

Temperature seasonality drives taxonomic and functional homogenization of tropical butterflies

Catherine M. Hulshof^{1,2}  | James D. Ackerman³ | Rosa A. Franqui⁴ |
 Akito Y. Kawahara^{2,5,6} | Carla Restrepo³

¹Department of Biology, Virginia Commonwealth University, Richmond, Virginia, USA

²Department of Entomology, Smithsonian National Museum of Natural History, Washington, DC, USA

³Department of Biology, University of Puerto Rico Rio Piedras, Rio Piedras, Puerto Rico

⁴Department of Agroenvironmental Sciences and Museo de Entomología y Biodiversidad Tropical, University of Puerto Rico Mayagüez, San Juan, Puerto Rico

⁵McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

⁶Entomology and Nematology Department, University of Florida, Gainesville, Florida, USA

Correspondence

Catherine M. Hulshof, Department of Biology, Virginia Commonwealth University, Richmond, VA 23284, USA.
 Email: cmhulshof@vcu.edu

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Abstract

Aim: To better understand the potential impact of climate change on butterfly assemblages across a tropical island, we model the potential for taxonomic and functional homogenization and determine climate- and trait-mediated shifts in projected species distributions.

Location: Puerto Rico.

Methods: We used thousands of museum records of diurnal Lepidoptera to model current (1970–2000) and forecast future (2061–2080) species distributions and combined these to test for taxonomic and functional homogenization. We then quantified climatic-mediated effects on current and forecasted taxonomic and functional composition and, specifically, whether temperature was a primary driver, as predicted by the temperature–size rule and the thermal melanism hypotheses. Finally, we measured wing traits important in thermoregulation (size and colour) and determined trait-mediated changes in forecasted species distributions over time.

Results: Based on ensemble model outputs, taxonomic and functional richness and turnover were predicted to vary across the island's complex topography. Our models projected an increase in taxonomic and functional richness over time, and a decrease in taxonomic and functional turnover – a signature of biotic homogenization. Under future climate scenarios, models projected a decrease in wing length and an increase in wing brightness at higher elevations. One variable, temperature seasonality, was the strongest predicted driver of both the current spatial distribution and the projected per cent change over time for not only wing traits but also taxonomic and functional richness and turnover.

Main conclusions: The species distribution models generated here identify several priority regions and species for future research and conservation efforts. Our work also highlights the role of seasonality and climatic variability on diverse tropical Lepidoptera assemblages, suggesting that climatic variability may be an important, albeit overlooked, driver of climate change responses.

KEY WORDS

biotic homogenization, Caribbean, ectotherm, Lepidoptera, melanism, SDM, trait

1 | INTRODUCTION

Worldwide shifts in species distributions in response to contemporary climate change are altering the taxonomic and functional composition of plant and animal communities, ultimately leading to biotic homogenization (i.e. the convergence of ecological communities over time; Parmesan, 2006; Wardle et al., 2011). Whereas taxonomic diversity describes the numbers and abundances of species, functional diversity describes the range of life history traits among species (McGill et al., 2006). The extent to which taxonomic and functional measures of diversity are linked is not entirely clear, but these connections may help understand mechanisms underlying the re-assembly of ecological communities under intensifying global change (Devictor et al., 2010; Green et al., 2022). At local scales, a growing number of field-based studies conducted mostly in temperate regions reveals shifts in species and trait distributions among diverse taxonomic groups (Green et al., 2022; MacLean & Beissinger, 2017), yet the rate of change between taxonomic and functional metrics often differs. At regional scales, data collected from networks of permanent plots show that relationships between taxonomic and functional diversity are idiosyncratic, varying across taxa (Hevia et al., 2016) and ranging from high covariation (Arnan et al., 2018; Reymond et al., 2013) to low or none (de Castro et al., 2020; Kaltsas et al., 2018; Nunes et al., 2017). These idiosyncrasies make it challenging to predict the re-assembly of ecological communities based on taxonomic patterns alone. A complementary approach to field-based sampling involves the use of species distribution models (SDMs) to predict both taxonomic and functional diversity patterns at larger spatial and temporal scales. In tropical regions, the application of such an approach is particularly urgent given that many animals are operating near their critical thermal maximum (Deutsch et al., 2008) and that narrow thermal tolerance breadths may constrain species' responses to shifting climates (Bota-Sierra et al., 2022). Documenting distribution shifts and testing trait-based hypotheses of rapid ecological change using a modelling approach is an obvious first step for understanding the complexity and consequences of climate change responses across the tree of life.

Insects are one of the most species-rich group of organisms on Earth, with an estimated 5.5 million species (Stork, 2018). As ectothermic organisms, insects are particularly sensitive to temperature (Deutsch et al., 2008; Huey & Stevenson, 1979; Kingsolver et al., 2011). Despite a shared sensitivity to temperature, changes in insect abundance, distribution and community composition differ worldwide. For example, some insect populations show rapid population declines over time (Halsch et al., 2021; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020), yet

others show the opposite trend or are stable (Roubik et al., 2021; Wagner et al., 2021; Willig et al., 2019). Similarly, insect species ranges have also both expanded in some regions and contracted in others globally (Wagner, 2020; Yang et al., 2021) and both upslope (e.g. Colwell et al., 2008; Moret et al., 2016; Wagner, 2020; Wu et al., 2019) and downslope (e.g. Lenoir et al., 2010; McCain & Garfinkel, 2021) distribution shifts have been reported in response to warming temperatures. These complex, and often opposing, responses are likely mediated by morphological and life history traits (Wagner, 2020), permitting the identification of winners and losers in the Anthropocene (sensu Dornelas et al., 2019; Wagner et al., 2021).

Two traits in particular – body size and melanization – are thought to play important roles in mediating responses to climate change. First, the temperature-size rule hypothesis posits that declining body size should emerge as a universal response to warming temperatures (Atkinson, 1994; Gardner et al., 2011; Ohlberger, 2013). As a result, body size is predicted to be smaller in warmer environments. This relationship holds even when elevation or latitude is used as a proxy for environmental temperature (Angilletta & Dunham, 2003). The temperature-size rule is thought to arise because larger organisms incur greater metabolic demands, have higher equilibrium body temperatures and gain and lose heat more slowly (Nijhout, 2003). Second, the thermal melanism hypothesis predicts that declining melanization (i.e. the reduction in pigment) may be another widespread response to warming temperature (Clusella-Trullas et al., 2008), given its relationship with solar absorption (MacLean et al., 2018). Thus, less melanization in ectotherms is favoured in warmer environments because it enables slower heating rates and lower body temperatures. For insects, some studies indicate warmer environments select for reduced body size (Attiwilli et al., 2022; Brehm et al., 2019; Henriques et al., 2022; Leingärtner et al., 2014; Xing et al., 2016) and melanization (Brakefield & de Jong, 2011; Stelbrink et al., 2019; Xing et al., 2016; Zeuss et al., 2014), while others report the opposite (MacLean et al., 2018) or show no relationship (Brehm & Fiedler, 2004; Dufour et al., 2018). In short, general patterns of insect body size or melanization responses to climate change have not yet emerged.

Butterflies are an excellent group of insects to model climatic- and trait-mediated responses to climate change as evidenced by efforts in temperate (e.g. Aguirre-Gutiérrez et al., 2017; Girardello et al., 2019; Mattila et al., 2011; Ockinger et al., 2010) and tropical (e.g. Meineke et al., 2018) regions. First, butterflies have many historical records and reliable identification guides. The multitude of occurrence records enables the quantification of current and future trends in taxonomic diversity and distributions at broad spatiotemporal scales. Furthermore, butterflies are well represented

in a two-dimensional image, facilitating the measurement of trait data from museum specimens. These data may then be used to understand the mechanisms underlying changes in species distributions and the re-assembly of ecological communities. Given that 90% of butterfly species are tropical (Bonebrake et al., 2010) and tropical ectotherms may be more vulnerable to warming (Deutsch et al., 2008; García-Robledo et al., 2016), climate change in the tropics may lead to rapid taxonomic and functional homogenization of the butterfly fauna, as certain species or traits are more favoured over others.

In this study, we use thousands of digitized collection records to model whether climate change will result in the taxonomic and functional homogenization of a tropical butterfly fauna by focusing on three questions. First, we ask if forecasts point to taxonomic or functional homogenization by modelling and comparing the current and future distribution of taxonomic and functional richness and turnover. Second, we ask what are the climatic-mediated effects on modelled taxonomic and functional composition, and specifically, does evidence support temperature as the primary driver of current and future changes of projected species and trait distributions? Lastly, we ask whether wing traits mediate changes in modelled species distributions, owing to their roles in thermoregulation, and examine interactions among species distributions, traits and climate. Across a topographically complex Caribbean island, we predicted that modelled taxonomic and functional richness and turnover would decline in cooler environments. This expectation was based on the idea that environmental selection favours species that are more melanized and larger-winged in cooler environments due to thermoregulatory constraints, per the temperature–body size rule and the thermal melanism hypothesis. As a result, under future climate scenarios, taxonomic and functional homogenization should increase in cooler environments due to upslope distributional shifts of lowland species. Simultaneously, warmer lowland environments may also exhibit reduced species and trait turnover due to biotic attrition. These expectations may be complicated by interactions among species distributions, traits and climate, which we model here, in addition to land use change, which we discuss further. Doing so can augment our understanding of potential shifts in species' distributions and the possible selection of functional traits under future climates. We can use these modelled results to develop testable hypotheses to identify species most at risk, anticipate cascading impacts on ecosystems

and guide conservation priorities, which could serve as important benchmarks for other Caribbean and tropical regions.

2 | METHODS

2.1 | Study site

The island of Puerto Rico is located within the Caribbean Biodiversity Hotspot, one of the 'hottest hotspots' (Myers, 2003). With an area of 8876 km², the island encompasses varied climatic, topographic and edaphic conditions over small spatial scales, creating a landscape that harbours diverse ecological and physiographic regions (Ewel & Whitmore, 1973; Helmer et al., 2002; Miller & Lugo, 2009). In Puerto Rico, variation in temperature is mostly driven by elevation (0–1340 m), whereas variation in precipitation is driven by a combination of prevailing winds from the north-east and interior mountains, producing a rain shadow effect where xeric conditions occur in the south and south-west and moist conditions in the north and north-east (Daly et al., 2003). Climatic variability determines the presence of lowland moist seasonal evergreen forests, submontane and lower montane wet evergreen sclerophyllous forests and lower montane wet evergreen forests (including both tall and elfin cloud forests) along the north and east sides and lowland dry semi-deciduous forests, lowland dry mixed evergreen drought-deciduous shrubland with succulents and lowland dry semi-deciduous forests along the south-west side (Helmer et al., 2002, and see Figure S1.1). These plant formations occur within three major physiographic regions (Murphy, 1916): the lowland coastal and interior plains; the Cordillera Central, a mountain range that extends in an east-west direction; and the Sierra de Luquillo, an isolated mountain range in the north-east. The karst formations in the northern region (mogotes), and the Sierra de Cayey – a south-eastern extension of the Cordillera Central and the Caguas-Juncos Valley, the largest interior valley on the island – are also identified as unique physiographic regions (Smith & Pico, 1976) (Figure 1).

