org/10.32614/RJ-2018-009

Pollock, L. J., O'Connor, L. M. J., Mokany, K., Rosauer, D. F., Talluto, M. V., & Thuiller, W. (2020). Protecting biodiversity (in all its complexity): new models and methods. *Trends in Ecology and Evolution*, *35*(12), 1119–1128. https://doi.org/10.1016/j.tree.2020.08.015

Pollock, L. J., Thuiller, W., & Jetz, W. (2017). Large conservation gains possible for global biodiversity facets. *Nature*, *546*(7656), 141–144. https://doi.org/10.1038/nature22368

Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C., & Gibbons, D. W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, *365*(6444), 335–337. https://doi.org/10.1038/365335a0

Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1456), 1947–1952. https://doi.org/10.1098/rspb.2000.1234

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rabinowitz, D. (1981). Seven forms of rarity. In H. Synge (Ed.), *Biological Aspects of Rare Plant Conservation* (pp. 205–217). John Wiley & Sons Ltd.

Rajão, R., Soares-Filho, B., Nunes, F., Börner, J., Machado, L., Assis, D., Oliveira, A., Pinto, L., Ribeiro, V., Rausch, L., Gibbs, H., & Figueira, D. (2020). The rotten apples of Brazil's agribusiness. *Science*, *369*(6501), 246–248. https://doi.org/10.1126/science.aba6646

Redding, D. W. (2003). *Incorporating genetic distinctness and reserve occupancy into a conservation priorisation approach*. Master's Thesis. University Of East Anglia, Norwich, UK.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, *142*(6), 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W., Warton, D. I., Wintle, B. A., Hartig, F., & Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, *40*(8), 913–929. https://doi.org/10.1111/ecog.02881

Robuchon, M., Pavoine, S., Véron, S., Delli, G., Faith, D. P., Mandrici, A., Pellens, R., Dubois, G., & Leroy, B. (2021). Revisiting species and areas of interest for conserving global mammalian phylogenetic diversity. *Nature Communications*, *12*(1), 1–11. https://doi.org/10.1038/s41467-021-23861-y

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G. R., Dabool, L., Das, I., Doan, T. M., Grismer, L. L., Hoogmoed, M., Itescu, Y., Kraus, F., Lebreton, M., … Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology and Evolution*, *1*(11), 1677–1682. https://doi.org/10.1038/s41559-017-0332-2

Rosser, N., Phillimore, A. B., Huertas, B., Willmott, K. R., & Mallet, J. (2012). Testing historical explanations for gradients in species richness in heliconiine butterflies of tropical America. *Biological Journal of the Linnean Society*, *105*(3), 479–497. https://doi.org/10.1111/j.1095-8312.2011.01814.x

Salcido, D. M., Forister, M. L., Garcia Lopez, H., & Dyer, L. A. (2020). Loss of dominant caterpillar genera in a protected tropical forest.

Scientific Reports, *10*(1), 1–10. https://doi.org/10.1038/s41598-019-57226-9

Sexton, J. O., Song, X. P., Feng, M., Noojipady, P., Anand, A., Huang, C., Kim, D. H., Collins, K. M., Channan, S., DiMiceli, C., & Townshend, J. R. (2013). Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with lidar-based estimates of error. *International Journal of Digital Earth*, *6*(5), 427–448. https://doi.org/10.1080/17538947.2013.786146

Sheldon, K. S., Yang, S., & Tewksbury, J. J. (2011). Climate change and community disassembly: Impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, *14*(12), 1191–1200. https://doi.org/10.1111/j.1461-0248.2011.01689.x

Sherratt, T. N. (2006). Spatial mosaic formation through frequency-dependent selection in Müllerian mimicry complexes. *Journal of Theoretical Biology*, *240*(2), 165–174. https://doi.org/10.1016/j.jtbi.2005.09.017

Sherratt, T. N. (2008). The evolution of Müllerian mimicry. *Naturwissenschaften*, *95*(8), 681–695. https://doi.org/10.1007/s00114-008-0403-y

Short, A. E. Z., Dikow, T., & Moreau, C. S. (2018). Entomological collections in the age of big data. *Annual Review of Entomology*, *63*, 513–530. https://doi.org/10.1146/annurev-ento-031616-035536

Sombroek, W. (2000). Amazon landforms and soils in relation to biological diversity. *Acta Amazonica*, *30*(1), 81. https://doi.org/10.1590/1809-43922000301100

Sonter, L. J., Herrera, D., Barrett, D. J., Galford, G. L., Moran, C. J., & Soares-Filho, B. S. (2017). Mining drives extensive deforestation in the Brazilian Amazon. *Nature Communications*, *8*(1), 1–7. https://doi.org/10.1038/s41467-017-00557-w

Stork, N. E. (2018). How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology*, *63*, 31–45. https://doi.org/10.1146/annurev-ento-020117-043348

Stork, N. E., & Habel, J. C. (2014). Can biodiversity hotspots protect more than tropical forest plants and vertebrates? *Journal of Biogeography*, *41*(3), 421–428. https://doi.org/10.1111/jbi.12223

