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**RISING MINIMUM TEMPERATURES CONTRIBUTED TO 50 YEARS OF SHIFTING NORTH AMERICAN ARCTIC AND BOREAL BUTTERFLY COMMUNITIES**

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**Abstract:** Global climate change has been identified as a major driver of potential insect declines yet in many regions, there are critical knowledge gaps for how communities are shifting in response to climate. Poleward regions are of particular interest because warming is most rapid, but biodiversity data are sparse. Building on recent advances in occupancy modeling approaches to presence-only data, we reconstructed 50 years (1970-2019) of butterfly occupancy trends in response to rising minimum temperatures in one of the most under sampled regions of the continent. Among 90 modeled species, we found that cold-adapted species are far more often in decline (probability of occupancy) compared to their warm-adapted, more southerly distributed counterparts. Further, in a post-hoc analysis using species’ traits, we find that species’ range-wide average annual temperature is a consistent predictor of occupancy decline/increase. Species with warmer ranges are likely to be increasing in occupancy, especially at the northern periphery of their ranges. Our results provide the first look at macroscale butterfly biodiversity shifts in a critically under sampled region of North America and highlight the potential of leveraging methods that can match recent increases in community science participation with more sparse historical data to reconstruct trends even in poorly sampled regions using presence-only data.

**Keywords:** arctic, biodiversity, boreal, butterflies, climate change, Lepidoptera

**Authorship Contributions:** VS came up with the study idea and design. NN obtained and processed climate data. VS conducted the analysis and original interpretation. RG, NN, and LR provided feedback on the analysis. VS wrote the original manuscript, and all authors edited the manuscript together.

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**1. INTRODUCTION**

Multiple lines of scientific evidence have pointed to the potential for an alarming recent decline in insect biodiversity across the planet (Cardoso *et al.* 2020; Wagner *et al.* 2021a, b). Major changes in the abundance and composition of insect populations increase the risk of losing vital insect-mediated ecosystem services, including pollination, decomposition, and pest control (Kremen *et al.* 2007), and the potential for collapse of some ecological networks (Dunne *et al.* 2002; Memmott *et al.* 2004; Grames *et al.* 2023). Although the list of potential agents driving insect decline is multifaceted , climate change has been put forth as a major contributor [(Wagner *et al.* 2021b)](https://www.zotero.org/google-docs/?8BW3yT). As ectotherms, insects are especially sensitive to both local and macroscale climatic conditions (Deutsch *et al.* 2008). Among insects, butterflies have by far the densest distribution and natural history data due to their high public profile and apparency in nature. Numerous foundational studies in global change biology have used butterflies to better understand how life history, ecological traits, and species interactions may drive responses to novel climatic conditions [(Parmesan *et al.* 1999; Poyry *et al.* 2009; Breed *et al.* 2013)](https://www.zotero.org/google-docs/?vZFL5N) .

Surface-level temperatures have risen more drastically in high-latitude regions than anywhere else (Holland & Bitz 2003), a trend that is expected to continue under nearly all climate change forecasts (ref). Under current, “business-as-usual” carbon-dioxide emission scenarios, surface temperatures are projected to increase in the Arctic by an average of 10° Celsius through 2100, roughly four times greater than other global regions (You *et al.* 2021). Further, this will likely result in rainier rather than snowy winters across polar region (Bintanja & Andry 2017; McCrystall *et al.* 2021). For butterflies in high-latitude regions to persist under such drastically shifting climatic conditions, they must be able to either move to where conditions are favorable, adapt to novel climates *in situ* or face significant risk of population declines (Corlett & Westcott 2013; Kellermann & van Heerwaarden 2019). The rapid climatic changes in this region and the potential for significant barriers to movement contribute to a high degree of “climate debt” for butterflies (Lewthwaite *et al.* 2018) or an increase in the disparity between current species ranges and the range shifts required to track climatic niche space under future climate change scenarios.

Despite the magnitude of change happening in high-latitude regions North American boreal and Arctic regions remain critically under sampled for butterflies, and available data are highly biased [(Shirey *et al.* 2021)](https://www.zotero.org/google-docs/?9tXWmg). These sampling gaps are major impediments to conservation, especially for invertebrates [(Cardoso *et al.* 2011)](https://www.zotero.org/google-docs/?CUS0Ah) . Data that do exist in this region come largely from natural history museum collections and community science platforms (such as records from online and mobile platforms like iNaturalist) and are almost all opportunistic “presence-only” (PO?) (hereafter, presence only). Presence-only data rarely reflect complete community sampling and may not capture all species in a broader community (Kelling *et al.* 2019). For example, collectors/observers may more often record species of particular interest or more detectable or a site may only have been ever visited one time while, cryptic, drab species may go under-reported (Meyer *et al.* 2016; Adamo *et al.* 2021). Finally, these data are highly biased because sampling intent are both unknown and unknowable. Uncorrected or mishandled biases in downstream analyses can cause problems when attempting to reconstruct ecological trends over large spatial extents and through time [(Guzman *et al.* 2021; Larsen & Shirey 2021)](https://www.zotero.org/google-docs/?oabnuy).

Fortunately, new advances in statistical modeling may be able to address this bias and unlock the potential of these data for broader research use. For example, occupancy-detection models, which are designed (MacKenzie *et al.* 2002; Kéry & Royle 2015) have long been used to reconstruct ecological signals over space and time from presence-absence or, more accurately, detection-non detection data, where sites were repeated visited and patterns in the series of detections and non-detections were used to disentangle the process of observation from underlying ecology (van Strien *et al.* 2013; Jönsson *et al.* 2021; Engelhardt *et al.* 2022; Jackson *et al.* 2022; Shirey *et al.* 2022a). Further, both simulation (Strayer 1999,Gaston et al., Kery and Royle book) and field studies ( ) have shown that detection-non detection data provide similar trends to surveys that document abundances (but see Dennis et al., 2019. This recent innovation that provides a pathway to use occupancy-detection models, especially in large regions with sparse, presence-only sampling is multiple, hierarchical spatial and temporal binning of data along with tests of community samples to build data sets that infer repeated sampling which are at the core of occupancy-detection models (Shirey et al., 2022).

Here, we used an occupancy-detection approach to account for a complex and undocumented detection process to reconstruct patterns of change in North America above 450 latitude over a 50-year period (1970-2019). Specifically, we examined the influence of changes in minimum temperature on species-specific occupancy patterns through space and time. Following prior work, we hypothesized that warm-associated species are likely faring, on average, better than their cold-associated counterparts as warmer winters support enhanced population establishment (Crozier 2003, 2004). In contrast, cold-adapted species may suffer if warm events lead to stress during or early termination of diapause followed by exposure to typical winter lows (Abarca *et al.* 2019; Klockmann & Fischer 2019). We split our modeled occupancy trends into three distinct spatial contexts per species: the southernmost locations, core/mid-latitude locations, and northernmost locations to provide additional information about range shifts in each of these regions of species’ ranges. Finally, we also aimed to test how key species’ traits such as affinity for disturbed habitats, wingspan, host plant breadth, overwintering life-stage, along with phylogeny predict overall occupancy shifts in a *post-hoc* analysis.

**2. METHODOLOGY**

The use of presence-only biodiversity data to reconstruct trends in communities presents several methodological challenges including unknown sample effort and intent, and often significant spatiotemporal and taxonomic biases (Troudet *et al.* 2017; Shirey *et al.* 2021; Bowler *et al.* 2022). Recently, much attention has been paid to developing better ways to analyze these data with recognition of their limitations (Ries *et al.* 2019; Guzman *et al.* 2021; Larsen & Shirey 2021; Belitz *et al.* 2022; Jackson *et al.* 2022; Larsen *et al.* 2022; Shirey *et al.* 2022a). Occupancy-detection models have emerged as one modeling approach that can be used to disentangle the process of observation from the underlying ecology (MacKenzie *et al.* 2002; van Strien *et al.* 2013; Kéry & Royle 2015). Further, multi-species occupancy models can be used to leverage community definitions of parameter values to model multiple species at the same time (Dorazio & Royle 2005). In a recent simulation study, these models have demonstrated the ability to accurately reconstruct ecological trends from presence-only datasets that meet certain pre-qualifying conditions (Shirey *et al.* 2022a).

To implement occupancy-detection models for this study, we established grids of 100×100 and 200×200-kilometer square cells across our study region to determine if the spatial grain of our study impacted our results. We set our analysis to the 50 years between 1970 and 2019 and divided this period into ten, five-year-long intervals. Previous simulation results found that five temporal bins were found to provide sufficient granularity to detect trends, while two time periods, a common method in these studies, often produced poor results (Shirey et al., 2022). In each of these periods we estimated the probability that a given species is an occupant of a specific grid cell. These “occupancy intervals” were further broken down into five one-year-long “visit intervals” to provide a basis for separate estimation of detection and occupancy, which requires tracking multiple visits as repeated trials within the larger occupancy interval (MacKenzie *et al.* 2002). A graphical representation of our workflow with details about our methods of inferring zeros is illustrated in Supplemental Figure 1.

***2.1 Species Occurrence, Range, Trait, and Phylogenetic Data***

First, species occurrence data were needed to infer detection/non-detection datasets across the 50 years of the study. Second, species range data were needed to constrain the analysis to regions where each species could plausibly occur. We also used range data to extract climatic traits for each species (e.g., average, range-wide temperature/precipitation). Along with this derived climatic trait data, we aggregated other ecological traits including wingspan, host plant family breadth, and disturbance affinity to test how these traits may predict declines/increases from the LepTraits database (Shirey et al., 2022). Finally, to test for a phylogenetic signal in species-specific trends over time, we required the phylogeny of the species in the region.

Species occurrence data for all butterflies above 45N from 1970 to 2019 were obtained from the Global Biodiversity Information Facility (GBIF)(GBIF.org 2022), Integrated Digitized Biocollections (iDigBio), and the Symbiota Collections of Arthropods Network (SCAN) (Heinrich *et al.* 2015) based on a list of species known to occur in high latitude regions. All extracted data are available in – supplementary material (?) . Duplicate records were filtered out. We removed records with exceptionally low coordinate precision (greater than 25 kilometers of a reported uncertainty radius). We reconciled the taxonomic names using the R package “taxize” (Scott Chamberlain & Eduard Szocs 2013) and, for non-matches, we resolved the taxonomy by hand where tractable (e.g. by matching unresolved synonymies to currently accepted names). We used the Lamas taxonomy as a backbone (Lamas 2015) and removed species where taxonomic ambiguity would lead to issues with species’ range assessments. We then limited our analysis to include only species with at least 500 reported occurrences across the spatiotemporal scope of our study. Finally, we removed all species from the analysis that are known migrants (*i.e.,* are not historically known to overwinter anywhere north of 45° in North America).

Species range map data were derived from published field guides on North American butterfly species, including The Kaufman Field Guide to Butterflies of North America (Brock & Kaufman 2006) and A Swift Guide to Butterflies of Mexico and Central America (Glassberg 2018). The range maps were digitized as part of work by Earl et al. (2021) and were re-used here. Range-wide average annual temperature/precipitation traits were extracted from each species’ range averaging conditions over each polygon using the BioClimI dataset (representing average climatic conditions from 1970-2000) [(Fick & Hijmans, 2017)](https://www.zotero.org/google-docs/?o92OvI). We also calculated the total area of the North American range for each species. To obtain information regarding wingspan, host plant breadth, and disturbance affinity, we obtained trait data for each species from LepTraits (Shirey *et al.* 2022b). The traits we obtained included disturbance affinity/avoidance, the number of host plant families the caterpillar can feed on, the average wingspan, and the overwintering life-stage of each species. Thus, the final dataset of butterfly traits consisted of range-wide average annual temperature, range-wide average annual precipitation, geographic range size, disturbance affinity/avoidance, host plant family breadth, average wingspan, and overwintering stage. Finally, we obtained a recently produced phylogeny (Earl *et al.* 2021) of North American butterfly species as a final data product to be used in our *post hoc* analysis of occupancy trends. We used this phylogeny to test for phylogenetic signal in our modeled occupancy results.