There are an estimated 100 butterfly species in Puerto Rico (Comstock, 1944; Forbes, 1930; Gleason & Cook, 1926; Pérez-Asso et al., 2009; Ramos, 1996; Wolcott, 1948). Most butterfly research in Puerto Rico has had a limited taxonomic and geographical scope, focusing on individual species (e.g. Bastardo Landrau, 1998; Carrión-Cabrera, 2003), single sites (e.g. Davila &

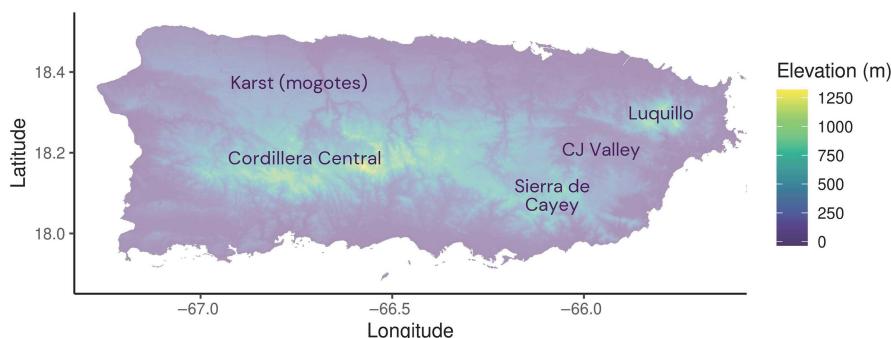


FIGURE 1 Elevation (m) in Puerto Rico and major physiographic regions including the northern karst formations (mogotes), Sierra de Luquillo, Caguas-Juncos (CJ) Valley, Cordillera Central and the Sierra de Cayey.

Asencio, 1992; Torres, 1992; Willig et al., 2019) or species catalogues (e.g. Pérez-Asso et al., 2009). Given the extent of predicted island-wide shifts in temperature and precipitation, there is a clear need to evaluate diversity patterns across the island by leveraging modelling approaches.

2.2 | Sources of butterfly data

The main source of data came from the Stuart J. Ramos Collection (SJRC; 3410 records; SJRC) which was donated by the late S. J. Ramos to the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History (MGCL) at the University of Florida, in Gainesville, Florida, USA. We supplemented occurrence records from additional sources including the Global Biodiversity Information Facility (GBIF; 2048 records; downloaded in January 2020, [GBIF.org](https://www.gbif.org)), iDigBio (1489 records; downloaded in March 2020, idigbio.org), the Museo de Entomología y Biodiversidad Tropical del Recinto Universitario de Mayagüez (MEBT; 626 records) and the Zoological Museum of the University of Puerto Rico at Rio Piedras (UPRRP; 620 records). Occurrence records span a range of collection years from 1830 to 2019, with most collected between 1980 and 2000 (Figure S1.2). Prior to our digitization of the Stuart J. Ramos Collection, only 158 Lepidoptera specimens from Puerto Rico had been digitized (<http://www.idigbio.org/portal2021>). Because of the importance of the Stuart J. Ramos Collection, we briefly describe the collection and its subsequent digitization.

The Stuart J. Ramos Collection is one of the largest, most extensively digitized butterfly collections in Puerto Rico (Franz & Yusseff Vanegas, 2009). The collection represents efforts of the late entomologist Stuart José Ramos Biaggi, an expert on the taxonomy, biogeography and ecology of Puerto Rican butterflies (Franz & Yusseff Vanegas, 2009; Ramos, 1996). We digitized the Stuart J. Ramos Collection following standardized protocols (iDigBio; www.idigbio.org), which included creating digital images of each specimen positioned on a standard grey background, with a colour card standard and scale, under constant light conditions. In addition, for each specimen, we transcribed the geographical location described by its pinned data label and georeferenced location data using the batch georeferencing tool (GeoLocate) in the Symbiota Collections of Arthropods Network (Gries et al., 2014; SCAN, 2019) where images and records are available.

2.3 | Species occurrences

The total number of compiled occurrence records was 8193. We examined records for accuracy and spatial bias, which resulted in the removal of 549 duplicate records and the elimination of records of unidentified species, species with less than 10 occurrences and nocturnal species. In addition, we spatially thinned species occurrence records using *spThin* (Aiello-Lammens et al., 2015) to reduce the effects of spatial sampling bias. This process takes the set of

occurrence records per species and identifies a new species-level subset that meets the specified minimum nearest-neighbour distance (5 km) while retaining the largest number of records. The final cleaned set of occurrence records totalled 2003 for 62 species belonging to 5 butterfly families (16 Hesperiidae, 4 Lycaenidae, 25 Nymphalidae, 1 Papilionidae and 16 Pieridae). These five families represent the most species-rich butterfly families in Puerto Rico (Ramos, 1996).

2.4 | Species distribution models (SDMs)

The 2003 records were used to generate SDMs which were created following a three-step procedure. First, we selected bioclimatic variables and checked for collinearity, eliminating highly correlated variables; second, we used the remaining variables to generate species distribution models using an ensemble approach; and lastly, we tested model performance. We describe each of these steps in more detail below. Current climate conditions were based on WorldClim (v 2.0; Hijmans et al., 2005) which includes elevation and 19 interpolated climatic variables. The WorldClim bioclimatic dataset has a spatial resolution of $\sim 1\text{ km}^2$ and represent annual trends (e.g. mean annual temperature and annual precipitation), seasonality and extreme conditions (e.g. temperature of the coldest and warmest month and precipitation of the wet and dry quarters) calculated as an average across a 30-year period (1970–2000). These 1- km^2 pixels were used to define our present-day butterfly communities (see Zurell et al., 2020). Future climate conditions were based on the Representative Concentration Pathway RCP 4.5, which is a more conservative scenario compared to other RCPs, and the global climate model HadGEM2-ES, which performs well at predicting bimodal seasonality for precipitation and temperature trends in Puerto Rico (Hayhoe, 2013), whereas many other GCMs do not. To reduce collinearity among predictor variables, we calculated variance inflation factors (VIF) with a threshold of less than two (Queen et al., 2002). As a result, six variables were included in species distribution models representing seasonality (isothermality, temperature and precipitation seasonality and temperature annual range); extreme conditions (precipitation of driest month and precipitation of the warmest quarter); and elevation. Together, these variables describe the bimodal precipitation and temperature seasonality characteristic of the island (Hayhoe, 2013).

We used the *biomod2* library in R to generate SDMs (Thuiller et al., 2016) using an ensemble approach under current and future climate conditions. The algorithms we chose to model species distributions were maximum entropy (MAXENT), random forest (RF) and a generalized linear model (GLM). Maximum entropy performs well with few occurrence records and was developed to model presence–background data (Phillips et al., 2006). Random forests are machine learning algorithms which use bootstrap-based classification and regression trees. They are widely used in SDMs and are robust to overfitting (Lawler et al., 2006). GLM is an extension of classic regression modelling, which uses linear or higher-degree

polynomials to model the relationship between response and predictor variables. Spatially thinned occurrence points were treated as presences, and 10,000 background points were randomly selected as pseudo-absences. We used 80% of presences and pseudo-absences for calibration; the remaining 20% of data were used to test model performance. We then calculated a consensus of predictions based on the weighted area under the curve (AUC) average of the three algorithms, selecting model outputs where the AUC values were greater than 0.6, based on 45 SDMs per species (2790 SDMs total). The number of models meeting or exceeding this threshold ranged from 2 to 43 models per species, which were averaged to create final species distribution maps. Lastly, we used the true skill statistic (TSS, Allouche et al., 2006) to evaluate models, discarding models with $TSS < 0.60$. TSS varies from -1 to 1, with values less than 0 representing no discrimination and 1 representing perfect discrimination (Araújo & New, 2007). We used default settings in *biomod2* (as suggested by Thuiller et al., 2009) to transform the ensemble model predictions (both current and future) into binary maps of presence/absence using species-specific thresholds that maximize specificity and sensitivity (Liu et al., 2011). Given the small area of Puerto Rico, its biogeographic history (most butterfly species dispersed to the island from elsewhere, Miller & Miller, 2001) and high forest cover (>50%, Helmer et al., 2002), we assumed perfect climate tracking (i.e. no dispersal limitations).

2.5 | Functional traits

While all specimen collections were sources of occurrence records, we only used the Stuart J. Ramos Collection to measure wing traits because it was (and is) the only digitized collection. We used FIJI (Abràmoff et al., 2004) to measure dorsal forewing length as the length between the forewing tip and the site of wing attachment on the thorax, and forewing width as the widest section of the forewing (Figure S1.3). To facilitate generalizations, we categorized species based on their wing length. Species with a forewing length less than the mean (3 cm) were classified as 'small-winged', while those with a forewing length greater than the mean were classified as 'large-winged'. We also measured hue, saturation and brightness (HSB) on a 1 cm^2 region of the dorsal forewing near the thorax, avoiding major veins and visible scale damage, as this region is important for thermoregulation (Kingsolver, 1987; Wasserthal, 1975; Watt, 1969). The HSB colour space provides a standardized metric for comparing colour values and is correlated with melanin content (Foster et al., 2023; McGraw et al., 2005). Hue represents the colour (i.e. red and yellow), saturation represents the intensity and brightness represents the lightness or darkness of the colour. Because melanin absorbs light, organisms with high melanin content will have lower HSB values (i.e. darker colours) and vice versa. Organisms with low melanin content will have higher HSB values (i.e. lighter colours). This method, however, emphasizes pigment colouration and ignores structural

colouration or iridescence. The impact of structural colouration on butterfly thermoregulation is not well known (Krishna et al., 2020). We focused on females because their parental investment and, thus, energetic requirements are often greater than those of males, and male colouration can be biased by sexual selection (Clutton-Brock & Parker, 1992). Of the 62 species, only 4 (all Nymphalidae) had visually noticeable size differences, with females being larger than males. In a few instances in which images of females were not available, or the sex could not be determined from visual characteristics such as markings or size differences, we selected individuals randomly within species for trait measurements (Female:Unknown = 48:14). We aimed for a maximum of 10 individuals per species when possible (median = 10; mean = 8.1 individuals per species).

2.6 | Data analysis

2.6.1 | Taxonomic and functional richness and turnover

To model the current and future distribution of taxonomic and functional composition across the island, we calculated taxonomic and functional richness and turnover for each grid cell (1 km^2 resolution) based on model outputs. Species richness was expressed as the number of species projected to occur in each grid cell. We obtained estimates of species richness by stacking and summing distribution maps. Taxonomic beta diversity accounts for differences in the numbers of species between sites (Baselga, 2010; Leprieur et al., 2012) and is partitioned into nestedness and turnover. Nestedness represents the difference in species richness between assemblages (Leprieur et al., 2012; McKnight et al., 2007), whereas turnover represents true species replacement between assemblages. The latter is insensitive to species richness gradients, such as those we expected to occur across the island's climatic gradients, and contributes more to beta diversity than nestedness (Baselga et al., 2012). We thus focused our analyses on turnover rather than nestedness and, towards this end, we used the Sørensen pairwise dissimilarity index among grid cells. A value of 0 indicates neighbouring pixels or communities had similar species composition, whereas a value of 1 indicates communities with distinct species composition.