Sumner, S., Law, G., & Cini, A. (2018). Why we love bees and hate wasps. *Ecological Entomology*, *43*(6), 836–845. https://doi.org/10.1111/een.12676

Ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van Der Hout, P., Daly, D. C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., Duivenvoorden, J., Adalardo De Oliveira, A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., … Morawetz, W. (2003). A spatial model of tree alpha-diversity and tree density for the Amazon. *Biodiversity and Conservation*, *12*, 2255–2277. https://doi.org/10.1023/A:1024593414624

Thuiller, W., Georges, D., Engler, R., & Breiner, F. (2020). biomod2: Ensemble Platform for Species Distribution Modeling. R package version 3.4.6. https://cran.r-project.org/package=biomod2

Toby Kiers, E., Palmer, T. M., Ives, A. R., Bruno, J. F., & Bronstein, J. L. (2010). Mutualisms in a changing world: An evolutionary perspective. *Ecology Letters*, *13*(12), 1459–1474. https://doi.org/10.1111/j.1461-0248.2010.01538.x

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., … Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*(6374), 466–469. https://doi.org/10.1126/science.aam9712

Uehara-Prado, M., & Freitas, A. V. L. (2009). The effect of rainforest fragmentation on species diversity and mimicry ring composition of ithomiine butterflies. *Insect Conservation and Diversity*, *2*(1), 23–28. https://doi.org/10.1111/j.1752-4598.2008.00025.x

Ulloa Ulloa, C., Acevedo-Rodríguez, P., Beck, S., Belgrano, M. J., Bernal, R., Berry, P. E., Brako, L., Celis, M., Davidse, G., Forzza, R. C., Gradstein, S. R., Hokche, O., León, B., León-Yánez, S., Magill, R. E., Neill, D. A., Nee, M., Raven, P. H., Stimmel, H., … Jørgensen, P. M. (2017). An integrated assessment of the vascular plant species of the Americas. *Science*, *358*(6370), 1614–1617. https://doi.org/10.1126/science.aao0398

Valavi, R., Elith, J., Lahoz-Monfort, J. J., & Guillera-Arroita, G. (2019). blockCV: An r package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. *Methods in Ecology and Evolution*, *10*(2), 225–232. https://doi.org/10.1111/2041-210X.13107

Vega, G. C., Pertierra, L. R., & Olalla-Tárraga, M. Á. (2017). Data Descriptor: MERRAclim, a high-resolution global dataset of remotely sensed bioclimatic variables for ecological modelling Background & Summary. *Scientific Data*, *4*(170078), 1–11. https://doi.org/10.1038/sdata.2017.78

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016a). Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific Data*, *3*(160067), 1–10. https://doi.org/10.1038/sdata.2016.67

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016b). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, *7*, 1–11. https://doi.org/10.1038/ncomms12558

Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C., & Pressey, R. (1996). A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology*, *10*(1), 155–174. https://doi.org/10.1046/j.1523-1739.1996.10010155.x

Williams, P. H., & Humphries, C. J. (1994). Biodiversity, taxonomic relatedness, and endemism in conservation. In P. L. Forey, C. J. Humphries, & R. I. Vane-Wright (Eds.), *Systematics and conservation evaluation* (pp. 269–287). Clarendon Press.

Willmott, K. R., & Freitas, A. V. L. (2006). Higher-level phylogeny of the Ithomiinae (Lepidoptera: Nymphalidae): classification, patterns of larval hostplant colonization and diversification. *Cladistics*, *22*(4), 297. https://doi.org/10.1111/j.1096-0031.2006.00108.x/full

Willmott, K. R., & Mallet, J. (2004). Correlations between adult mimicry and larval host plants in ithomiine butterflies. *Proceedings of the Royal Society B: Biological Sciences*, *271*(Suppl_5), S266–S269. https://doi.org/10.1098/rsbl.2004.0184

Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., Mouillot, D., Mouquet, N., Renaud, J., & Thuiller, W. (2014). Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. *Diversity and Distributions*, *20*(6), 674–685. https://doi.org/10.1111/ddi.12186

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., … Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*(9), 1261–1277. https://doi.org/10.1111/ecog.04960

BIOSKETCH

The research team has a long-standing interest in ithomiine 'clearwing' butterflies, spanning systematics, diversification patterns and processes, the role of host plants and mimetic interactions from micro- to macroevolutionary scale, community ecology and phylogenetics, and historical biogeography. This paper is the result of over 30 years of collaborative efforts to collect, describe and classify Ithomiini butterflies and their mimicry patterns in order to unravel the mechanisms at play in species distribution, community assemblages, and mimicry patterns and niche evolution. The first author, Maël Doré, is a PhD student interested in the interplay between community ecology, phylogenetics and macroecological patterns in tropical environments. To this end, he employs various tools ranging from systematics to species distribution models and comparative phylogenetic methods.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Doré, M., Willmott, K., Leroy, B., Chazot, N., Mallet, J., Freitas, A. V. L., Hall, J. P. W., Lamas, G., Dasmahapatra, K. K., Fontaine, C., & Elias, M. (2021). Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group. *Diversity and Distributions*, 00, 1–19. https://doi.org/10.1111/ddi.13455