***2.2 Climate Data***

We used minimum temperatures and precipitation climate data to inform the ecological process of our occupancy-detection model. Land use is also a strong contributor to the occupancy of butterflies across our study region, but to our knowledge, no comprehensive dataset of land cover exists for high-latitude regions of North America extending back into the 1970s or from even more recent time periods that would allow for our 5-year temporal grain. Thus, we opted to inform our models solely with climatic predictors.

Monthly minimum temperatures from 1970 to 2015 were extracted from the National Oceanic and Atmospheric Administration's (NOAA) 20th-century reanalysis, 20CRv3 (Slivinski *et al.* 2019). These data are available at 0.1-degree spatial and monthly temporal resolution from 1836 to 2015. Since NOAA data were not yet available for 2016 onward, variables for these years were obtained from the Climate Prediction Center (CPC) (Climate Prediction Center 2022). These data are available at 0.5-degree spatial and monthly temporal resolution. Monthly data were extracted from the Climate Research Unit (CRU) TS4.04 global precipitation dataset (Harris *et al.* 2020a, b). The CRU data are available at \_\_\_ spatial resolution back to 1900. . Minimum average temperatures increased over the vast majority of our study range, up to 4C over the 50 year period (Fig. 1a) while precipitation (brief summary) (Supplementary Fig. ? – or see supplementary figs – but a fig in the supplements would be nice if not already there).

Climate raster data reflecting monthly average minimum temperature and monthly precipitation for the years 1970 through 2019 were read into R using the package “raster” (Hijmans *et al.* 2015). The raster data were then reprojected to the project coordinate reference system (North America Albers Equal Area Conic) also used as the base projection for all other spatial data in this analysis. The raster data were further summarized within each grid cells using the mean value of all raster values within a given occupancy interval weighted by their coverage of the cell. Thus, average minimum temperature and average precipitation reflect the area-weighted mean of a given five-year occupancy interval (e.g., 1970-1974). Finally, exploration of our climate data revealed that average minimum temperature and average precipitation were highly correlated (Pearson’s r = 0.67 for the 100×100-kilometer scale and Pearson’s r = 0.73 for the 200×200-kilometer scale), thus we opted to include a single climate predictor, average minimum temperature, in our main models. We decided on temperature over precipitation as prior research has demonstrated temperature to be especially important for range dynamics in butterflies (Keret *et al.* 2020). We also ran precipitation-only models and include those results in the Supplementary Material

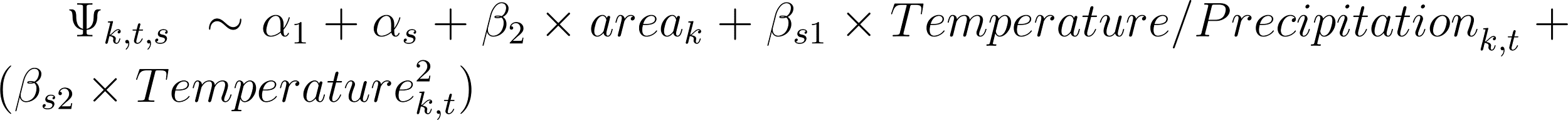
***2.3 Inferring Detection from Presence-only Observations***

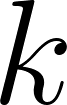
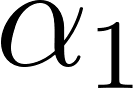
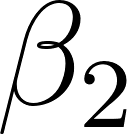
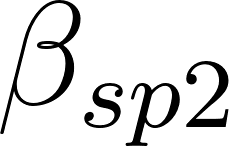
Occupancy-detection models use detection/non-detection data to reconstruct occupancy trends (MacKenzie *et al.* 2002; Kéry & Royle 2015). This poses methodological challenges regarding when it is appropriate to infer non-detections from presence-only data. Our methods for imputing non-detection is adapted in Supplement 1 from Shirey et al. (2022). We assume, for this study, fthat the detection of at least two distinct species in a given cell/visit Iinterval is enough to impute non-detection data for all other species that could potentially occur at that grid cell (*i.e.,* their range plus a 100-kilometer buffer intersects the cell) (Supplemental Figure S1). Both simulation and empirical studies have relied on this assumption and, in particular, simulation studies show that such an approach generates results that match simulated trends (Shirey et al., 2021 – any others that did something similar?). Further, these simulations also demonstrate that occupancy-detection models are robust to violations of this assumption (e.g. an inferred non-detection came from a location/time period where not all species were looked for), but generally, at least half of all sampling events should have intended to capture the entire community of species in order to produce accurate inferences (Shirey *et al.* 2022a).

To proxy this probability of community-focused sampling events (events where all potentially occurring species were looked for) in our dataset, we spatiotemporally aggregated all of our occurrence data at the point level. The occurrence records must have been collected during the same year and must also have been collected/observed within 5 kilometers of one another to be included in an aggregate cluster. We then used the number of species in these spatiotemporal aggregations as a means to classify clusters. “Community clusters” were point aggregate clusters where more than one distinct species was reported; “singleton clusters” were point clusters or single points where only one species was reported. We took the percentage of points that fell within community clusters compared to the entire occurrence dataset as the proxy of community-focused visitation probability. This percentage was 69.64% and which was above a 50% found to be a sufficient cutoff in simulation studies (Shirey et al., 2021).

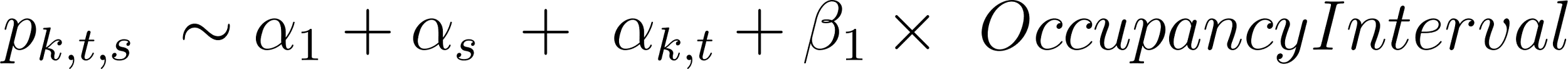
***2.4 Occupancy-detection Modeling***

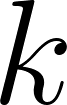
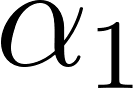
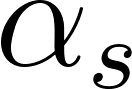
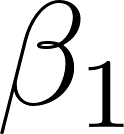
We specified a model that was used across all detection/non-detection datasets described above. For the occupancy subcomponent of our model, we included two environmental predictors of occupancy, average minimum temperature (or average precipitation) across a 5-year-long period (e.g., 1970-1974, as species-specific slopes), and the terrestrial surface area of the grid cell (to account for cells along coastlines or with other large bodies of water). We also included a species-specific intercept in our model to account for differences in baseline occupancy among species. Thus, the occupancy component of our model is:

[](https://www.codecogs.com/eqnedit.php?latex=%5Cmathrm%7B%5CPsi%7D_%7Bk%2Ct%2Cs%7D%5C%20%5Csim%20%5Calpha_1%2B%5Calpha_%7Bs%7D%2B%5Cbeta_2%5Ctimes%7Barea%7D_k%2B%5Cbeta_%7Bs1%7D%5Ctimes%7BTemperature%2FPrecipitation%7D_%7Bk%2Ct%7D%2B(%5Cbeta_%7Bs2%7D%5Ctimes%7BTemperature%7D_%7Bk%2Ct%7D%5E2)#0)

where [](https://www.codecogs.com/eqnedit.php?latex=%7B%5CPsi%7D_%7Bk%2Ct%2Cs%7D#0) is the probability that a given species, [](https://www.codecogs.com/eqnedit.php?latex=s#0), is an occupant of cell [](https://www.codecogs.com/eqnedit.php?latex=k#0) in occupancy interval [](https://www.codecogs.com/eqnedit.php?latex=t#0); [](https://www.codecogs.com/eqnedit.php?latex=%5Calpha_1#0) is the mean occupancy probability for butterflies (on a linear scale); [](https://www.codecogs.com/eqnedit.php?latex=%5Calpha_%7Bsp%7D#0) is a species-specific intercept; [](https://www.codecogs.com/eqnedit.php?latex=%5Cbeta_2#0) is the effect of terrestrial surface area on occupancy probability; and [](https://www.codecogs.com/eqnedit.php?latex=%5Cbeta_%7Bsp1%7D#0) is the species-specific effect (slope) of minimum temperature/precipitation on occupancy. The parameter [](https://www.codecogs.com/eqnedit.php?latex=%5Cbeta_%7Bsp2%7D#0) is only estimated in the temperature model to estimate the potential quadratic effect of minimum temperature on occupancy probability. For all parameters, we assumed the values were to be drawn from normal distributions with a mean of zero and a variance that was estimated at the parameter level from a uniform distribution.

The detection component of our model was informed by a random-effects structure which included an average intercept value estimated across all grid cell, occupancy interval, and species combinations, a fixed-effect of occupancy interval on detection (to account for potentially increasing detectability due to modern survey methods and digital platforms such as iNaturalist), and two random intercepts that varies by (a) species and (b) cell by occupancy interval. Mathematically, our detection component is defined as:

[](https://www.codecogs.com/eqnedit.php?latex=p_%7Bk%2Ct%2Cs%7D%5C%20%5Csim%20%5Calpha_1%2B%5Calpha_s%5C%20%2B%5C%20%5Calpha_%7Bk%2Ct%7D%2B%5Cbeta_1%5Ctimes%5C%20Occupancy%20Interval#0)

where [](https://www.codecogs.com/eqnedit.php?latex=p_%7Bk%2Ct%2Cs%7D#0) is the detection probability of a given species, [](https://www.codecogs.com/eqnedit.php?latex=s#0), during a given occupancy interval, [](https://www.codecogs.com/eqnedit.php?latex=t#0), at a particular cell, [](https://www.codecogs.com/eqnedit.php?latex=k#0); the parameter [](https://www.codecogs.com/eqnedit.php?latex=%5Calpha_1#0) is the mean detection probability for all butterflies (on a linear scale); [](https://www.codecogs.com/eqnedit.php?latex=%5Calpha_s#0) is a random species-specific intercept; [](https://www.codecogs.com/eqnedit.php?latex=%5Calpha_%7Bk%2Ct%7D#0) is a cell by occupancy interval random intercept; and [](https://www.codecogs.com/eqnedit.php?latex=%5Cbeta_1#0) is the effect of occupancy interval (OI) on detection probability. For all parameters, we assumed the values were to be drawn from normal distributions with a mean of zero and a variance that was estimated at the parameter level. Finally, the likelihood in our model was defined by the product of the latent occupancy state (either present or absent per a Bernoulli draw of the calculated occupancy probability [](https://www.codecogs.com/eqnedit.php?latex=%7B%5CPsi%7D_%7Bk%2Ct%2Cs%7D#0)) and the probability of detection, [](https://www.codecogs.com/eqnedit.php?latex=p_%7Bk%2Ct%2Cs%7D#0).

We ran our occupancy models using JAGS (Plummer 2003) on each detection/non-detection dataset for 150,000 iterations, 50,000 of which were discarded as “burn-in,” sampling every 100 iterations across four chains for a total of 4,000 samples from the posterior distribution. We assessed convergence across these chains by examining both Gelman-Rubin diagnostic values (Gelman & Rubin 1992) (using 1.1 as an upper threshold), and by visually inspecting the trace plots for all parameters (provided in the Supplementary Material). We used the R packages “jagsUI” (Kellner 2021) and “MCMCvis” (Youngflesh 2018) to complete the majority of this work. Visualizations of model performance metrics are included in the Supplemental Material.

***2.5 Post-hoc Trait Analysis***

Species’ traits have been demonstrated to be associated with changes in species’ ranges over time and in the relative risk of decline (Keinath et al., 2017) or extinction (Fagan et al., 2001). We thus conducted two trait-based analyses on our occupancy model output. We examined if average annual range-wide temperature and other traits such as wingspan, host plant family breadth, overwintering life-stage, and disturbance affinity predicted mean occupancy shifts from the 1970s to 2010s.