Functional richness and turnover were calculated following a similar approach. Functional richness was calculated as the total branch length of a tree linking all projected species occurring within a grid cell, which was calculated using functions in the *betapart* and *BAT* packages (Baselga, 2010; Baselga & Orme, 2012; Cardoso et al., 2015). The tree was calculated using a hierarchical cluster analysis using trait values for species within each grid cell. Functional turnover or beta diversity was then calculated as the turnover of traits between a focal grid cell and its eight neighbouring cells using the Sørensen pairwise dissimilarity index (Sørensen, 1948; following Petchey & Gaston, 2006; Safi et al., 2011) using the *speciesRaster* package (Title 2017). As with species turnover, a value of 0 indicates

that neighbouring pixels or communities have similar functional trait composition, and a value of 1 indicates that communities have distinct (i.e. no overlap in their) functional composition.

The relative per cent change (RPC) between projected current and future taxonomic and functional richness and turnover, distribution area, elevational range and maximum elevation was calculated for each pixel according to [Equation 1](#):

$$RPC = (PF_i - PP_i) / PP_i \times 100 \quad (1)$$

where PF_i and PP_i are the projected future and projected present values of pixel i respectively. Pixel values were plotted as histograms to visualize pixel-level gains and losses in taxonomic and functional richness and turnover. We used a two-sided z -test ($H_0: \mu=0$) or a Mann-Whitney U -test (for non-normal distributions) to identify statistically significant gains or losses in pixel-level taxonomic and functional richness and turnover and wing trait values.

2.6.2 | Climatic-mediated effects on species and trait distributions

Our next set of analyses was aimed at examining environmental drivers, in particular temperature, on present and relative per cent change in projected butterfly taxonomic and functional richness and turnover, as well as wing trait variation across Puerto Rico. We used generalized additive models (GAMs; [Hastie & Tibshirani, 1986](#)) in which bioclimatic variables from WorldClim were used as predictors and layers for taxonomic and functional richness and turnover were used as responses. Similar to the species distribution models, multicollinearity among bioclimatic variables was removed using a VIF of less than 2 ([Queen et al., 2002](#)), resulting in four predictor variables (temperature seasonality, temperature annual range, precipitation of the warmest quarter and elevation). Because this was a pixel-scale analysis, these four variables differed from the six variables used for species distribution models (derived based on occurrence records rather than pixels). The four variables were scaled and centred to a mean of 0 and a standard deviation of 1. GAMs were fitted using the *mgcv* package ([Wood & Wood, 2015](#)) with a thin-plate spline smoother (which tends to have better RMSE performance) and default dimension (k) of the basis for the smoothing term. Estimation of smoothing penalties was performed using restricted maximum likelihood (method = 'REML') which has been shown to perform better than other methods and treats the model as a mixed effects model with the non-linear parts of the spline treated as special random effects. We generated all possible additive models using *MuMIn* ([Barton & Barton, 2015](#)) and used model selection according to the Akaike information criterion (AIC, [Burnham & Anderson, 2004](#)). Because GAMs use smooth functions that can be complex and non-linear, interpreting model coefficients can be complicated ([Hastie & Tibshirani, 1986](#)), making it difficult to understand how the predictor variables affect the response variables. Because of this, we also fit an ordinary least squares (OLS) regression to aid in interpreting the relative effect size and direction (i.e. negative and positive) of

relationships between response and predictor variables. This dual approach can help avoid misinterpreting the importance of predictor variables.

2.6.3 | Trait-mediated effects on species distributions

Our third and final set of analyses was aimed at testing whether traits mediate projected distribution changes including upslope migration, leading to taxonomic or functional homogenization. To this end, we first ran a principal component analysis (PCA) on all traits (i.e. wing length, hue, saturation and brightness) to interpret a reduced number of axes of variation more easily. All variables were scaled to a mean of 0 and a standard deviation of 1 prior to analyses (z-score transformation) due to differences in magnitudes and units among variables. We calculated Spearman correlation coefficients among PCA scores and area, elevational range, maximum elevation, mean elevation and minimum elevation for projected present and future distributions (and relative per cent change) based on binary transformed ensemble model predictions.

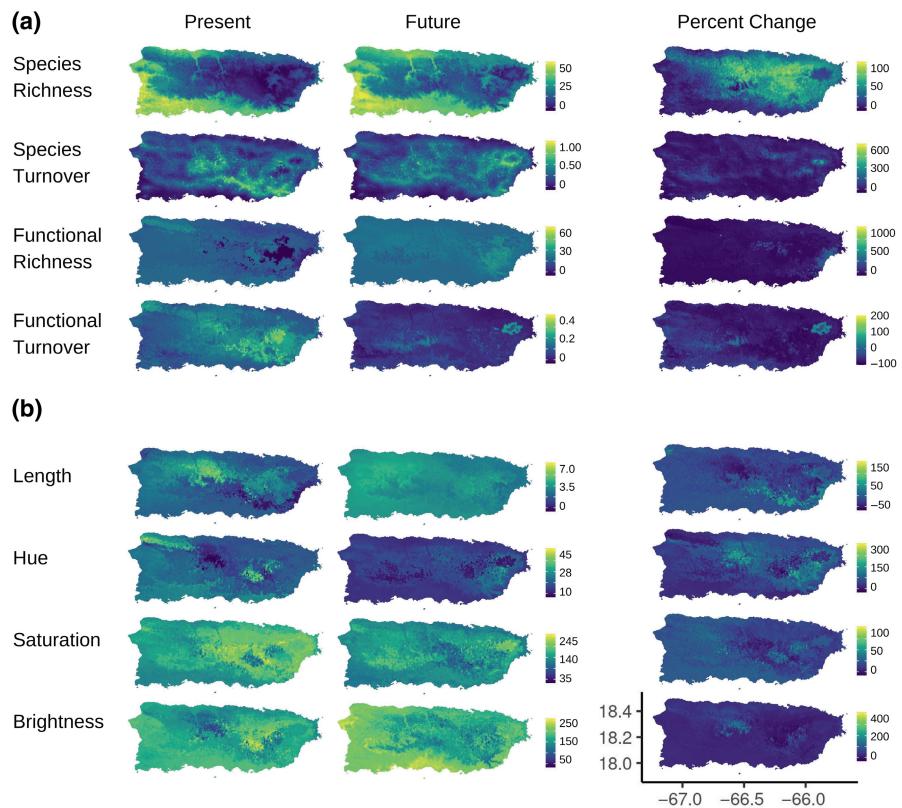
3 | RESULTS

3.1 | Taxonomic and functional richness and turnover

Modelled taxonomic and functional richness and turnover were variable across the island, both under current and future climate scenarios. Under current conditions, species richness was projected to be the highest in the southern and western lowlands, whereas species turnover was projected to be the highest in the Cordillera Central and the Sierra de Cayey ([Figure 2a](#)). In contrast, functional richness was projected to be the highest in the north-west karst region, and functional turnover was projected to be the highest in the large Caguas-Juncos eastern valley ([Figure 2a](#)). Wing length was projected to be the highest along the northern karst region where hue values were also projected to be highest in the yellow range ([Figure 2b](#)), whereas saturation and brightness were projected to be the highest in the eastern portions of the Cordillera Central.

The patterns described above exhibited important changes under future conditions. In general, our models projected an overall increase in species richness at the site level. The largest increases in species richness occurred in the northern karst region and the Cordillera Central. In contrast, our models projected a decrease in species turnover, with the greatest decreases in species turnover projected to occur along the western and southern coasts. Likewise, our models projected an increase in functional richness across the island, although the greatest increases were projected to occur in the eastern Caguas-Juncos Valley ([Figure 2a](#)). Functional turnover, like species turnover, was projected to decrease at the site level across the island, yet the greatest decreases were projected to occur

FIGURE 2 Modelled present (1970–2000), future (2061–2080) and per cent change (%) of (a) species richness (number of species), functional richness (sum of the trait-distance matrix branch lengths), species and functional turnover (Sørensen pairwise dissimilarity index) and (b) wing length (cm), hue, saturation and brightness (colour metrics all unitless, range 0–255) for 62 butterfly species using stacked ensemble distribution models. Note the different units and scales for each panel.



in the northern karst region and the eastern Caguas-Juncos Valley (Figure 2a). Although functional turnover was projected to decrease at the site level across the island, it was projected to increase in the Sierra de Luquillo (Figure 2a). Wing traits also exhibited variable patterns across the island; however, all traits were most notably projected to change in the northern karst region or the eastern Caguas-Juncos Valley (Figure 2b).

These patterns are best summarized by examining the relative per cent change between modelled future and current taxonomic and functional richness and turnover at the island level.

Over time our models projected (1) an increase in mean site-level species richness by about six species or 20% (Figure 3a, z -test: 450.45, $p < .001$); (2) an increase of mean site-level functional richness by 28% (Figure 3c, z -test: 45.93, $p < .001$); (3) a decrease of mean site-level species turnover by 41% (Figure 3b, z -test: -6.28, $p < .001$); and (4) a decrease in mean site-level functional turnover by 59% (Figure 3d, z -test: -13.406, $p < .001$). Functional homogenization was projected to exceed taxonomic homogenization, on average, especially in lowland areas (Figure S1.4). Furthermore, wing length was projected to slightly decrease by 6% (Figure 3e; z -test: -12.793, $p < .001$), hue was projected to increase by 25% from orange-to-yellow hues (Figure 3f; z -test: 436.5, $p < .001$), saturation to decrease by 8% (Figure 3g; z -test: -995.59, $p < .001$) and brightness to slightly increase by 1% (Figure 3h; z -test: 65.17, $p < .001$).

The extent to which taxonomic and functional measures of diversity are linked is not well studied. Here, we found that projected taxonomic richness was positively correlated with projected functional richness ($R^2 = .41$, $p < .001$), taxonomic turnover was positively

correlated with functional turnover ($R^2 = .51$, $p < .001$), but richness was negatively correlated with turnover for both taxonomic ($R^2 = .38$, $p < .001$) and functional indices ($R^2 = .33$, $p < .001$) (i.e. taxonomic richness was negatively correlated with taxonomic turnover and functional richness was negatively correlated with functional turnover; Figures S1.4 and S1.5).

3.2 | Climatic-mediated effects on species and trait distributions

Based on results from both GAMs and OLS regressions, temperature seasonality (bio4) was the strongest predictor of projected current taxonomic and functional richness and turnover, although with opposing effects (Table 1). Temperature seasonality was negatively associated with projected measures of richness (based on OLS regressions; species: $\beta = -5.61$, $p < .001$; functional: $\beta = -0.29$, $p < .001$) and positively associated with those of turnover (species: $\beta = -0.06$, $p < .001$; functional: $\beta = 0.04$, $p < .001$). Similarly, temperature seasonality was the strongest predictor of projected relative per cent change in species richness ($\beta = 3.49$, $p < .001$), functional richness ($\beta = 0.45$, $p < .001$) and functional turnover ($\beta = -0.37$, $p < .001$), but not projected changes in species turnover (Table 1). Temperature seasonality was positively associated with projected change in species ($\beta = 3.49$, $p < .001$) and functional richness ($\beta = 0.45$, $p < .001$), and negatively associated with projected change in functional turnover ($\beta = -0.37$, $p < .001$). Projected change in species turnover was more strongly (and positively)

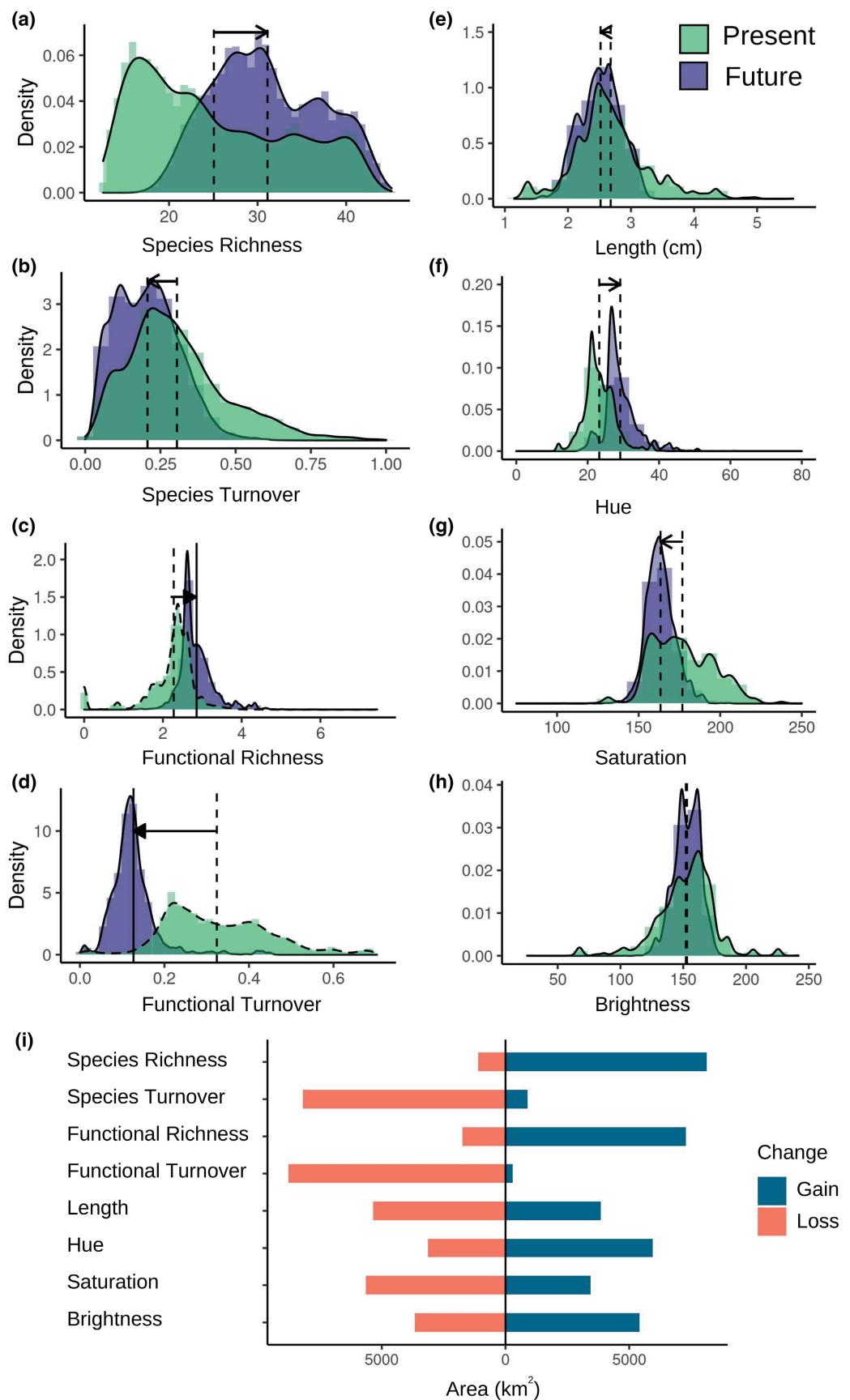


FIGURE 3 Density histogram plots showing changes in modelled (a-d) species and functional richness and turnover; (e-h) wing length, hue, saturation and brightness over time. Values represent pixel-level values calculated based on mean traits for all species with at least 65% probability of occurring in each cell. Pixels are $\sim 1 \text{ km}^2$ spatial resolution ($883 \times 923 \text{ m}$), and (i) total area (km^2) exhibiting gains or losses in each response variable.

TABLE 1 Results of generalized additive models (GAM) and ordinary least squares regression (OLS) of projected present and projected change in response variables: taxonomic and functional richness and turnover, and wing length, hue, saturation and brightness and explanatory variables: elevation, precipitation of the warmest quarter (bio18), temperature seasonality (bio4) and temperature annual range (bio7).

	Species richness	Functional richness	Species turnover	Functional turnover	Wing length	Hue	Saturation	Brightness
GAM present								
Degrees of freedom	36.02	33.2	34.59	35.1	34.65	34.63	35.14	31.69
R^2_{adj}	.94	.40	.53	.54	.39	.45	.6	.45
Dev (%) explained	94.1	40.1	52.9	54	39.1	44.8	60.5	44.7
OLS present								
Elevation	-0.96	0.22	-0.004	0.0004	0.065	-0.46	1.82	-9.52
P Warm Q (bio18)	-2.36	-0.21	0.04	-0.005	0.03	-0.58	8.16	5.26
T Season (bio4)	-5.61	-0.29	0.06	0.04	-0.01	-1.84	6.21	-9.37
T Range (bio7)	2.04	0.02	0.01	-0.01	0.20	-0.08	-1.01	-2.41
R^2_{adj}	.71	.28	.18	.15	.22	.24	.43	.29
p Value	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001
GAM change								
Degrees of freedom	35.41	35.51	34.38	35.1	33.1	34.16	34.25	32.12
R^2_{adj}	.8	.46	.34	.57	.14	.44	.39	.27
Dev (%) explained	79.6	46.3	34.3	56.9	13.9	44.4	39.1	26.8
OLS change								
Elevation	-0.81	-0.26	0.03	0.18	-0.02	-0.32	-0.11ns	4.28
P Warm Q (bio18)	-0.08	0.21	0.01	0.11	0.02	0.13ns	-0.37	-6.11
T Season (bio4)	3.49	0.45	-0.02	-0.37	-0.04	4.09	-7.24	3.70
T Range (bio7)	-0.07	-0.02	-0.01	0.11	-0.03	-0.42	1.91	3.17
R^2_{adj}	.49	.22	.10	.18	.01	.24	.18	.10
p Value	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001

Note: For brevity, degrees of freedom (df) and, as measures of overall fit, the adjusted R^2 and the deviance explained are presented for GAMs (see Table S1.1 for F-values for each variable). Estimates of the regression coefficients are presented for OLS regressions. All coefficients were significant ($p < .001$) unless otherwise noted ('ns'). Bold values indicate non-significance ($p > .05$).

associated with elevation ($\beta = 0.03$, $p < .001$). Under current conditions, predictors of wing traits varied by trait (Table 1). In contrast, temperature seasonality was the strongest predictor of projected change in all wing trait values, but the direction of the relationship varied from negative (length and saturation) to positive (hue and brightness, Table 1).

3.3 | Trait-mediated effects on species distributions

Species were primarily separated by wing hue, saturation and brightness along Axis 1 of the PCA and secondarily by wing length along Axis 2 (Figure S1.6, Table S1.2). Spearman correlation coefficients among PC scores indicated significant relationships among the second PC axis (strongly associated with wing length), current distribution area (rho: .26, $p < .05$) and modelled future elevation including modelled future maximum elevation and change in elevational range (Tables S1.3 and S1.4). Wing length was negatively correlated with projected changes in maximum elevation ($R^2 = -.34$, $p < .01$) and

elevational range ($R^2 = -.34$, $p < .01$). Wing saturation was positively correlated with wing length ($R^2 = .28$, $p < .01$) and negatively correlated with hue ($R^2 = -.49$, $p < .0001$; Table S1.4). Notably, larger-winged species were projected to exhibit decreased distribution area with declines in maximum elevation, whereas smaller-winged species were projected to exhibit increased distribution area with upslope expansion (Figure 4).

4 | DISCUSSION

We used digitized museum collections and species distribution models to model the extent to which climate change could lead to taxonomic and functional homogenization of tropical butterfly communities. The modelling approach used here pointed to both taxonomic and functional homogenization, as well as a negative relationship between wing length and temperature seasonality. Finally, we found that changes in modelled distribution area were negatively correlated with wing length. Altogether, our work indicates that temperature seasonality is a prominent driver of biotic homogenization

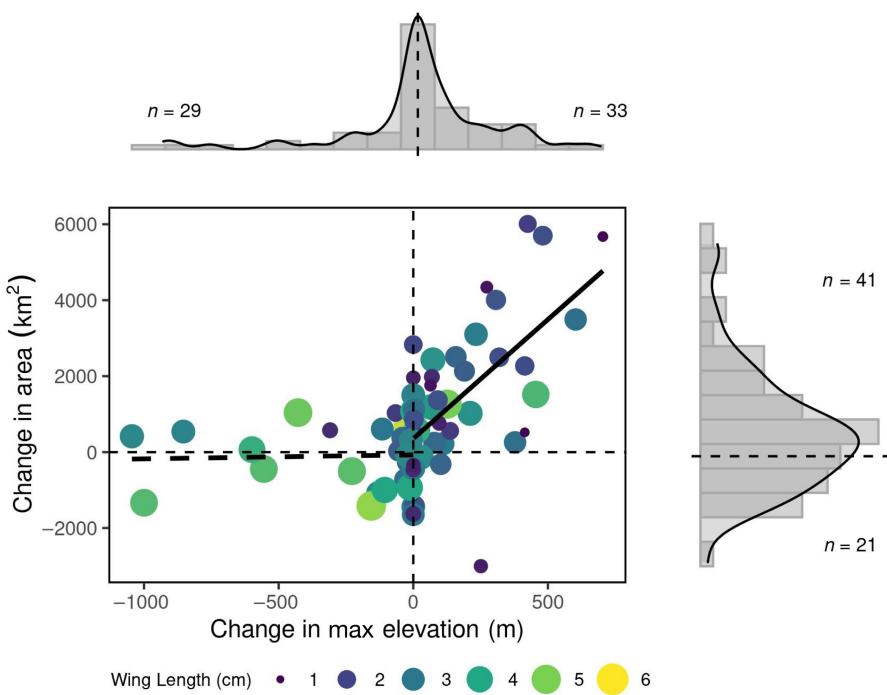


FIGURE 4 Local regression between modelled change in area and modelled change in maximum elevation for 62 butterfly species based on current (1970–2000) and future (2061–2080) environmental conditions, showing that predicted declines in maximum elevation are not associated with changes in distribution area. In contrast, predicted increases in maximum elevation are associated with predicted increases in distribution area ($R^2 = .35$, $p < .001$). Histogram and density distributions for predicted change in distribution area (km^2) and predicted change in maximum elevation (m) are shown along the corresponding axes. Most species with small wings were predicted to expand their habitat area and shift to higher elevations. Size and colour of data points indicate wing length (cm). Notably, species which were predicted to exhibit declines in maximum elevation were predominantly larger winged.

by favouring smaller, less melanized species that expand their distributions upslope.