Our post-hoc models were based on several core hypotheses about what might be the most important predictive variable for a species’ occupancy trend. Our first model, Model A, or an ecological “null” model, is an intercept-only model that assumes occupancy trend is best predicted by a singular mean value across all species. To this model, we added species-specific intercept terms that are correlated by a variance-covariance matrix from our phylogeny. We call is model Model B, or the “null + phylogenetic intercept” model. The following models (Models C-N) follow a similar structure (e.g., with/without phylogenetic intercept terms), but in these cases we select trait(s) that we believe may be especially informative for predicting occupancy trend. In Models C/D we use species range-wide average annual temperature as a predictor operating under the assumption that species with warmer ranges will fare better than those with colder ranges due to increasing minimum temperatures. In Models E/F we use species range size as a predictor operating under the assumption that species with larger ranges will, on average, have larger ecological niches and be able to colonize new habitats/sustain populations more easily in those habitats over time. This hypothesis was born from trends estimated in prior work for many of these species (). In Models G/H we used average wingspan as a predictor operating under the assumption that wingspan is a proxy for dispersal capability and that larger wingspans/dispersal capability will predict occupancy increases (). In Models I/J we used the average number of reported host plant families as a predictor, operating under the assumption that species with greater family-level host plant breadth will be more likely to colonize new habitats/sustain populations due to larger resource availability (). In Models K/L, we used range-wide average annual temperature, overwintering life stage, and the interaction between these two predictors. We included an interaction term here since \_\_\_ (). Finally, in Models M/N, we used all available trait information (described in our data collection phase above). A summary table of these models including the rational for each is included in the Supplemental Material.

After running our models, we then compared them using leave-one-out (LOO) cross-validation in order to select the top candidate model (Vehtari *et al.* 2017). From our LOOIC scores, we calculated the expected log pointwise predictive density (ELPD-LOO) or a measure of predictive accuracy (Vehtari *et al.* 2017). Higher values of this metric are preferred. Phylogenetic signal among occupancy estimates was measured using Pagel’s [](https://www.codecogs.com/eqnedit.php?latex=%5Clambda#0) where values close to zero indicate no phylogenetic signal in the response and values close to one indicate strong correlation with phylogeny (Pagel 1999; Freckleton *et al.* 2002). This work was performed using the R package “brms” which interfaces with Stan (Bürkner 2017). We ran all of our models for 200,000 iterations, discarding 100,000 as “burn-in” and thinning by 50 across four chains for a total of 4,000 samples from the posterior. We assessed convergence by using the Gelman-Rubin diagnostic values and by inspecting trace plots (provided in the Supplementary Material).

**3. RESULTS**

We modeled the response of 90 species of butterfly to changes to temperature from 1970-2019 and x percent showed a trend (defined here by the credible intervals not overlapping zero) . Overall, occupancy probability increased with increasing minimum temperature across all species (Fig. 2). Not surprisingly, warm-adapted species showed the greatest increase with rises in minimum temperature and cold adapted species showed acute declines (Fig. 2). However, model results also showed an unexpected reversal in trend when temperatures increased (Fig. 2), although confidence was much lower for that pattern (Fig. 2).Notably, several cold-adapted species exhibit average occupancy declines across their modeled ranges including *Boloria freija* (BOLFRE, -7.5% in mid-latitude sites), *B. chariclea* (BOLCHA, -6.8% in mid-latitude sites), *Boloria eunomia* (BOLEUN, -5.9% in mid-latitude sites), and *Agriades glandon* (AGRGLA, -3.1% in mid-latitude sites). In contrast, warm-adapted/southern species have, in general, exhibited occupancy mean stability or increases alongside rising minimum temperatures (Figure 3). For example, the species, *Pieris rapae* (PIERAP), *Pterourus rutulus* (PTERUT) and *Cercyonis pegala* (CERPEG) have all exhibited average occupancy increases of roughly 4% or greater across all geographic components of their modeled range. Several species for which occupancy trends appear to marginally increase/decrease or that have remained relatively stable compared to the 1970s include *Coenonympha tullia* (COETUL) and *Glaucopsyche lygdamus* (GLALYG).

In sum, we find trends at the northern third of each species’ model range are generally more positive than trends at the southern third (average northern occupancy shifts are greater than southern shifts for 60 species compared to 29 species where average southern occupancy shifts are greater than those in the northern subcomponent of their range). Due to the very small number of sites modeled for *P. glaucus*, a comparison could not be made between northern and southern sites. A full account of average occupancy shifts as well as maps reproducing the shifts from the 1970s for each species are included in the supplementary material for all models.

Our top candidate model for the relationship between phylogeny, species’ traits and occupancy trend was the model that used species’ range-wide temperature as a predictor (Model C/D). In many cases, according to LOOIC, Model C and Model D (a model that included species’ range-wide temperature and a phylogenetic intercept term) were equivalent (Supplemental Table S2-4). Our analysis of LOOIC scores in the southernmost context of species’ ranges revealed that Model C was equivalent to Model A (“null” intercept only model), Model B (intercept only model with an additional phylogenetic intercept), Model D, and, to a lesser extent, Model F (a model with additional species traits and a phylogenetic intercept term) (Supplemental Material S4). tThe estimated effect of range-wide temperature on 50-year occupancy trend across geographic subranges becomes stronger with increasing latitude. In other word, species with warmer North American ranges are likely to exhibit more positive occupancy shifts in the northernmost part of their range followed by core/mid-latitude sites and finally by southern sites (Figure 4). Overall, there is a positive association between warmer range and increasing occupancy probability across all geographic contexts.

**4. DISCUSSION**

Our models demonstrate that minimum temperature (and in corollary, precipitation) predicts the overall 50-year occupancy trajectory of butterfly species in our study region. On average, minimum temperatures have increased by an average of 0.86 degrees Celsius between the 1970s and 2010s (Figure 1). Such increases may be related to occupancy via two distinct effects on butterflies. First, elevated minimum temperatures may be detrimental to cold-adapted species as lack of snow cover and/or false phenological cues of winter termination may increase the risk of exposure of diapausing butterflies to harsh winter temperatures and early spring frosts (). Second, elevated minimum temperatures are likely beneficial to more southern-distributed species as previously harsh winters become milder, allowing for northward range expansion (). Indeed, poleward shifts are a commonly noted phenomenon among species elsewhere as they aim to track their thermal optima with a changing climate (). The estimated effect of minimum temperature on species-specific occupancy from our model supports this trend (Figure 2), and as evidenced by cold-associated species generally declining in occupancy as minimum temperatures rise (Figure 3). In contrast, many of the warm-associated species in our study benefit from the same increasing minimum temperatures (Figure 2). Spatially, our results confirm that stronger positive shifts in species occupancy are occurring for a majority of species (n = 60 or roughly 66%) in the northern geographic context of their modeled range.

Our post-hoc analysis of species traits revealed that a species’ range-wide temperature is the best predictor of 50-year occupancy shift across our study region (Model C/D, Figure 4). Additionally, the estimated effect of range-wide temperature in predicting occupancy trend becomes stronger along and south-to-north gradient within a given species’ range. Specifically, species’ that could be considered “warm-adapted” (*i.e.,* have warmer North American ranges) exhibit stronger increases in occupancy in the northernmost geographic component of their modeled range. In contrast to the increasing occupancy of warm-adapted species, cold-adapted butterflies are faring worse and often across all geographic components of their ranges (Figure 3). This result makes sense ecologically and parallels prior studies conducted in Europe where structured monitoring data are more common in boreal and Arctic region (Parmesan *et al.* 1999; Poyry *et al.* 2009). The natural conclusion of the present work as well as past inference suggests that the composition of butterfly communities in high-latitude North America may turnover to reflect more warm-adapted, southern-distributed species in the future.

We expected that other traits would also serve as predictors of occupancy trend in our analysis; however, the top two candidate models (with the exception of the southern geographic model) consistently indicated that a model including range-wide temperature alone was the best model for predicting average occupancy shift. This result may be unsurprising since we modeled occupancy trends based on temperature and that species’ thermal niches are nearly ubiquitous predictors of range shifts across taxa (McMahon & Hays 2006; Scridel *et al.* 2017; Braschler *et al.* 2020). Secondly, a recent review suggests that the ability of traits to predict range shifts may be limited by a multitude of factors including potentially complex, interactive, and potentially non-linear dynamics (Beissinger & Riddell 2021). Thus, at the scale of our analysis, species’ traits may not be good predictors of occupancy outcomes. Further analysis at finer spatiotemporal resolution may reveal more nuanced evidence for the important of species’ traits and life-history in predicting population trends. Experimental designs that aim to test for potentially complex relationships governing species’ responses to increasing temperature, for example, the interplay between hostplant quality and thermal stress, are likely the best way to elucidate these dynamics (Abarca 2019; Abarca *et al.* 2019; Litchman & Thomas 2023).

A full examination of our post-hoc model suite revealed that Model D (a model that included range-wide temperature and phylogenetic intercepts) was equivalent to Model C (discussed above) in the northern and southern geographic contexts (Supplemental Material S2-4). Despite this model scoring on par with Model C, our estimates of Pagel’s from Model D revealed no strong phylogenetic signal in our occupancy trends regardless of geographic context (South = 0.01 [0, 0.05 95% CRI]; Core = 0 [0, 0.01 95% CRI]; North = 0 [0, 0.01 95% CRI]). Despite this, some notable groups do exhibit declines across our study region including members of the genus *Boloria*, *Erebia,* and *Oeneis* (Figure 3, Supplemental Table S1).

While we examined the impacts of climate on species-specific occupancy trends, the importance of changing land-cover/use on boreal and Arctic butterflies cannot be ignored. Butterflies are especially sensitive to habitat type and disturbance as well as the availability of corridors to navigate to new, suitable habitats. In boreal Canada, butterfly abundance and species richness increases along human-made cutlines (Riva *et al.* 2018a). Additionally, increasing frequency and intensity of forest fire in the region may also contribute to both opportunities and challenges for high-latitude butterflies (Girardin & Mudelsee 2008; Hanes *et al.* 2019). Forest fire (of varying severity) may contribute to initial negative butterfly abundance patterns, but over time, butterflies may benefit from the presence of early successional and open canopy habitats (Johansson *et al.* 2020; Mason Jr *et al.* 2021; Ulyshen *et al.* 2022). Further, open canopy areas (including roadsides, smaller cutlines, and trails) may act as corridors for butterfly movement (Haddad 1999; Haddad & Tewksbury 2005; Riva *et al.* 2018b). Low connectivity of habitat/mobility of species can make it more challenging for more southern distributed butterflies to navigate and colonize new habitats as they track their thermal tolerances (Hodgson *et al.* 2012). Limited ability to colonize newly available habitat in this region is the leading hypothesis surrounding why so much climate debt has accrued for butterflies (Lewthwaite *et al.* 2017, 2018).

**5. CONCLUSION**

Global climate change is impacting high-latitude butterfly communities across North America, However, it is important to recognize that not all species are being impacted equally. Our research, in tandem with recent occupancy analyses of other groups demonstrates the importance of understanding how climatic shifts will impact insects on a species-specific level. Further, we show that occupancy-detection models can be used with sparse, presence-only data to extract clear ecological signals over large spatiotemporal scales. As such, occupancy-detection models will be an important tool for ecologists and conservation biologists, especially for hyperdiverse groups like insects, where structured monitoring data are often unavailable. While an overall perspective shows that rising minimum temperatures may benefit butterflies; cold-adapted species typically do not benefit and are likely being forced to the northern periphery of their ranges. Species’ range-wide average annual temperature is the strongest predictor of modeled occupancy trend while other traits did not strongly predict the same trends. Further research on the interplay of traits including the role of intraspecific variation in thermal tolerance, phenological and morphological adaptation, and genetic variation/effective population size are needed to contextualize these broad scale patterns further.

**Conflict of Interests**

The authors declare no conflict of interest in completing this work.

**Data Availability Statement**

The code utilized in this analysis are freely available via GitHub at xxx and via Zenodo at the following DOI: xxx. Model inference can be found on GitHub and also at DataDryad via the following DOI: xxx. Range maps used in this analysis can be made available upon request.

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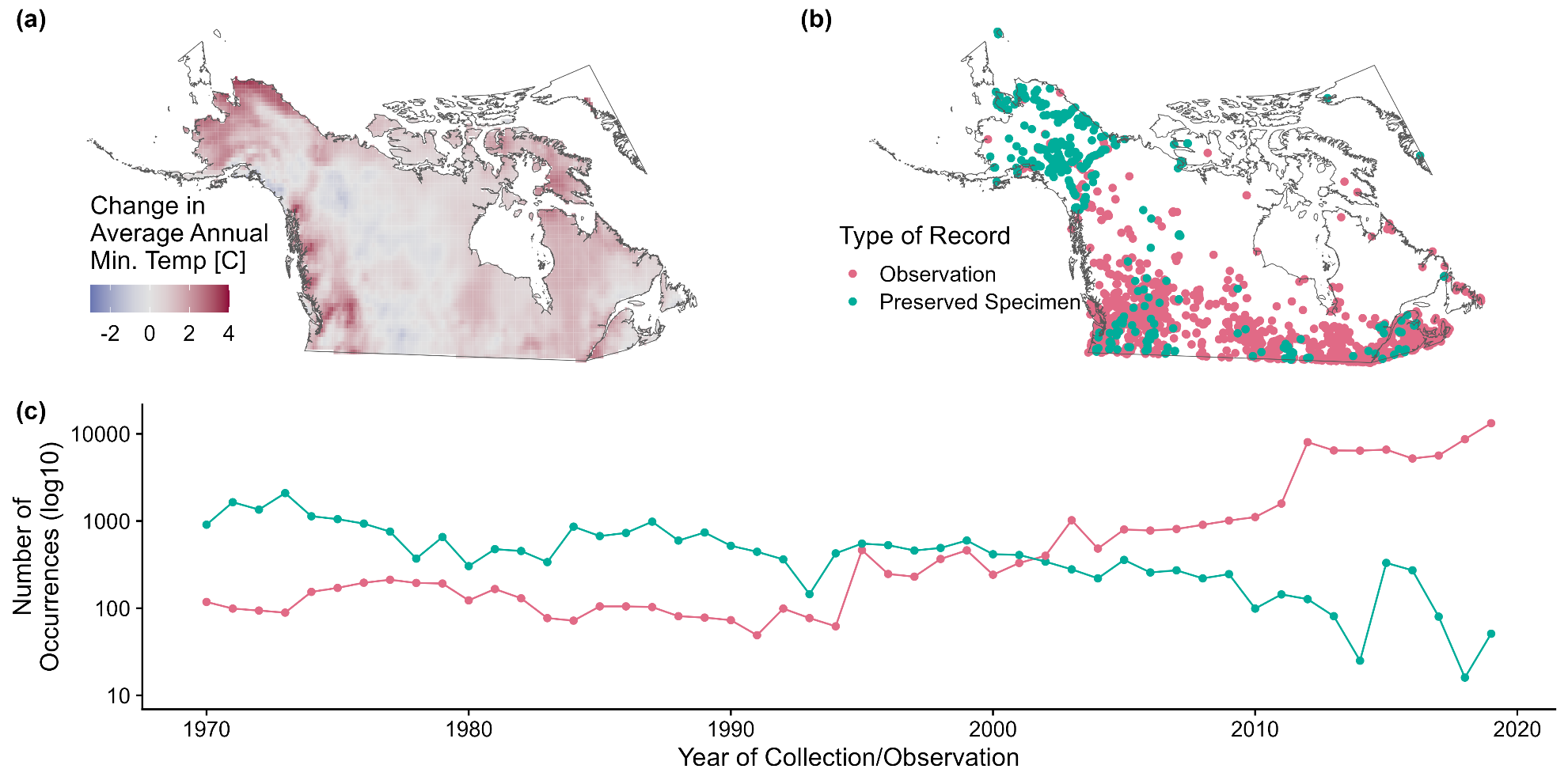
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**FIGURES**

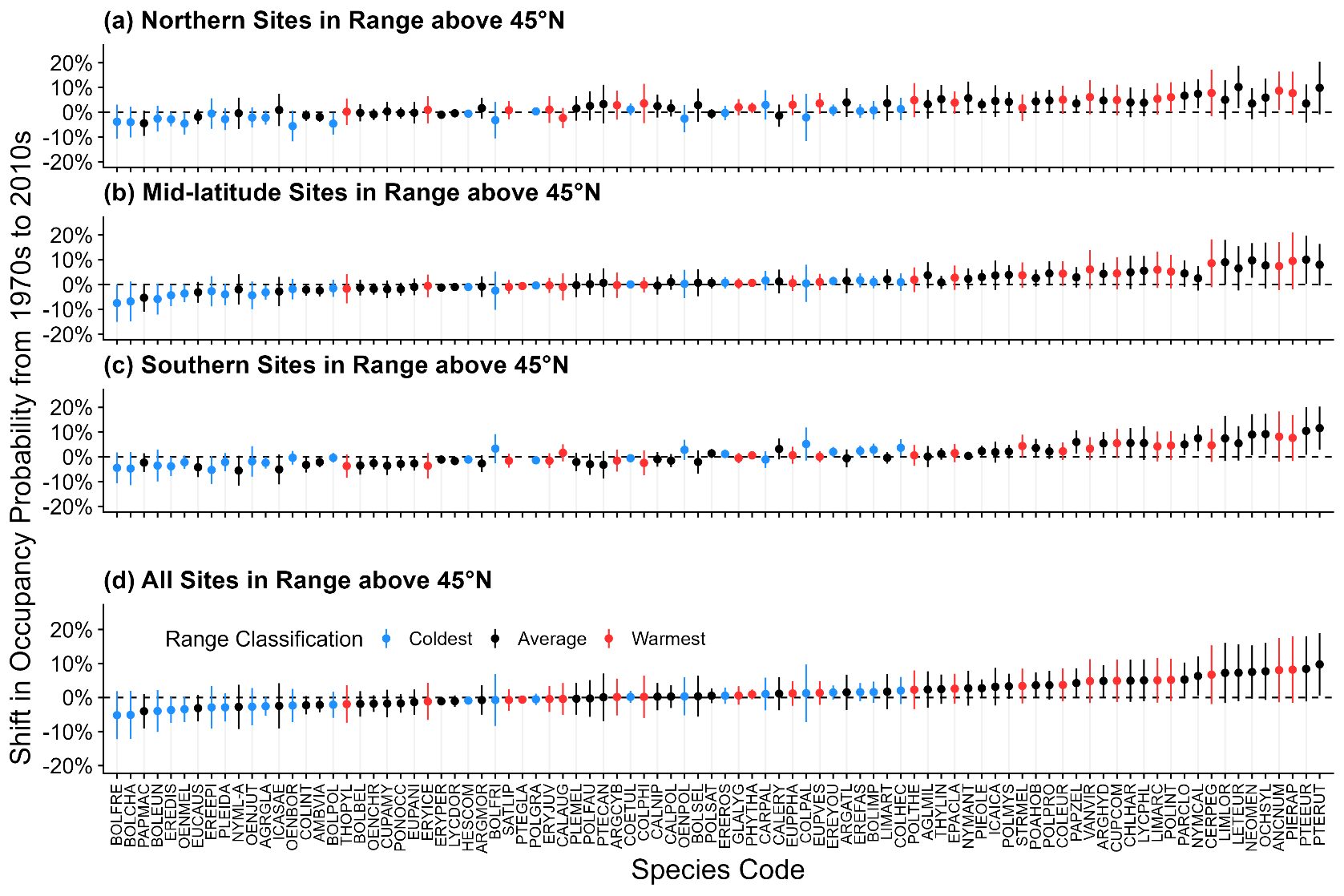


**Figure 1.** An overview of the study region encompassed by our analysis including (a) the change in average annual minimum temperature from the 1970s to 2010s, (b) the spatial distribution of occurrence records from natural history collections and community science platforms, and (c) the number of occurrence records from natural history museum collections and community science platforms by year over the same 50-year timeframe. A random sample of 5,000 of the occurrence records (c) are shown to indicate spatial biase in available records while avoiding overplotting.

Chart

Description automatically generated

**Figure 2.** Species-specific responses to average minimum temperature (faded, grey lines) as well as the response of the butterflies with the coldest quartile of North American ranges (blue, n = 23), warmest quartile of North American ranges (red, n = 23), and middle quartile of species or those species with average range-wide temperatures (grey, n = 44). Species-specific responses are shown only for the range of temperatures that species has experienced within its range (above 45°N) between 1970-2019. All lines are derived from model estimated parameters (linear and quadratic) of species to the average minimum temperature covariate.



**Figure 3.** Species-specific occupancy shifts from the 1970s to 2010s where points indicate the mean occupancy shift and lines indicate one standard deviation of the variation in occupancy shift among (a) the northernmost third of sites within that species’ range in the study region, (b) the mid-latitude third of sites within that species’ range, (c) the southernmost third of sites within that species’ range, and (d) all of the sites within that species’ range (all ranges truncated at 45°N). Species are colored by quartiles of the average annual temperature in their North American ranges (same as in Figure 2).

Chart, scatter chart

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**Figure 4.** The predictive relationship between species’ (a) range-wide average annual temperature and (b) average wingspan and mean occupancy probability shift from the 1970s to 2010s. Shaded regions indicate Bayesian credible intervals while points represent species in our post-hoc analysis.

**SUPPLEMENTAL MATERIAL**

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**Mathematical Definition of Post-hoc Trait Models**

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**Supplemental Table S5.** Model selection for post-hoc 200-km temperature analysis

**Supplemental Table S8.** Model selection for post-hoc 100-km precipitation analysis

**Supplemental Table S11.** Model selection for post-hoc 200-km precipitation analysis

**Supplemental Figure S1.** Graphical illustration of the approach used in this study

**Supplemental Figure S2.** Occupancy trends from the 200km temperature model

**Supplemental Figure S3.** Occupancy trends from the 100km precipitation model

**Supplemental Figure S4.** Occupancy trends from the 200km precipitation model

**Supplemental Figure S5.** Parameter estimates for the 200km temperature post-hoc Model C

**Supplemental Figure S6.** Parameter estimates for the 200km temperature post-hoc Model H

**Supplemental Figure S7.** Parameter estimates for the 100km precipitation post-hoc Model

**Supplemental Figure S8.** Parameter estimates for the 200km precipitation post-hoc Model C.

**ADDITIONAL SUPPLEMENTARY MATERIAL FILES**

**Supplemental File S1:** Trace plots and other model assessment metrics for our 100-kilometer temperature occupancy-detection model.

**Supplemental File S2:** Trace plots and other model assessment metrics for our 200-kilometer temperature occupancy-detection model.

**Supplemental File S3:** Trace plots and other model assessment metrics for our 100-kilometer precipitation occupancy-detection model.

**Supplemental File S4:** Trace plots and other model assessment metrics for our 200-kilometer precipitation occupancy-detection model.

**Supplementary File S5.** Mean occupancy shift maps for species modeled using across all models (denoted by specific .pdf files names for each, default is the 100-kilometer temperature model).