4.1 | Taxonomic and functional richness and turnover

The first goal of this study was to model current and projected trends in taxonomic and functional richness and turnover across the topographically complex island of Puerto Rico. Under current climate conditions, butterfly species richness was projected to be the highest along the south-west coast, mirroring patterns of bird diversity (Acevedo & Restrepo, 2008; Campos-Cerqueira et al., 2021; Kepler & Kepler, 1970; Smith et al., 2017). A combination of high precipitation seasonality and reduced abundance of amphibians competing with birds for invertebrate prey is suggested as an explanation for high bird richness in this region (Kepler & Kepler, 1970). In comparison, butterfly species turnover was projected to be the highest across two main mountain ranges, namely the Cordillera Central and the Sierra de Cayey. High species turnover in mountainous terrain is not uncommon (e.g. Dewan et al., 2022) and can be attributed to environmental heterogeneity (Wilson & Fox, 2021). Functional richness was projected to be the greatest in the humid, north-west region of the island, where taxonomic richness was also projected to be high. This region is characterized by limestone hills or haystacks

(mogotes), consisting of narrow valleys surrounded by hills with steep slopes (Lugo et al., 2001). In general, high biodiversity in this region (including endemic birds, amphibians and reptiles) is attributed to protection from strong winds and reduced agricultural impact on steep terrain (Rivera & Aide, 1998). These conditions have led to persistent forest cover which may insulate populations from disturbances and this stability may, over long periods of time, result in greater diversity (e.g. Roubik et al., 2021; Willig et al., 2019). Finally, functional turnover was projected to be the greatest in the humid and fertile Caguas-Juncos valley, an alluvial valley once used for cattle and sugarcane. As in other tropical regions (e.g. Bush et al., 2015), land-use legacies influence contemporary patterns of plant species composition (Pascarella et al., 2000) and thus suitable host plant distributions, which likely play a role in the high butterfly functional turnover found in the Caguas-Juncos valley. In Puerto Rico, the legacy of deforestation and land use continues to impact plant species richness and distributions (Grau et al., 2003) with cascading effects on insects that depend or specialize on different plants (Acevedo & Restrepo, 2008; Barberena-Arias & Aide, 2003). For example, one study found that although secondary forests in Puerto Rico became structurally similar to old-growth forests, they differed in plant species composition, often dominated by non-indigenous species (Aide et al., 2000; Zimmerman et al., 2000). Although occurrence records span a range of collection years from 1830 to 2019, most were collected between 1980 and 2000. During this 20-year

period, widespread agricultural abandonment led to forest recovery, and by the early 2000s, forest cover in Puerto Rico reached 55%, even though these novel forests are dominated by non-indigenous plants at the expense of indigenous ones (Brandeis & Turner, 2013; Rojas-Sandoval et al., 2022). It is possible that changes in forest cover and plant abundances during this time led to shifts in butterfly abundances from early successional species specializing in agricultural crops to later successional species, supporting a more generalist butterfly fauna given the increase in non-indigenous plant species composition. Furthermore, forest regeneration combined with frequent hurricane disturbance leads to complex successional processes (Flynn et al., 2010), which may further play a role in the high butterfly functional turnover found in the Caguas-Juncos valley – a region which receives more direct impact from east-to-west moving hurricanes. More detailed analyses could potentially use the Lepidoptera collection record to model shifts in species' abundances over time (e.g. Gotelli et al., 2023) by, for example, dividing records into different time periods. However, this approach would require confronting additional challenges (e.g. computational time and the paucity of butterfly records post-2000). A related caveat is that the butterfly species included in our modelling approach encompasses a bit more than half of the total estimated number of butterfly species on the island (see Figure S1.7). The included butterfly species reflect those with at least 10 occurrence records and tend to be more common. Thus, understanding whether rarity in the collection record translates to rarity in abundance could better determine whether our results underestimate patterns of richness and turnover.

Compared to diversity patterns of current modelled butterfly communities, future butterfly communities were projected to become more taxonomically and functionally similar or homogeneous. Biotic homogenization was projected to occur throughout the island but especially in the coastal lowlands and interior valleys. These results are in stark contrast with those for the flora of Puerto Rico where a greater floristic homogenization was projected to occur at higher elevations (Henareh Khalyani et al., 2019), which may be explained by differences in the bioclimatic variables used in the SDMs. Henareh Khalyani et al. (2019) used annual means of temperature and precipitation, whereas we used metrics describing their variation (seasonality, range), extremes (water availability during the warmest quarter) and elevation (a major determinant of temperature on the island; Daly et al., 2003). Shifting climatic variables have interacting effects on insect growth and mortality (Pureswaran et al., 2018), so more detailed studies on how climate means and variability interact is a pressing challenge. Another possibility is that plants and insects have different abiotic limitations, and higher elevation habitats are currently too cold or climatically variable for the butterfly species studied here, pointing to potential future spatial mismatches between insects and their host plants under future climate scenarios (e.g. Gérard et al., 2020; Schweiger et al., 2008). Alternatively, these contrasting findings may be driven by differences in plant and butterfly diversity patterns or differences in the degree of host plant specialization. Lowland habitats are warmer, supporting a diverse butterfly community but reduced

plant diversity (Weaver & Murphy, 1990), perhaps because the butterfly assemblage there consists of more generalists. In comparison, upland habitats harbour fewer butterfly species even though these areas are floristically more diverse (Gould et al., 2006; Weaver & Murphy, 1990), pointing to a more specialized butterfly assemblage. Given that species distributions reflect a range of variables in addition to climate, actual species re-distributions will depend on life histories, behaviour, dispersal and concomitant shifts in other species including host plants, predators, parasitoids and pathogens as well as changes in land use. For example, behavioural thermoregulation can diminish the direct impacts of warming and facilitate species persistence in unfavourable thermal environments (Bonebrake et al., 2014; Wenda et al., 2021). Additionally, in this study, we estimated adult butterfly responses but caterpillar responses may have equally important consequences for population persistence in warming climates (e.g. Agosta et al., 2017; Fenberg et al., 2016; Van Dyck et al., 2015; Wilson et al., 2019). Finally, the results shown here may be influenced by evolutionary relationships with certain families exhibiting greater sensitivity to changes in climatic variability or, conversely, exhibiting greater sensitivity to the presence of particular host plants (which differ across environments), confounding the observed linkages between traits and climate.

4.2 | Climatic-mediated effects on species and trait distributions

The second goal of our study was to understand possible climatic-mediated effects on taxonomic and functional richness and turnover and wing traits. Overall, we found that current and future-modelled measures of richness and turnover were driven primarily by temperature seasonality followed by elevation. In addition, we found that under current conditions, wing size and melanization increased with elevation. In other words, butterflies were larger and more melanized at higher elevations. However, future climatic conditions favoured smaller, less melanized species, particularly in the high Central Cordillera. In other words, butterfly assemblages became smaller and lighter at higher elevations. Our results are in line with three sets of studies. The first reported larger wing size and greater wing melanization at higher elevations (Brehm et al., 2019; Henriques et al., 2022; Leingärtner et al., 2014; Xing et al., 2016), both among temperate and tropical Lepidoptera. The second reported declining body size across temperate (Bowden et al., 2015; Wonglersak et al., 2020; Zeuss et al., 2014) and tropical (Wu et al., 2019) insects as a universal response to climate warming (Gardner et al., 2011; Ohlberger, 2013). Although the latter study set primarily focuses on within-species changes in body size using museum specimens and historical temperature records, we demonstrate these changes can also occur at an assemblage level. Taken together, the emerging importance of thermoregulatory constraints on wing size and colour (e.g. Clusella Trullas et al., 2007; Kingsolver, 1983) suggests that future warming is likely to favour smaller, less melanized species. The third set of

studies demonstrates the prominent, and often overlooked, role of climatic variability on species and functional diversity. In our study, current modelled taxonomic and functional richness and turnover, as well as projected changes in these and wing traits, were primarily driven by temperature seasonality: modelled species and functional richness increased with decreasing temperature seasonality. Thus, thermal stability promotes species and functional diversity. In line with other studies, thermal stability was strongly correlated with species richness in our study, possibly reflecting reduced extinction risks (Huntley et al., 2016). However, our results also showed greater trait variation among species in thermally stable environments, which contradicts empirical results across latitude and taxa (e.g. Deutsch et al., 2008) and predictions from the climatic variability hypothesis (e.g. Janzen, 1967) which argues that trait variation should be greater in thermally variable environments. One explanation for this result is that climatic stability favours specialization (Vázquez & Stevens, 2004) and, consequently, greater specialization results in finer niche partitioning, allowing more species to co-exist (MacArthur, 1972). Another possibility is that thermal stability reduces selection for traits that cope with unstable temperature regimes and these traits then vary simply by genetic drift. The impact of temperature seasonality on species turnover is much less understood, and on functional turnover even less so (Dewan et al., 2022). Seasonality may impact species and functional turnover through its impact on resource availability (Gaston & Chown, 1999). Indeed, the seasonality of resource availability was a major influence on weevil body size variation (Chown & Klok, 2003) and may be especially important for the Puerto Rican Lepidoptera assemblage given that their abundances vary between wet and dry seasons (Davila & Asencio, 1992).

4.3 | Trait-mediated effects on species distributions

The final question we asked was whether traits mediate projected changes in species distributions. Our comparisons of wing colour and size with species' projected changes in distributions showed that shifts in species distributions were associated with wing size and, to a lesser extent, wing brightness. Specifically, smaller-winged species were projected to exhibit the greatest increases in distribution area, that is, expansion of their ranges, primarily through upslope migration. In contrast, larger-winged species were projected to exhibit the greatest declines in distribution area, that is, contraction of their ranges, via downslope shifts in distribution. Examining the degree of specialization among small and larger-winged species could provide additional insight into these differences, for example, if smaller-winged species tend to be wide-ranging generalists. A phylogenetic approach could further determine whether these results are driven by specific families (e.g. small-winged Lycaenids). Interestingly, the widest-ranging species exhibited the poorest model performance. Many of these were skippers (Hesperiidae), pointing to mechanisms that may

promote broad ranges or determine population-level responses to changing climate (see Figure S1.8). Furthermore, our results are in sharp contrast with a recent meta-analysis across latitudes that showed that traits, including body size, are weak predictors of distribution shifts across taxa (Beissinger & Riddell, 2021). Perhaps it is easier to detect the role of traits at smaller scales rather than the global scale of meta-analyses. The present study was restricted to a small topographically complex island, and the modelled distribution shifts occurred across elevation rather than latitude. The meta-analysis by Beissinger and Riddell (2021) also contradicts other studies on Lepidoptera that report body size as an important predictor of distribution shifts. For example, large body size predisposed species to distribution declines among butterflies in Finland (Mattila et al., 2011) and population declines among moths in England (Coulthard et al., 2019). Thus, for mobile taxa such as Lepidoptera, traits such as wing size may be good predictors of climate change-induced shifts in species distributions, as we have modelled here. Even though large body size is positively associated with dispersal ability (MacLean & Beissinger, 2017), and thus might be expected to promote distribution expansions, selection against larger wing size may be driven by thermoregulation. Warming temperatures are expected to favour smaller wing sizes, reducing thermal loads and metabolic demands. Yet the downslope shifts of larger-winged species from cooler uplands to warmer lowlands, projected here, seemingly challenge a thermoregulatory explanation. These results may point to interactive effects of wing size on temperature tolerance and desiccation resistance (Chown et al., 2011), with larger wings conferring greater drought tolerance (Hooper et al., 1999; Kellermann & van Heerwaarden, 2019; Parkash et al., 2009). Modelled distribution shifts were also explained by wing brightness, although to a lesser extent than wing size. Colour may translate into differences in heat loads and exposure to climatic conditions, which further underscores the idea that thermoregulatory constraints drive predicted species distributions in the butterfly fauna studied here. Here, we focused on species-level traits but intraspecific variation in wing size or colouration (e.g. Ellers & Boggs, 2004; Kingsolver, 1995) would be worth examining further (and the images are available for doing so). Local adaptation or plasticity could be important mechanisms for responding to climate change in situ.