***Mathematical Definitions of Post-hoc Trait and Phylogeny Models***

We specified eight potential models to examine the predictive relationship between species traits, phylogeny and mean occupancy trend. The equations below illustrate the specific models in more detail (*RangePrecip* substituted *RangeTemp* for the precipitation analysis).

|  |  |  |
| --- | --- | --- |
| **Model ID** | **Model Specification** | **Rationale** |
| A  “Null” |  | Ecological “null” model, *i.e.,* all occupancy trends are predicted by an average intercept. |
| B  “Null + Phylo” |  | Model A with a phylogenetic random intercept term, *i.e.,* species occupancy trends are predicted by an average intercept and species-specific, phylogenetic intercept. |
| C  “Temp” |  | Occupancy trends are best predicted by species’ range-wide average annual temperature. Warmer, southern species will exhibit increases in occupancy probability. |
| D  “Temp + Phylo” |  | Occupancy trends are best predicted by species’ range-wide average annual temperature and a species-specific, phylogenetic intercept. Warmer, southern species will exhibit increases in occupancy probability. |
| E  “Range” |  | Occupancy trends are best predicted by species’ range-size. Widely distributed species will exhibit increases in occupancy probability due to wider environmental tolerance. |
| F  “Range + Phylo” |  | Occupancy trends are best predicted by species’ range-size and a species-specific phylogenetic intercept. Widely distributed species will exhibit increases in occupancy probability due to wider environmental tolerance. |
| G  “Size” |  | Occupancy trends are best predicted by species’ average wingspan. Larger species will exhibit increases in occupancy probability due to greater mobility. |
| H  “Size + Phylo” |  | Occupancy trends are best predicted by species’ average wingspan and a species-specific phylogenetic intercept. Larger species will exhibit increases in occupancy probability due to greater mobility. |
| I  “Resource” |  | Occupancy trends are best predicted by species’ family-level host plant breadth. Species with greater host plant breadth will exhibit increases in occupancy probability due to broader resource availability. |
| J  “Resource + Phylo” |  | Occupancy trends are best predicted by species’ family-level host plant breadth and a species-specific phylogenetic intercept. Species with greater host plant breadth will exhibit increases in occupancy probability due to broader resource availability. |
| K  “Overwinter” |  | Occupancy trends are best predicted by range-wide temperature, overwintering life stage, and the interaction between those two factors. Temperature preference and overwintering life stage may contribute to occupancy trend. |
| L  “Overwinter + Phylo” |  | Occupancy trends are best predicted by range-wide temperature, overwintering life stage, the interaction between those two factors and a species-specific, phylogenetic intercept. Temperature preference and overwintering life stage may contribute to occupancy trend. |
| M  “Complex” |  | Occupancy trends are best predicted by a model that includes all available trait information. Many traits predict occupancy trend. |
| N  “Complex + Phylo” |  | Occupancy trends are best predicted by a model that includes all available trait information and a species-specific, phylogenetic intercept. Many traits predict occupancy trend. |

**Supplemental Table S1.** Mean occupancy trend for modeled butterfly species across all occupancy-detection models in this analysis. Occupancy trends reflect the overall average trend at each site +/- one standard deviation of the variance across all sites modeled for that species. Inferences from each model type are denoted by column headers (100T = 100km temperature, 200T = 200km temperature, 100P = 100km precipitation, and 200P = 200km precipitation. Cells are conditionally formatted by the direction and magnitude of decline/increase.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **CODE** | **SCIENTIFIC NAME** | **100T MODEL** | **200T MODEL** | **100P MODEL** | **200P MODEL** |
| AGLMIL | *Aglais milberti* | 2.4% (+/-5.4%) | 2.8% (+/-5.8%) | 0.0% (+/-0.1%) | 0.1% (+/-0.3%) |
| AGRGLA | *Agriades glandon* | -2.5% (+/-2.7%) | -2.2% (+/-2.3%) | -0.2% (+/-0.6%) | -0.1% (+/-0.4%) |
| AMBVIA | *Amblyscirtes vialis* | -2.2% (+/-2.1%) | -0.7% (+/-0.8%) | -0.7% (+/-1.6%) | -0.2% (+/-0.7%) |
| ANCNUM | *Ancyloxypha numitor* | 8.1% (+/-9.5%) | 6.3% (+/-7.7%) | 0.9% (+/-0.8%) | 0.9% (+/-0.9%) |
| ARGATL | *Argynnis atlantis* | 1.5% (+/-5.2%) | 1.8% (+/-6.0%) | -0.1% (+/-0.3%) | 0.1% (+/-0.3%) |
| ARGCYB | *Argynnis cybele* | 0.2% (+/-5.4%) | 0.5% (+/-4.6%) | -0.4% (+/-0.9%) | -0.2% (+/-0.8%) |
| ARGHYD | *Argynnis hydaspe* | 4.9% (+/-4.7%) | 4.2% (+/-4.6%) | 2.3% (+/-1.8%) | 2.5% (+/-2.1%) |
| ARGMOR | *Argynnis mormonia* | -0.7% (+/-4.3%) | 0.0% (+/-3.7%) | -0.6% (+/-0.7%) | -0.4% (+/-0.5%) |
| BORBEL | *Boloria bellona* | -1.9% (+/-3.7%) | -1.2% (+/-3.0%) | -0.9% (+/-3.5%) | -0.3% (+/-2.3%) |
| BOLCHA | *Boloria chariclea* | -5.1% (+/-7.1%) | -3.6% (+/-6.1%) | -0.9% (+/-2.4%) | -0.5% (+/-1.9%) |
| BOLEUN | *Boloria eunomia* | -3.9% (+/-6.1%) | -3.2% (+/-4.8%) | -0.7% (+/-1.9%) | -0.2% (+/-1.3%) |
| BOLFRE | *Boloria freija* | -5.2% (+/-7.1%) | -4.4% (+/-6.3%) | -1.7% (+/-3.7%) | -1.1% (+/-3.4%) |
| BOLFRI | *Boloria frigga* | -0.7% (+/-7.6%) | -1.4% (+/-7.6%) | -1.4% (+/-2.9%) | -0.9% (+/-3.3%) |
| BOLIMP | *Boloria improba* | 1.6% (+/-3.1%) | -1.8% (+/-3.7%) | -2.2% (+/-2.3%) | -1.9% (+/-2.7%) |
| BOLPOL | *Boloria polaris* | -2.1% (+/-3.8%) | -4.4% (+/-5.8%) | -3.0% (+/-3.5%) | -2.0% (+/-4.8%) |
| BOLSEL | *Boloria selene* | 0.4% (+/-6.0%) | 2.1% (+/-6.6%) | 1.1% (+/-2.2%) | 0.5% (+/-1.4%) |
| CALAUG | *Callophrys augustinus* | -0.4% (+/-4.7%) | 0.1% (+/-4.1%) | 0.6% (+/-1.3%) | 0.6% (+/-1.6%) |
| CALERY | *Callophrys eryphon* | 1.1% (+/-4.9%) | 1.3% (+/-4.4%) | 0.3% (+/-0.4%) | 0.2% (+/-0.6%) |
| CALNIP | *Callophrys niphon* | 0.3% (+/-4.0%) | 1.8% (+/-4.0%) | 0.3% (+/-0.3%) | 0.8% (+/-1.2%) |
| CALPOL | *Callophrys polios* | 0.3% (+/-3.4%) | 0.9% (+/-3.9%) | -0.2% (+/-0.5%) | 0.0% (+/-0.2%) |
| CARPAL | *Carterocephalus palaemon* | 1.0% (+/-4.8%) | 1.7% (+/-4.9%) | 0.9% (+/-2.0%) | 0.7% (+/-1.5%) |
| CERPEG | *Cercyonis pegala* | 6.7% (+/-8.6%) | 5.7% (+/-7.2%) | -0.1% (+/-0.3%) | 0.0% (+/-0.2%) |
| CHLHAR | *Chlosyne harrisii* | 4.9% (+/-6.2%) | 4.5% (+/-5.3%) | 2.5% (+/-2.2%) | 2.3% (+/-2.2%) |
| COETUL | *Coenonympha tullia* | 0.2% (+/-1.8%) | 0.9% (+/-3.4%) | 0.0% (+/-0.2%) | 0.0% (+/-0.1%) |
| COLEUR | *Colias eurytheme* | 3.7% (+/-4.8%) | 3.4% (+/-5.1%) | -0.3% (+/-0.9%) | -0.1% (+/-0.8%) |
| COLHEC | *Colias hecla* | 2.1% (+/-4.0%) | -2.2% (+/-5.8%) | -2.8% (+/-3.0%) | -2.4% (+/-3.9%) |
| COLINT | *Colias interior* | -2.3% (+/-2.7%) | -0.8% (+/-4.2%) | -0.5% (+/-1.8%) | -0.1% (+/-0.9%) |
| COLPAL | *Colias palaeno* | 1.3% (+/-8.4%) | 0.0% (+/-6.6%) | -3.0% (+/-5.1%) | -1.2% (+/-3.8%) |
| COLPHI | *Colias philodice* | 0.2% (+/-6.2%) | 1.1% (+/-8.6%) | -0.1% (+/-1.0%) | 0.0% (+/-0.9%) |
| CUPAMY | *Cupido amyntula* | -1.7% (+/-4.0%) | -0.4% (+/-3.5%) | -0.3% (+/-1.1%) | -0.1% (+/-0.5%) |
| CUPCOM | *Cupido comyntas* | 4.9% (+/-6.2%) | 6.3% (+/-8.0%) | 1.5% (+/-1.3%) | 1.0% (+/-0.9%) |
| EPACLA | *Epargyreus clarus* | 2.6% (+/-4.4%) | 1.4% (+/-2.5%) | 0.0% (+/-0.0%) | -0.4% (+/-0.4%) |
| EREDIS | *Erebia discoidalis* | -3.7% (+/-3.8%) | -3.2% (+/-2.9%) | -1.4% (+/-2.5%) | -0.7% (+/-2.0%) |
| EREEPI | *Erebia epipsodea* | -2.9% (+/-6.3%) | -1.8% (+/-6.0%) | -0.6% (+/-1.0%) | -0.3% (+/-0.6%) |
| EREFAS | *Erebia fasciata* | 1.6% (+/-2.7%) | -2.1% (+/-4.8%) | -2.4% (+/-2.5%) | -2.9% (+/-3.2%) |
| EREROS | *Erebia rossii* | 0.6% (+/-2.4%) | 0.1% (+/-4.7%) | -2.6% (+/-2.9%) | -2.5% (+/-3.1%) |
| EREYOU | *Erebia youngi* | 1.5% (+/-2.1%) | -0.1% (+/-2.4%) | -2.4% (+/-2.1%) | -2.5% (+/-2.3%) |
| ERYICE | *Erynnis icelus* | -1.1% (+/-5.4%) | -0.1% (+/-6.0%) | -0.1% (+/-1.6%) | 0.0% (+/-0.6%) |
| ERYJUV | *Erynnis juvenalis* | -0.4% (+/-3.8%) | 0.5% (+/-3.1%) | 0.8% (+/-0.6%) | 0.7% (+/-0.6%) |
| ERYPER | *Erynnis persius* | -1.1% (+/-0.9%) | -0.2% (+/-0.4%) | -0.2% (+/-0.5%) | 0.1% (+/-0.3%) |
| EUCAUS | *Euchloe ausonides* | -3.1% (+/-3.9%) | -2.2% (+/-4.4%) | -1.0% (+/-2.5%) | -0.3% (+/-1.9%) |
| EUPANI | *Euphydryas anicia* | -1.3% (+/-3.7%) | 0.1% (+/-2.8%) | -0.3% (+/-0.2%) | 0.2% (+/-0.2%) |
| EUPPHA | *Euphydryas phaeton* | 1.2% (+/-3.6%) | 2.8% (+/-4.5%) | 2.8% (+/-2.1%) | 3.2% (+/-2.7%) |
| EUPVES | *Euphyes vestris* | 1.4% (+/-3.5%) | 0.4% (+/-2.0%) | 2.5% (+/-3.2%) | 2.4% (+/-3.2%) |
| GLALYG | *Glaucopsyche lygdamus* | 0.6% (+/-2.7%) | 1.2% (+/-3.6%) | 0.1% (+/-0.1%) | 0.1% (+/-0.3%) |
| HESCOM | *Hesperia comma* | -0.9% (+/-0.9%) | -0.1% (+/-0.3%) | 0.1% (+/-0.2%) | 0.2% (+/-1.0%) |
| ICAICA | *Icaricia icarioides* | 3.2% (+/-5.5%) | 2.8% (+/-3.3%) | -0.6% (+/-0.4%) | 0.2% (+/-0.2%) |
| ICASAE | *Icaricia saepiolus* | -2.4% (+/-6.7%) | -1.2% (+/-5.6%) | -0.8% (+/-2.1%) | -0.3% (+/-1.1%) |
| LETEUR | *Lethe eurydice* | 7.3% (+/-8.3%) | 6.7% (+/-7.5%) | 1.6% (+/-1.5%) | 1.4% (+/-1.7%) |
| LIMARC | *Limenitis archippus* | 5.1% (+/-6.6%) | 5.0% (+/-6.3%) | 1.2% (+/-2.2%) | 0.8% (+/-1.9%) |
| LIMART | *Limenitis arthemis* | 1.7% (+/-5.2%) | 2.3% (+/-5.0%) | 0.7% (+/-1.9%) | 0.4% (+/-1.7%) |
| LIMLOR | *Limenitis lorquini* | 7.2% (+/-8.9%) | 7.1% (+/-8.8%) | 3.8% (+/-3.3%) | 3.6% (+/-3.3%) |
| LYCDOR | *Lycaena dorcas* | -1.0% (+/-1.7%) | -0.8% (+/-2.4%) | -0.2% (+/-0.5%) | 0.0% (+/-0.1%) |
| LYCPHL | *Lycaena phlaeas* | 5.1% (+/-6.2%) | 4.2% (+/-5.5%) | 0.9% (+/-1.7%) | 0.6% (+/-2.0%) |
| NEOMEN | *Neophasia menapia* | 7.5% (+/-7.8%) | 6.6% (+/-8.5%) | 3.7% (+/-3.1%) | 3.3% (+/-3.0%) |
| NYMANT | *Nymphalis antiopa* | 2.7% (+/-5.1%) | 2.5% (+/-4.5%) | 1.1% (+/-2.4%) | 0.7% (+/-2.4%) |
| NYMCAL | *Nymphalis californica* | 6.3% (+/-5.7%) | 6.4% (+/-5.6%) | 0.8% (+/-0.5%) | 1.1% (+/-0.8%) |
| NYML-A | *Nymphalis l-album* | -2.7% (+/-6.5%) | -2.5% (+/-6.8%) | -1.0% (+/-2.6%) | -0.4% (+/-1.9%) |
| OCHSYL | *Ochlodes sylvanoides* | 7.7% (+/-8.4%) | 6.4% (+/-7.7%) | 2.5% (+/-2.2%) | 2.6% (+/-2.3%) |
| OENBOR | *Oeneis bore* | -2.3% (+/-4.9%) | -6.4% (+/-7.1%) | -2.7% (+/-3.7%) | -1.2% (+/-4.0%) |
| OENCHR | *Oeneis chryxus* | -1.8% (+/-2.5%) | -0.5% (+/-2.8%) | -0.4% (+/-1.2%) | 0.0% (+/-0.1%) |
| OENJUT | *Oeneis jutta* | -2.7% (+/-5.5%) | -1.9% (+/-3.8%) | -0.5% (+/-1.7%) | -0.1% (+/-0.6%) |
| OENMEL | *Oeneis melissa* | -3.4% (+/-3.7%) | -4.0% (+/-4.3%) | -1.3% (+/-2.1%) | -0.6% (+/-2.1%) |
| OENPOL | *Oeneis polixenes* | 0.3% (+/-5.6%) | -2.8% (+/-5.2%) | -1.3% (+/-2.2%) | -0.5% (+/-1.9%) |
| PAPMAC | *Papilio machaon* | -4.0% (+/-5.1%) | -3.6% (+/-4.1%) | -1.4% (+/-2.9%) | -0.8% (+/-2.9%) |
| PAPZEL | *Papilio zelicaon* | 4.3% (+/-4.3%) | 4.3% (+/-4.1%) | 1.7% (+/-1.6%) | 1.5% (+/-1.3%) |
| PARCLO | *Parnassius clodius* | 5.3% (+/-5.0%) | 6.4% (+/-6.1%) | 2.6% (+/-1.8%) | 1.7% (+/-1.4%) |
| PHYTHA | *Phyciodes tharos* | 0.9% (+/-1.4%) | 0.7% (+/-1.2%) | 0.1% (+/-0.1%) | 0.0% (+/-0.2%) |
| PIEOLE | *Pieris oleracea* | 2.8% (+/-2.6%) | 1.8% (+/-2.0%) | 1.1% (+/-2.2%) | 0.5% (+/-2.0%) |
| PIERAP | *Pieris rapae* | 8.2% (+/-9.7%) | 8.2% (+/-9.1%) | 0.6% (+/-1.2%) | 0.8% (+/-1.9%) |
| PLEIDA | *Plebejus idas* | -2.9% (+/-4.2%) | -1.5% (+/-3.9%) | -0.7% (+/-1.6%) | -0.2% (+/-0.9%) |
| PLEMEL | *Plebejus melissa* | -0.3% (+/-4.7%) | -2.0% (+/-3.4%) | -3.0% (+/-3.1%) | -2.5% (+/-2.4%) |
| POAHOB | *Poanes hobomok* | 3.6% (+/-3.8%) | 3.9% (+/-4.3%) | 2.6% (+/-2.8%) | 2.0% (+/-2.8%) |
| POLMYS | *Polites mystic* | 3.3% (+/-3.7%) | 2.1% (+/-2.8%) | 1.1% (+/-1.8%) | 0.9% (+/-1.8%) |
| POLTHE | *Polites themistocles* | 2.3% (+/-5.7%) | 1.6% (+/-3.8%) | 0.0% (+/-0.3%) | 0.2% (+/-0.3%) |
| POLFAU | *Polygonia faunus* | -0.3% (+/-5.4%) | 0.6% (+/-5.9%) | 0.2% (+/-0.6%) | 0.2% (+/-0.7%) |
| POLGRA | *Polygonia gracilis* | -0.5% (+/-1.7%) | -0.2% (+/-2.2%) | 0.0% (+/-0.1%) | 0.1% (+/-0.3%) |
| POLINT | *Polygonia interrogationis* | 5.2% (+/-6.2%) | 3.4% (+/-4.5%) | 3.1% (+/-3.3%) | 2.4% (+/-2.7%) |
| POLPRO | *Polygonia progne* | 3.6% (+/-4.2%) | 4.2% (+/-5.3%) | 0.4% (+/-0.7%) | 0.3% (+/-0.9%) |
| POLSAT | *Polygonia satyrus* | 0.5% (+/-2.2%) | 1.3% (+/-2.2%) | 0.0% (+/-0.1%) | 0.1% (+/-0.6%) |
| PONOCC | *Pontia occidentalis* | -1.7% (+/-2.8%) | -1.1% (+/-2.5%) | -0.6% (+/-1.7%) | -0.2% (+/-1.2%) |
| PTECAN | *Pterourus canadensis* | 0.1% (+/-7.0%) | 0.8% (+/-7.4%) | 0.5% (+/-1.2%) | 0.2% (+/-0.8%) |
| PTEEUR | *Pterourus eurymedon* | 8.4% (+/-9.6%) | 6.9% (+/-8.5%) | 3.1% (+/-2.5%) | 3.0% (+/-2.6%) |
| PTEGLA | *Pterourus glaucus* | -0.6% (+/-0.6%) | 0.1% (+/-1.2%) | -3.6% (+/-0.8%) | -0.2% (+/-0.4%) |
| PTERUT | *Pterourus rutulus* | 9.7% (+/-9.2%) | 8.3% (+/-9.4%) | 3.4% (+/-3.2%) | 2.8% (+/-2.9%) |
| SATLIP | *Satyrium liparops* | -0.7% (+/-3.2%) | -0.6% (+/-2.8%) | 1.6% (+/-1.5%) | 1.8% (+/-2.0%) |
| STRMEL | *Strymon melinus* | 3.4% (+/-5.1%) | 5.9% (+/-6.1%) | 0.1% (+/-0.1%) | 0.2% (+/-0.3%) |
| THOPYL | *Thorybes pylades* | -1.9% (+/-5.5%) | -2.0% (+/-5.3%) | -0.6% (+/-1.4%) | -0.3% (+/-1.6%) |
| THYLIN | *Thymelicus lineola* | 2.5% (+/-4.3%) | 3.7% (+/-6.5%) | 0.9% (+/-1.0%) | 0.6% (+/-0.9%) |
| VANVIR | *Vanessa virginiensis* | 4.8% (+/-6.4%) | 2.8% (+/-3.9%) | 3.0% (+/-3.3%) | 2.7% (+/-3.2%) |

**Supplemental Table S2.** Model comparison metrics for models predicting average core/mid-latitude occupancy shift since the 1970s. Results are shown for the 100-kilometer scale, temperature analysis. Top candidate model is underlined and in bold. We considered models equivalent if the difference in ELPD +/- the standard error of the ELPD estimate overlapped zero and favored models which used fewer predictors if this was the case.

|  |  |  |  |
| --- | --- | --- | --- |
| **MODEL** | **ELDP-LOO** | **DELTA ELPD** | **SE DELTA ELPD** |
| A | 145.6 | -5.1 | 2.5 |
| B | 147.0 | -3.7 | 3.2 |
| **C** | **150.7** | **0.0** | **0.0** |
| **D** | **150.1** | **-0.6** | **1.5** |
| E | 144.7 | -6.1 | 2.9 |
| F | 145.9 | -4.9 | 3.6 |
| **G** | **147.5** | **-3.3** | **3.8** |
| **H** | **147.1** | **-3.7** | **4.0** |
| I | 144.1 | -6.6 | 2.6 |
| J | 145.6 | -5.1 | 3.3 |
| K | 144.3 | -6.4 | 2.9 |
| L | 145.0 | -5.8 | 2.6 |
| M | 146.0 | -4.7 | 4.3 |
| N | 145.1 | -5.7 | 4.4 |

**Supplemental Table S5.** Model comparison metrics for models predicting average core/mid-latitude occupancy shift since the 1970s. Results are shown for the 200-kilometer scale, temperature analysis. Top candidate model is italic and bold. We considered models equivalent if the difference in ELPD was less than four.

|  |  |  |  |
| --- | --- | --- | --- |
| **MODEL** | **ELDP-LOO** | **DELTA ELPD** | **SE DELTA ELPD** |
| A |  |  |  |
| B |  |  |  |
| C |  |  |  |
| D |  |  |  |
| E |  |  |  |
| F |  |  |  |
| G |  |  |  |
| H |  |  |  |
| I |  |  |  |
| J |  |  |  |
| K |  |  |  |
| L |  |  |  |
| M |  |  |  |
| N |  |  |  |

**Supplemental Table S8.** Model comparison metrics for models predicting average core/mid-latitude occupancy shift since the 1970s. Results are shown for the 100-kilometer scale, precipitation analysis. Top candidate model is italic and bold. We considered models equivalent if the difference in ELPD was less than four.

|  |  |  |  |
| --- | --- | --- | --- |
| **MODEL** | **ELDP-LOO** | **DELTA ELPD** | **SE DELTA ELPD** |
| A |  |  |  |
| B |  |  |  |
| C |  |  |  |
| D |  |  |  |
| E |  |  |  |
| F |  |  |  |
| G |  |  |  |
| H |  |  |  |
| I |  |  |  |
| J |  |  |  |
| K |  |  |  |
| L |  |  |  |
| M |  |  |  |
| N |  |  |  |