5 | CONCLUSION

Using digitized museum specimen records, we generated species and trait distribution models to examine the potential for taxonomic and functional homogenization among a tropical butterfly assemblage. Our modelling approach points to biotic homogenization resulting from shifts in species and trait distributions. Results also consistently showed that island-wide shifts in modelled species distributions were primarily driven by temperature seasonality and mediated by wing size. These projected relationships are tempered by the recognition that distribution shifts do not occur in isolation

of biotic interactions, human impacts, changes in land use, time lags, phenotypic plasticity, phenological shifts or evolutionary change. Although limitations of species distribution modelling are well known (e.g. Guisan & Thuiller, 2005), it remains a useful tool for delineating suitable habitats for species of interest. When paired with museum data, species distribution models generate useful baseline predictions that can be treated as hypotheses (Lee-Yaw et al., 2022). The resulting hypotheses are particularly beneficial in regions where long-term field research or population monitoring remains scarce such as in the tropics where climate change is accelerating rapidly.

The predictions generated here identify several priority focal areas for future research. Specifically, research should prioritize further understanding the impact of seasonality and climatic variability on tropical butterfly assemblages. The importance of climatic variability on butterfly (and more broadly insect) assemblages may help explain contradictory reports of population declines worldwide – sites perhaps differing in the rate of change of seasonality. Additionally, butterflies are an ideal system for understanding shifts in biotic interactions under future climate scenarios and, although beyond the scope of the present study, herbarium data could be coupled with collection records to examine whether butterfly distributions are further constrained by the limits of their host plants under the same climate scenarios. Phylogenetic approaches may provide additional insight into whether the relationships shown here are confounded by other factors or whether certain families are more sensitive to climate change predicted for this region.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13814>.

DATA AVAILABILITY STATEMENT

All data are deposited in Dryad which can be accessed at: doi: [10.5061/dryad.ngf1vhzz](https://doi.org/10.5061/dryad.ngf1vhzz). All digitized images are available in the Symbiota Collections of Arthropods Network (SCAN; <https://scan-bugs.org/portal/>).

ORCID

Catherine M. Hulshof  <https://orcid.org/0000-0002-2200-8076>

REFERENCES

Abràmoff, M. D., Magalhães, P. J., & Ram, S. J. (2004). Image processing with ImageJ. *Biophotonics International*, 11(7), 36–42.

Acevedo, M. A., & Restrepo, C. (2008). Land-cover and land-use change and its contribution to the large-scale organization of Puerto Rico's bird assemblages. *Diversity and Distributions*, 14(1), 114–122.

Agosta, S. J., Hulshof, C. M., & Staats, E. G. (2017). Organismal responses to habitat change: Herbivore performance, climate and leaf traits in regenerating tropical dry forests. *Journal of Animal Ecology*, 86(3), 590–604.

Aguirre-Gutiérrez, J., Wallis De Vries, M. F., Marshall, L., van't Zelfde, M., Villalobos-Arámbula, A. R., Boekelo, B., Bartholomeus, H., Franzén, M., & Biesmeijer, J. C. (2017). Butterflies show different functional and species diversity in relationship to vegetation structure and land use. *Global Ecology and Biogeography: A Journal of Macroecology*, 26(10), 1126–1137.

Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., & Marcano-Vega, H. (2000). Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. *Restoration Ecology*, 8(4), 328–338.

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38(5), 541–545.

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *The Journal of Applied Ecology*, 43(6), 1223–1232.

Angilletta, M. J., Jr., & Dunham, A. E. (2003). The temperature-size rule in ectotherms: Simple evolutionary explanations may not be general. *The American Naturalist*, 162(3), 332–342.

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22(1), 42–47.

Arnan, X., Arcoverde, G. B., Pie, M. R., Ribeiro-Neto, J. D., & Leal, I. R. (2018). Increased anthropogenic disturbance and aridity reduce phylogenetic and functional diversity of ant communities in Caatinga dry forest. *The Science of the Total Environment*, 631–632, 429–438.

Atkinson, D. (1994). Temperature and organism size: A biological law for ectotherms? *Advances in Ecological Research*. <http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=4124219>

Attiwilli, S., Karmakar, T., Isvaran, K., & Kunte, K. (2022). Habitat preference and functional traits influence responses of tropical butterflies to varied habitat disturbance. *International Journal of Tropical Insect Science*, 42(1), 855–864.

Barberena-Arias, M. F., & Aide, T. M. (2003). Species diversity and trophic composition of litter insects during plant secondary succession. *Caribbean Journal of Science*, 39(2), 161–169.

Barton, K., & Barton, M. K. (2015). Package "mumin". Version. <https://cran.hafro.is/web/packages/MuMin/MuMin.pdf>

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography: A Journal of Macroecology*, 19(1), 134–143.

Baselga, A., Gómez-Rodríguez, C., & Lobo, J. M. (2012). Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. *PLoS One*, 7(2), e32341.

Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808–812.

Bastardo Landrau, R. H. (1998). *Estructura y dinamica de poblacion de Ascia monuste eubotea (Godart, 1819) (Lepidoptera: Pieridae) en Puerto Rico*. University of Puerto Rico. <https://search.proquest.com/openview/d0a9086152d887950127c3cf6e94fd50/1?pq-origsite=gscholar&cbl=18750&diss=y>

Beissinger, S. R., & Riddell, E. A. (2021). Why are species' traits weak predictors of range shifts? *Annual Review of Ecology, Evolution, and Systematics*, 52(1), 47–66.

Bonebrake, T. C., Boggs, C. L., Stamberger, J. A., Deutsch, C. A., & Ehrlich, P. R. (2014). From global change to a butterfly flapping: Biophysics and behaviour affect tropical climate change impacts. *Proceedings of the Royal Society B: Biological Sciences*, 281(1793), 20141264.

Bonebrake, T. C., Ponisio, L. C., Boggs, C. L., & Ehrlich, P. R. (2010). More than just indicators: A review of tropical butterfly ecology and conservation. *Biological Conservation*, 143(8), 1831–1841.

Bota-Sierra, C. A., García-Robledo, C., Escobar, F., Novelo-Gutiérrez, R., & Londoño, G. A. (2022). Environment, taxonomy and morphology constrain insect thermal physiology along tropical mountains. *Functional Ecology*, 36(8), 1924–1935.

Bowden, J. J., Eskildsen, A., Hansen, R. R., Olsen, K., Kurle, C. M., & Høy, T. T. (2015). High-Arctic butterflies become smaller with rising temperatures. *Biology Letters*, 11(10), e20150574. <https://doi.org/10.1098/rsbl.2015.0574>

Brakefield, P. M., & de Jong, P. W. (2011). A steep cline in ladybird melanism has decayed over 25 years: A genetic response to climate change? *Heredity*, 107(6), 574–578.

Brandeis, T. J., & Turner, J. A. (2013). Puerto Rico's forests, 2009. *Resource bulletin SRS-191*. U. S. Department of Agriculture Forest Service, Southern Research Station. 85 p.

Brehm, G., & Fiedler, K. (2004). Bergmann's rule does not apply to geotropical moths along an elevational gradient in an Andean montane rain forest. *Global Ecology and Biogeography: A Journal of Macroecology*, 13(1), 7–14.

Brehm, G., Zeuss, D., & Colwell, R. K. (2019). Moth body size increases with elevation along a complete tropical elevational gradient for two hyperdiverse clades. *Ecography*, 42(4), 632–642.

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33(2), 261–304.

Bush, M. B., McMichael, C. H., Piperno, D. R., Silman, M. R., Barlow, J., Peres, C. A., Power, M., & Palace, M. W. (2015). Anthropogenic influence on Amazonian forests in pre-history: An ecological perspective. *Journal of Biogeography*, 42(12), 2277–2288.

Campos-Cerdeira, M., Terando, A. J., Murray, B. A., Collazo, J. A., & Aide, T. M. (2021). Climate change is creating a mismatch between protected areas and suitable habitats for frogs and birds in Puerto Rico. *Biodiversity and Conservation*, 30(12), 3509–3528.

Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT – Biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution/British Ecological Society*, 6, 232–236. <https://doi.org/10.1111/2041-210X.12310>

Carrión-Cabrera, J. E. (2003). *Estatus de Atlantea tulita (Dewitz, 1877) en Puerto Rico*. [scholar.uprm.edu]. <https://scholar.uprm.edu/handle/20.500.11801/1007>

Chown, S. L., & Klok, C. J. (2003). Altitudinal body size clines: Latitudinal effects associated with changing seasonality. *Ecography*, 26(4), 445–455.

Chown, S. L., Sørensen, J. G., & Terblanche, J. S. (2011). Water loss in insects: An environmental change perspective. *Journal of Insect Physiology*, 57(8), 1070–1084.

Clusella-Trullas, S., van Wyk, J. H., & Spotila, J. R. (2007). Thermal melanism in ectotherms. *Journal of Thermal Biology*, 32(5), 235–245.

Clusella-Trullas, S., Terblanche, J. S., Blackburn, T. M., & Chown, S. L. (2008). Testing the thermal melanism hypothesis: A macrophysiological approach. *Functional Ecology*, 22(2), 232–238.

Clutton-Brock, T. H., & Parker, G. A. (1992). Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology*, 67(4), 437–456.

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, 322(5899), 258–261.

Comstock, W. P. (1944). *Insects of Porto Rico and the Virgin Islands, Rhopalocera or butterflies. Scientific survey of Porto Rico and the Virgin Islands*. New York Academy of Sciences.

Coulthard, E., Norrey, J., Shortall, C., & Harris, W. E. (2019). Ecological traits predict population changes in moths. *Biological Conservation*, 233, 213–219.

Daly, C., Helmer, E. H., & Quiñones, M. (2003). Mapping the climate of Puerto Rico, Vieques and Culebra. *International Journal of Climatology*, 23(11), 1359–1381.

David, E. N., & Asencio, C. I. (1992). Lepidopteros del Bosque Estatal de Maricao (Lepidoptera: Rhopalocera). *Acta Científica*, 6(1–3), 77–86.

de Castro, F. S., Da Silva, P. G., Solar, R., Fernandes, G. W., & Neves, F. d. S. (2020). Environmental drivers of taxonomic and functional diversity of ant communities in a tropical mountain. *Insect Conservation and Diversity/Royal Entomological Society of London*, 13(4), 393–403.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghilambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 105(18), 6668–6672.

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.

Dewan, S., Sanders, N. J., & Acharya, B. K. (2022). Turnover in butterfly communities and traits along an elevational gradient in the eastern Himalaya, India. *Ecosphere*, 13(3), e3984. <https://doi.org/10.1002/ecs2.3984>

Dornelas, M., Gotelli, N. J., Shimadzu, H., Moyes, F., Magurran, A. E., & McGill, B. J. (2019). A balance of winners and losers in the Anthropocene. *Ecology Letters*, 22(5), 847–854.

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.

Ellers, J., & Boggs, C. L. (2004). Functional ecological implications of intraspecific differences in wing melanization in *Colias* butterflies. *Biological Journal of the Linnean Society*, 82, 79–87.

Ewel, J. J., & Whitmore, J. L. (1973). The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service, Institute of Tropical Forestry, Research Paper ITF-018, 018. <https://www.fs.usda.gov/treesearch/pubs/5551>

Fenberg, P. B., Self, A., Stewart, J. R., Wilson, R. J., & Brooks, S. J. (2016). Exploring the universal ecological responses to climate change in a univoltine butterfly. *Journal of Animal Ecology*, 85(3), 739–748.

Flynn, D. F. B., Uriarte, M., Crk, T., Pascarella, J. B., Zimmerman, J. K., Aide, T. M., & Caraballo Ortiz, M. A. (2010). Hurricane disturbance alters secondary forest recovery in Puerto Rico: Secondary forest recovery. *Biotropica*, 42(2), 149–157.

Forbes, W. T. M. (1930). Insects of Porto Rico and the Virgin Islands. Heterocera or moths (excepting the Noctuidae, Geometridae, and Pyralidae). Insects of Porto Rico and the Virgin Islands. <https://www.cabdirect.org/cabdirect/abstract/20057003454>

Foster, B. J., McCulloch, G. A., Foster, Y., Kroos, G. C., King, T. M., & Waters, J. M. (2023). Ebony underpins Batesian mimicry in melanic stoneflies. *Molecular Ecology*, 32(18), 4986–4998.

Franz, N. M., & Yusseff Vanegas, S. Z. (2009). The university of Puerto Rico at mayagüez insect collection – Then and now. *Entomological News*, 120(4), 401–408.

García-Robledo, C., Kuprewicz, E. K., Staines, C. L., Erwin, T. L., & Kress, W. J. (2016). Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 113(3), 680–685.

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, 26(6), 285–291.

Gaston, K. J., & Chown, S. L. (1999). Elevation and climatic tolerance: A test using dung beetles. *Oikos*, 86(3), 584–590.

Gérard, M., Vanderplanck, M., Wood, T., & Michez, D. (2020). Global warming and plant–pollinator mismatches. *Emerging Topics in Life Sciences*, 4(1), 77–86.

Girardello, M., Chapman, A., Dennis, R., Kaila, L., Borges, P. A. V., & Santangeli, A. (2019). Gaps in butterfly inventory data: A global analysis. *Biological Conservation*, 236, 289–295.

Gleason, H. A., & Cook, M. T. (1926). *Scientific survey of Puerto Rico and the Virgin Islands, vol. VII, part 1: Plant ecology of Puerto Rico*. New York Academy of Sciences (issued Feb. 22, 1927).

Gotelli, N. J., Booher, D. B., Urban, M. C., Ulrich, W., Suarez, A. V., Skelly, D. K., Russell, D. J., Rowe, R. J., Rothendler, M., Rios, N., Rehan, S. M., Ni, G., Moreau, C. S., Magurran, A. E., Jones, F. A. M., Graves, G. R., Fiera, C., Burkhardt, U., & Primack, R. B. (2023). Estimating species relative abundances from museum records. *Methods in Ecology and Evolution*, 14(2), 431–443.

Gould, W. A., González, G., & Carrero Rivera, G. (2006). Structure and composition of vegetation along an elevational gradient in Puerto Rico. *Journal of Vegetation Science*, 17(5), 653–664.

Grau, H. R., Aide, T. M., Zimmerman, J. K., Thominson, J. R., Helmer, E., & Zou, X. (2003). The ecological consequences of socioeconomic and land-use changes in Postagriculture Puerto Rico. *Bioscience*, 53(12), 1159.

Green, S. J., Brookson, C. B., Hardy, N. A., & Crowder, L. B. (2022). Trait-based approaches to global change ecology: Moving from description to prediction. *Proceedings. Biological Sciences/The Royal Society*, 289(1971), 20220071.

Gries, C., Gilbert, M. E. E., & Franz, N. M. (2014). Symbiota – A virtual platform for creating voucher-based biodiversity information communities. *Biodiversity Data Journal*, 2, e1114.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009.

Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 118(2), e2002543117. <https://doi.org/10.1073/pnas.2002543117>

Hastie, T., & Tibshirani, R. (1986). Generalized additive models. *Statistical Science: A Review Journal of the Institute of Mathematical Statistics*, 1(3), 297–310.

Hayhoe, K. (2013). Quantifying key drivers of climate variability and change for Puerto Rico and the Caribbean. *Caribbean Landscape*.

Helmer, E. H., Ramos, O., López, T. D. M., Quinones, M., & Diaz, W. (2002). Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. *Caribbean Journal of Science*, 38(3–4), 165–183.

Henareh Khalyani, A., Gould, W. A., Falkowski, M. J., Muscarella, R., Uriarte, M., & Yousef, F. (2019). Climate change increases potential plant species richness on Puerto Rican uplands. *Climatic Change*, 156(1), 15–30.

Henriques, N. R., Lourenço, G. M., Diniz, É. S., & Cornelissen, T. (2022). Is elevation a strong environmental filter? Combining taxonomy, functional traits and phylogeny of butterflies in a tropical mountain. *Ecological Entomology*, 47(4), 613–625.

Hevia, V., Carmona, C. P., Azcárate, F. M., Torralba, M., Alcorlo, P., Ariño, R., Lozano, J., Castro-Cobo, S., & González, J. A. (2016). Effects of land use on taxonomic and functional diversity: A cross-taxon analysis in a Mediterranean landscape. *Oecologia*, 181, 959–970.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978.

Hooper, R. E., Tsubaki, Y., & Siva-Jothy, M. T. (1999). Expression of a costly, plastic secondary sexual trait is correlated with age and condition in a damselfly with two male morphs. *Physiological Entomology*, 24(4), 364–369.

Huey, R. B., & Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *American Zoologist*, 19(1), 357–366.

Huntley, B., Collingham, Y. C., Singarayer, J. S., Valdes, P. J., Barnard, P., Midgley, G. F., Altweig, R., & Ohlemüller, R. (2016). Explaining patterns of avian diversity and endemism: Climate and biomes of southern Africa over the last 140,000 years. *Journal of Biogeography*, 43(5), 874–886.

Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *The American Naturalist*, 101(919), 233–249.

Kaltsas, D., Dede, K., Giannaka, J., Nasopoulou, T., Kechagioglou, S., Grigoriadou, E., Raptis, D., Damos, P., Vasiliadis, I., Christopoulos, V., Loukaki, E., Frantes, R., Vlachaki, D., & Avtzis, D. N. (2018). Taxonomic and functional diversity of butterflies along an altitudinal gradient in two NATURA 2000 sites in Greece. *Insect Conservation and Diversity/Royal Entomological Society of London*, 11(5), 464–478.

Kellermann, V., & van Heerwaarden, B. (2019). Terrestrial insects and climate change: Adaptive responses in key traits. *Physiological Entomology*, 44(2), 99–115.

Kepler, C. B., & Kepler, A. K. (1970). Preliminary comparison of bird species diversity and density in Luquillo and Guanica forests. In H. T. Odum & R. F. Pigeon (Eds.), *A tropical rain forest: A study of irradiation and ecology at El Verde* (pp. 183–186). Puerto Rico.

Kingsolver, J. G. (1983). Thermoregulation and flight in *Colias* butterflies: E elevational patterns and mechanistic limitations. *Ecology*, 64(3), 534–545.

Kingsolver, J. G. (1987). Evolution and coadaptation of thermoregulatory behavior and wing pigmentation pattern in pierid butterflies. *Evolution*, 41(3), 472–490.

Kingsolver, J. G. (1995). Viability selection on seasonally polyphenic traits: Wing melanin pattern in western white butterflies. *Evolution*, 49(5), 932–941.

Kingsolver, J. G., Woods, H. A., Buckley, L. B., Potter, K. A., MacLean, H. J., & Higgins, J. K. (2011). Complex life cycles and the responses of insects to climate change. *Integrative and Comparative Biology*, 51(5), 719–732.

Krishna, A., Nie, X., Warren, A. D., Llorente-Bousquets, J. E., Briscoe, A. D., & Lee, J. (2020). Infrared optical and thermal properties of microstructures in butterfly wings. *Proceedings of the National Academy of Sciences of the United States of America*, 117(3), 1566–1572.

Lawler, J. J., White, D., Neilson, R. P., & Blaustein, A. R. (2006). Predicting climate-induced range shifts: Model differences and model reliability. *Global Change Biology*, 12(8), 1568–1584.

Lee-Yaw, J. A., McCune, J. L., Pironon, S., & Sheth, S. N. (2022). Species distribution models rarely predict the biology of real populations. *Ecography*, 2022(6), e05877.

Leingärtner, A., Krauss, J., & Steffan-Dewenter, I. (2014). Species richness and trait composition of butterfly assemblages change along an altitudinal gradient. *Oecologia*, 175(2), 613–623.

Lenoir, J., Gégout, J. C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., & Svenning, J. C. (2010). Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33(2), 295–303.

Leprieur, F., Albouy, C., De Bortoli, J., Cowman, P. F., Bellwood, D. R., & Mouillot, D. (2012). Quantifying phylogenetic beta diversity: Distinguishing between "true" turnover of lineages and phylogenetic diversity gradients. *PLoS One*, 7(8), e42760.

Liu, C., White, M., & Newell, G. (2011). Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography*, 34(2), 232–243.

Lugo, A. E., Castro, L. M., Vale, A., López, T. D. M., Hernández Prieto, E., García Martinó, A., Puente Rolón, A. R., Tossas, A. G., McFarlane, D. A., Miller, T., & Rodríguez, A. (2001). Puerto Rican karst – A vital resource. General Technical Report WO-65, August 2001. <http://www.fs.fed.us/global/iitf/karst.pdf>

MacArthur, R. H. (1972). In H. Row (Ed.), *Geographical ecology: Patterns in the distribution of species* (p. 269). Princeton University Press.

MacLean, H. J., Nielsen, M. E., Kingsolver, J. G., & Buckley, L. B. (2018). Using museum specimens to track morphological shifts through climate change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 374(1763), 20170404. <https://doi.org/10.1098/rstb.2017.0404>

MacLean, S. A., & Beissinger, S. R. (2017). Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology*, 23(10), 4094–4105.

Mattila, N., Kaitala, V., Komonen, A., Päivinen, J., & Kotiaho, J. S. (2011). Ecological correlates of distribution change and range shift in butterflies. *Insect Conservation and Diversity/Royal Entomological Society of London*, 4(4), 239–246.

McCain, C. M., & Garfinkel, C. F. (2021). Climate change and elevational range shifts in insects. *Current Opinion in Insect Science*, 47, 111–118.

McGill, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185.

McGraw, K. J., Safran, R. J., & Wakamatsu, K. (2005). How feather colour reflects its melanin content. *Functional Ecology*, 19(5), 816–821.