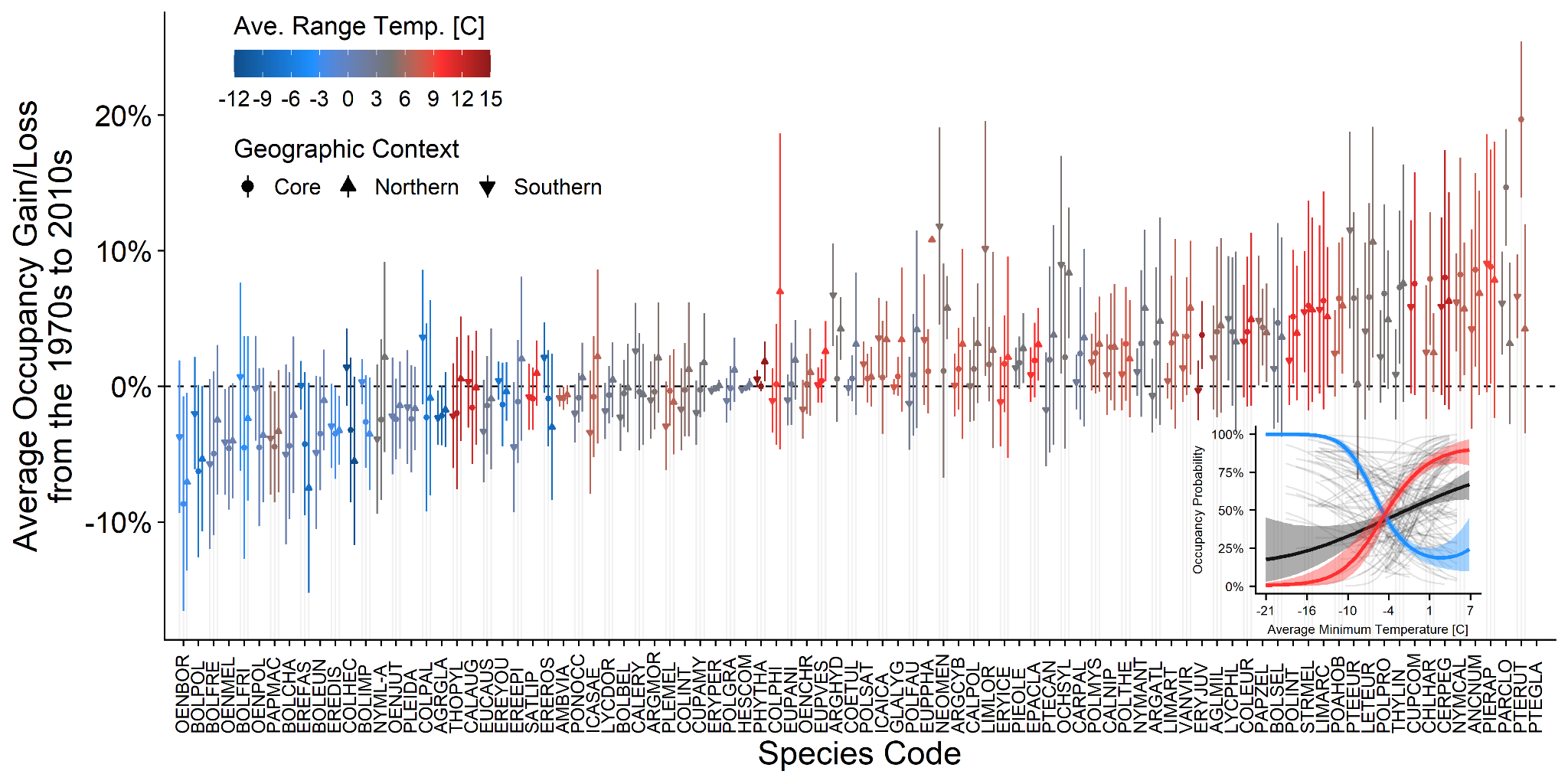
**Supplemental Table S11.** Model comparison metrics for models predicting average core/mid-latitude occupancy shift since the 1970s. Results are shown for the 200-kilometer scale, precipitation analysis. Top candidate model is italic and bold. We considered models equivalent if the difference in ELPD was less than four.

|  |  |  |  |
| --- | --- | --- | --- |
| **MODEL** | **ELDP-LOO** | **DELTA ELPD** | **SE DELTA ELPD** |
| A |  |  |  |
| B |  |  |  |
| C |  |  |  |
| D |  |  |  |
| E |  |  |  |
| F |  |  |  |
| G |  |  |  |
| H |  |  |  |
| I |  |  |  |
| J |  |  |  |
| K |  |  |  |
| L |  |  |  |
| M |  |  |  |
| N |  |  |  |

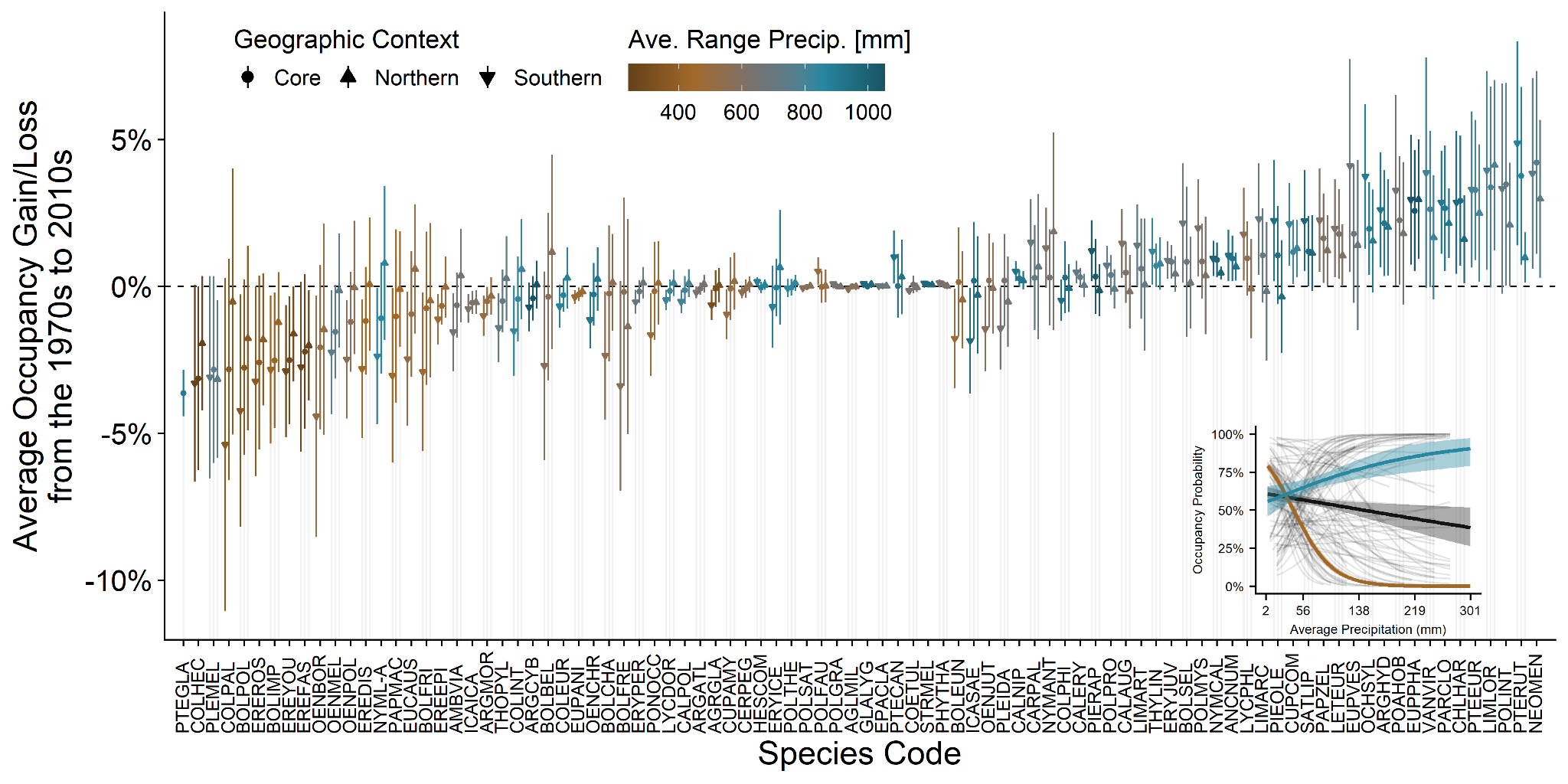
**Graphical user interface, application

Description automatically generated**

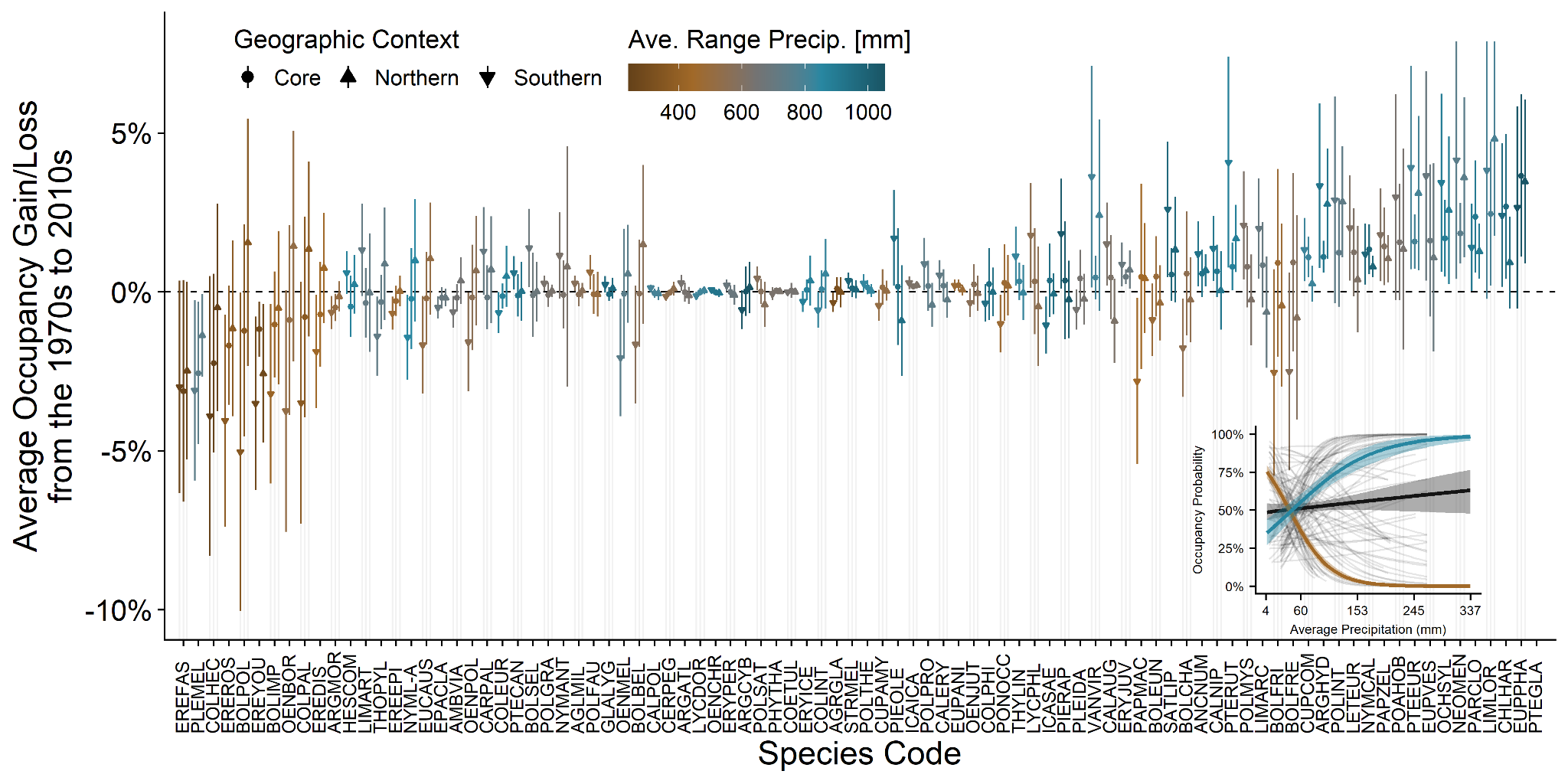
**Supplemental Figure S1.** A summary of the methodological workflow used in this study from data compilation to non-detection imputation and occupancy-detection modeling. The post-hoc analysis using species traits and phylogeny is also visualized.

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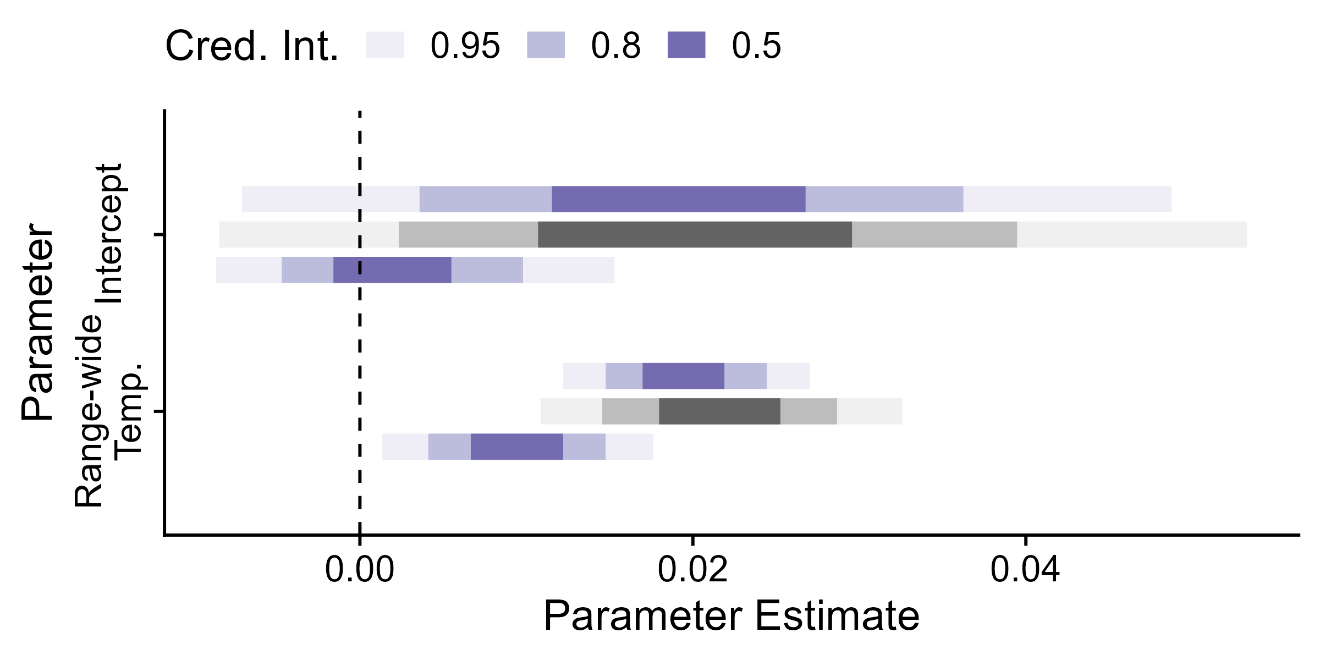
**Supplemental Figure S2.** Species-specific occupancy shifts from the 1970s where points indicate the average occupancy shift for a given geographic context (core/mid-latitude, southern, and northern grid cells) and lines indicate one standard deviation of variation among relevant sites. The inset panel illustrates the relationship between minimum temperature and occupancy probability for each species (thin, grey lines), all butterflies on average (black line), the species with the coldest quarter of ranges (blue line), and the species with the warmest quarter of ranges (red line). Only temperatures that each species has experienced in its range are shown by the species-specific lines. Results shown here are from the 200 kilometer temperature model. Note that there were too few sites to model *Pterourus glaucus* at this scale*.*

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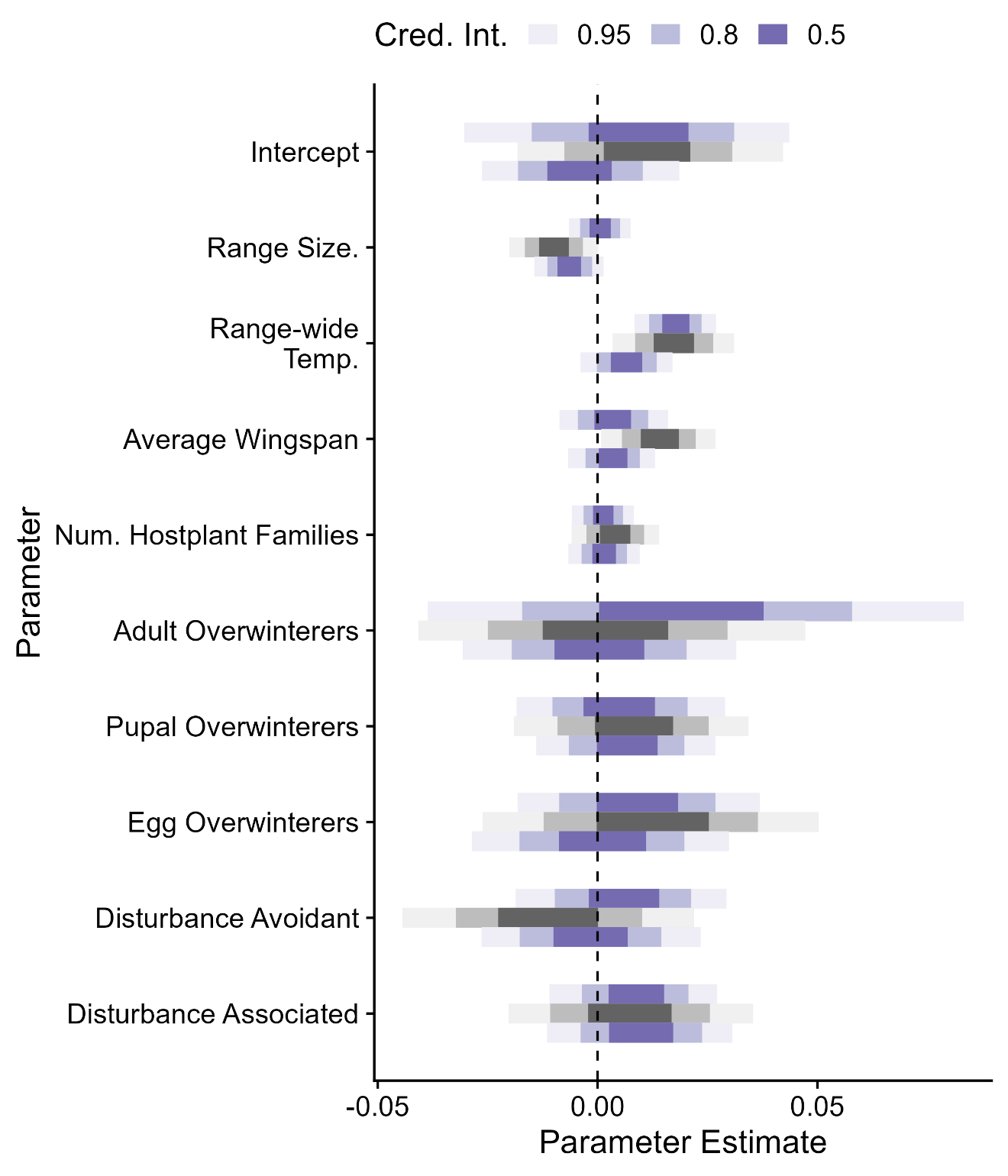
**Supplemental Figure S3.** Species-specific occupancy shifts from the 1970s where points indicate the average occupancy shift for a given geographic context (core/mid-latitude, southern, and northern grid cells) and lines indicate one standard deviation of variation among relevant sites. The inset panel illustrates the relationship between precipitation and occupancy probability for each species (thin, grey lines), all butterflies on average (black line), the species with the wettest quarter of ranges (blue line), and the species with the driest quarter of ranges (brown line). Only precipitation that each species has experienced in its range are shown by the species-specific lines. Results shown here are from the 100 kilometer precipitation model.

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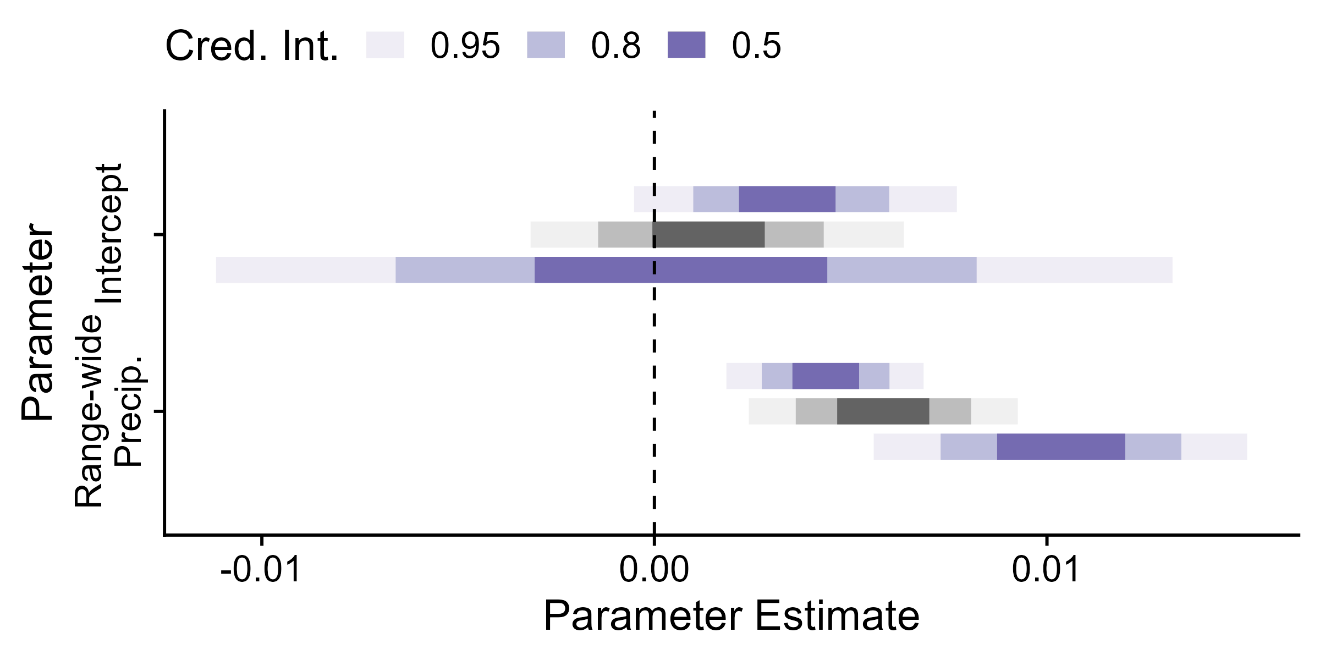
**Supplemental Figure S4.** Species-specific occupancy shifts from the 1970s where points indicate the average occupancy shift for a given geographic context (core/mid-latitude, southern, and northern grid cells) and lines indicate one standard deviation of variation among relevant sites. The inset panel illustrates the relationship between precipitation and occupancy probability for each species (thin, grey lines), all butterflies on average (black line), the species with the wettest quarter of ranges (blue line), and the species with the driest quarter of ranges (red line). Only precipitation that each species has experienced in its range are shown by the species-specific lines. Results shown here are from the 200 kilometer precipitation model.

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**Supplemental Figure 5.** Parameter estimates for model intercept (Model D) and covariate (range-wide temperature) when predicting mean occupancy shift from the 1970s across the three geographic components of each species’ modeled range: lower/purple are parameter estimates for the southernmost part of the species’ range, middle/grey is the core/mid-latitude third of the species’ range, and upper/purple is the northernmost part of the species range. Results are shown here for the 200-kilometer temperature analysis. Pagel’s mean estimates were 0.0 (0.0 – 0.01 95% CRI, South); 0.01 (0.0 – 0.03 95% CRI, Core); and 0.03 (0.0 – 0.13 95% CRI, North).

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**Supplemental Figure S6.** Parameter estimates for model intercept (Model H) and covariate (range-wide temperature) when predicting mean occupancy shift from the 1970s across the three geographic components of each species’ modeled range: lower/purple are parameter estimates for the southernmost part of the species’ range, middle/grey is the core/mid-latitude third of the species’ range, and upper/purple is the northernmost part of the species range. Results are shown here for the 200-kilometer temperature analysis. Pagel’s mean estimates were 0.0 (0.0 – 0.01 95% CRI, South); 0.00 (0.0 – 0.01 95% CRI, Core); and 0.05 (0.0 – 0.22 95% CRI, North).



**Supplemental Figure S7.** Parameter estimates for model intercept (Model D) and covariate (range-wide temperature) when predicting mean occupancy shift from the 1970s across the three geographic components of each species’ modeled range: lower/purple are parameter estimates for the southernmost part of the species’ range, middle/grey is the core/mid-latitude third of the species’ range, and upper/purple is the northernmost part of the species range. Results are shown here for the 100-kilometer precipitation analysis. Pagel’s mean estimates were 0.01 (0.0 – 0.02 95% CRI, South); 0.0 (0.0 – 0.0 95% CRI, Core); and 0.0 (0.0 – 0.01 95% CRI, North).

Chart, timeline

Description automatically generated

**Supplemental Figure S8.** Parameter estimates for model intercept (Model D) and covariate (range-wide temperature) when predicting mean occupancy shift from the 1970s across the three geographic components of each species’ modeled range: lower/purple are parameter estimates for the southernmost part of the species’ range, middle/grey is the core/mid-latitude third of the species’ range, and upper/purple is the northernmost part of the species range. Results are shown here for the 200-kilometer precipitation analysis. Pagel’s mean estimates were 0.01 (0.0 – 0.02 95% CRI, South); 0.0 (0.0 – 0.01 95% CRI, Core); and 0.0 (0.0 – 0.0 95% CRI, North).