McKnight, M. W., White, P. S., McDonald, R. I., Lamoreux, J. F., Sechrest, W., Ridgely, R. S., & Stuart, S. N. (2007). Putting beta-diversity on the map: Broad-scale congruence and coincidence in the extremes. *PLoS Biology*, 5(10), e272.

Meineke, E. K., Davies, T. J., Daru, B. H., & Davis, C. C. (2018). Biological collections for understanding biodiversity in the anthropocene. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 374(1763), 20170386. <https://doi.org/10.1098/rstb.2017.0386>

Miller, G., & Lugo, A. E. (2009). *Guide to the ecological systems of Puerto Rico*. International Institute of Tropical Forestry General Technical Report. IITF-GTR-35. <https://doi.org/10.2737/IITF-GTR-35>

Miller, J. Y., & Miller, L. D. (2001). The biogeography of the west Indian butterflies (Lepidoptera): An application of a vicariance/dispersalist model. In *Biogeography of the West Indies* (pp. 127–156). CRC Press.

Moret, P., Aráuz, M. d. L. Á., Gobbi, M., & Barragán, Á. (2016). Climate warming effects in the tropical Andes: First evidence for upslope shifts of Carabidae (coleoptera) in Ecuador. *Insect Conservation and Diversity/Royal Entomological Society of London*, 9(4), 342–350.

Murphy, L. S. (1916). *Forests of Porto Rico: Past, present, and future and their physical and economic environment*. U.S. Department of Agriculture.

Myers, N. (2003). Biodiversity hotspots revisited. *Bioscience*, 53(10), 916–917.

Nijhout, H. F. (2003). The control of body size in insects. *Developmental Biology*, 261(1), 1–9.

Nunes, C. A., Quintino, A. V., & Constantino, R. (2017). Patterns of taxonomic and functional diversity of termites along a tropical elevational gradient. *Biotropica*, 49, 186–194. <https://doi.org/10.1111/btp.12365>

Ockinger, E., Schweiger, O., Crist, T. O., Debinski, D. M., Krauss, J., Kuussaari, M., Petersen, J. D., Pöyry, J., Settele, J., Summerville, K., S., & Bommarco, R. (2010). Life-history traits predict species responses to habitat area and isolation: A cross-continental synthesis. *Ecology Letters*, 13(8), 969–979.

Ohlberger, J. (2013). Climate warming and ectotherm body size – From individual physiology to community ecology. *Functional Ecology*, 27(4), 991–1001.

Parkash, R., Singh, S., & Ramnivas, S. (2009). Seasonal changes in humidity level in the tropics impact body color polymorphism and desiccation resistance in *Drosophila jambulina* – Evidence for melanism-desiccation hypothesis. *Journal of Insect Physiology*, 55(4), 358–368.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 637–669.

Pascarella, J. B., Aide, T. M., Serrano, M. I., & Zimmerman, J. K. (2000). Land-use history and Forest regeneration in the Cayey Mountains, Puerto Rico. *Ecosystems*, 3(3), 217–228.

Pérez-Asso, A. R., Genaro, J. A., & Garrido, O. H. (2009). *Butterflies of Puerto Rico*. 140 p. Editorial Cocuyo, J & J Press.

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, 9(6), 741–758.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3), 231–259.

Pureswaran, D. S., Roques, A., & Battisti, A. (2018). Forest insects and climate change. *Current Forestry Reports*, 4, 35–50.

Queen, J. P., Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge University Press.

Ramos, S. J. (1996). An annotated checklist of the butterflies of Puerto Rico. *Annals of the New York Academy of Sciences*, 776(1), 217–238.

Reymond, A., Purcell, J., Cherix, D., Guisan, A., & Pellissier, L. (2013). Functional diversity decreases with temperature in high elevation ant fauna. *Ecological Entomology*, 38(4), 364–373.

Rivera, L. W., & Aide, T. M. (1998). Forest recovery in the karst region of Puerto Rico. *Forest Ecology and Management*, 108(1), 63–75.

Rojas-Sandoval, J., Ackerman, J. D., Marcano-Vega, H., & Willig, M. R. (2022). Alien species affect the abundance and richness of native species in tropical forests: The role of adaptive strategies. *Ecosphere*, 13(12), e4291.

Roubik, D. W., Basset, Y., Lopez, Y., Bobadilla, R., Perez, F., & Ramírez, S. J. A. (2021). Long-term (1979–2019) dynamics of protected orchid bees in Panama. *Conservation Science and Practice*, 3, e543.

Safi, K., Cianciaruso, M. V., Loyola, R. D., Brito, D., Armour-Marshall, K., & Diniz-Filho, J. A. F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366(1577), 2536–2544.

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8–27.

SCAN. (2019). *Biodiversity occurrence data accessed through SCAN Data Portal*. <https://scan-bugs.org/portal/index.php>

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I. (2008). Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, 89(12), 3472–3479.

Smith, C. T., & Pico, R. (1976). The geography of Puerto Rico. *The Geographical Journal*, 142(1), 148.

Smith, R. L., Beard, K. H., & Koons, D. N. (2017). Invasive coqui frogs are associated with greater abundances of nonnative birds in Hawaii, USA. *The Condor*, 120(1), 16–29.

Sorensen, T. A. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter/Kongelige Danske Videnskabernes Selskab*, 5, 1–34.

Stelbrink, P., Pinkert, S., Brunzel, S., Kerr, J., Wheat, C. W., Brandl, R., & Zeuss, D. (2019). Colour lightness of butterfly assemblages across North America and Europe. *Scientific Reports*, 9(1), 1760.

Stork, N. E. (2018). How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology*, 63, 31–45.

Thuiller, W., Georges, D., & Engler, M. (2016). Package "biomod2". Species distribution modeling within an ensemble forecasting framework. <https://cran.microsoft.com/snapshot/2016-05-25/web/packages/biomod2/biomod2.pdf>

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD – A platform for ensemble forecasting of species distributions. *Ecography*, 32(3), 369–373.

Torres, J. A. (1992). Lepidoptera outbreaks in response to successional changes after the passage of hurricane Hugo in Puerto Rico. *Journal of Tropical Ecology*, 8(3), 285–298.

Van Dyck, H., Bonte, D., Puls, R., Gotthard, K., & Maes, D. (2015). The lost generation hypothesis: Could climate change drive ectotherms into a developmental trap? *Oikos*, 124(1), 54–61.

Vázquez, D. P., & Stevens, R. D. (2004). The latitudinal gradient in niche breadth: Concepts and evidence. *The American Naturalist*, 164(1), E1–E19.

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, 65, 457–480.

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America*, 118(2), e2023989118.

Wardle, D. A., Bardgett, R. D., Callaway, R. M., & Van der Putten, W. H. (2011). Terrestrial ecosystem responses to species gains and losses. *Science*, 332(6035), 1273–1277.

Wasserthal, L. T. (1975). The role of butterfly wings in regulation of body temperature. *Journal of Insect Physiology*, 21(12), 1921–1930.

Watt, W. B. (1969). Adaptive significance of pigment polymorphisms in *colias* butterflies, II. Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*. *Proceedings of the National Academy of Sciences of the United States of America*, 63(3), 767–774.

Weaver, P. L., & Murphy, P. G. (1990). Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica*, 22(1), 69–82.

Wenda, C., Xing, S., Nakamura, A., & Bonebrake, T. C. (2021). Morphological and behavioural differences facilitate tropical butterfly persistence in variable environments. *Journal of Animal Ecology*, 90(12), 2888–2900.

Willig, M. R., Woolbright, L., Presley, S. J., Schowalter, T. D., Waide, R. B., Heartsill Scalley, T., Zimmerman, J. K., González, G., & Lugo, A. E. (2019). Populations are not declining and food webs are not collapsing at the Luquillo experimental Forest [Review of populations are not declining and food webs are not collapsing at the Luquillo experimental Forest]. *Proceedings of the National Academy of Sciences of the United States of America*, 116(25), 12143–12144.

Wilson, R. J., Brooks, S. J., & Fenberg, P. B. (2019). The influence of ecological and life history factors on ectothermic temperature-size responses: Analysis of three Lycaenidae butterflies (Lepidoptera). *Ecology and Evolution*, 9(18), 10305–10316.

Wilson, R. J., & Fox, R. (2021). Insect responses to global change offer signposts for biodiversity and conservation. *Ecological Entomology*, 46(4), 699–717.

Wolcott, G. N. (1948). Insects of Puerto Rico. *The Journal of Agriculture of the University of Puerto Rico*, 32, 1–224.

Wonglersak, R., Fenberg, P. B., Langdon, P. G., Brooks, S. J., & Price, B. W. (2020). Temperature-body size responses in insects: A case study of British Odonata. *Ecological Entomology*, 45(4), 795–805.

Wood, S., & Wood, M. S. (2015). Package 'mgcv'. R Package Version, 1(29), 729.

Wu, C.-H., Holloway, J. D., Hill, J. K., Thomas, C. D., Chen, I.-C., & Ho, C.-K. (2019). Reduced body sizes in climate-impacted Borneo moth assemblages are primarily explained by range shifts. *Nature Communications*, 10(1), 4612.

Xing, S., Bonebrake, T. C., Tang, C. C., Pickett, E. J., Cheng, W., Greenspan, S. E., Williams, S. E., & Scheffers, B. R. (2016). Cool habitats support darker and bigger butterflies in Australian tropical forests. *Ecology and Evolution*, 6(22), 8062–8074.

Yang, L. H., Postema, E. G., Hayes, T. E., Lippey, M. K., & MacArthur-Waltz, D. J. (2021). The complexity of global change and its effects on insects. *Current Opinion in Insect Science*, 47, 90–102.

Zeuss, D., Brandl, R., Brändle, M., Rahbek, C., & Brunzel, S. (2014). Global warming favours light-coloured insects in Europe. *Nature Communications*, 5, 3874.

Zimmerman, J. K., Pascarella, J., & Aide, T. M. (2000). Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology*, 8, 350–360.

Zurell, D., Zimmerman, N. E., Gross, H., Baltensweiler, A., Sattler, T., & Wüest, R. O. (2020). Testing species assemblage predictions from stacked and joint species distribution models. *Journal of Biogeography*, 47(1), 101–113.

BIOSKETCHES

Catherine M. Hulshof is a tropical ecologist who combines empirical, trait-based and modelling approaches to understand biodiversity patterns and global change responses of plants and Lepidoptera. <https://biodiversityresearchlab.com/>.

James D. Ackerman is the director of the University of Puerto Rico Rio Piedras herbarium and zoological collections. He works on floristics, population biology, biogeography, invasive species and orchid biology.

Rosa A. Franqui is the director of the Museo de Entomología y Biodiversidad Tropical at the University of Puerto Rico Mayagüez.

Akito Y. Kawahara is the director of the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida. He works on the phylogeny and conservation of Lepidoptera.

Carla Restrepo is a landscape ecologist who combines quantitative methods, satellite imagery, spatial data and field work to examine processes that modify the spatial structure of tropical landscapes.

Author contributions: CMH and CR devised the project and conceptual framework. JDA, RAF and AYK provided access to collection databases. AYK facilitated image and record deposition in SCAN. CMH collected the data, ran the models and analysed the results. CMH and CR wrote the manuscript, with contributions from all authors.

SUPPORTING INFORMATION

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

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