USING BIOCLIMATIC INDICATORS TO ANALYSE THE PRESENCE OF CLIMATIC MISMATCHES AMONGST LOCAL AMPHIBIAN ASSEMBLAGES OF AMERICA

USO DE INDICADORES BIOCLIMÁTICOS PARA ANALIZAR LA PRESENCIA DE DESAJUSTES CLIMÁTICOS EN LOS ENSAMBLES LOCALES DE ANFIBIOS EN AMÉRICA

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Received: 2024-01-02. **Accepted**: 2024-11-19. **Published**: 2025-03-13.
Editor: Carlos A. Navas, Brasil.

Resumen.– Las especies se enfrentan de forma constante al aumento de la temperatura en las últimas décadas. Esto conduce a un desequilibrio entre las tolerancias térmicas de las comunidades de especies y la magnitud del calentamiento climático. En los casos donde las especies no logran adaptarse a los cambios climáticos, las comunidades exhiben una respuesta retrasada y, por lo tanto, acumulan una deuda climática. La información actual sobre estos desajustes climáticos se concentra principalmente en las comunidades de plantas, insectos y aves en regiones templadas. Aquí, examinamos la variación del desajuste climático en 80 ensambles de anfibios de la familia Hylidae en todo el continente americano. Para nuestros análisis, calculamos el desajuste climático para cada ensamblaje como la diferencia entre los índices de temperatura de la comunidad (ITC) y las temperaturas históricas promedio tanto para los valores máximos como para los mínimos. Utilizando modelos mixtos lineales generalizados, evaluamos un conjunto potencial de variables predictoras ambientales que impulsan los desajustes climáticos. Las tendencias en las respuestas de los ensamblajes eran visibles y variaban según los sitios. Los valores de desajuste climático negativo se concentran en ensambles en regiones tropicales sugiriendo que en estos sitios las especies pueden enfrentar dificultades para adaptarse a las temperaturas crecientes, por lo tanto, podrían tener intervalos térmicos más bajos. Los ensamblajes en zonas templadas y subtropicales mostraron desajustes climáticos positivos, lo que sugiere un menor riesgo de extinción hasta el momento. Sin embargo, de todas las variables probadas, solo la latitud absoluta, la elevación y la velocidad climática pasada explicaron el desajuste climático para la temperatura mínimo. Estos resultados podrían sugerir que la escala de nuestra investigación fue demasiado gruesa, por lo que sugerimos que se realicen análisis adicionales a escalas regional y local, así como investigación adicional sobre la compleja naturaleza del retraso climático y las variables que dan forma al efecto de las dinámicas de retraso.

Palabras clave.– Anura, cambio climático, conservación, deuda climática, Hylidae.

Abstract.– Species are facing an ongoing struggle to keep up with rising temperatures. This is leading to a disequilibrium between species communities' thermal tolerances and the magnitude of climatic warming. In cases where species fail to adapt to climatic shifts, they exhibit a lagged response and, therefore, accumulate a climatic debt. Current information is primarily focused on plant, insect, and bird communities in temperate regions. Here, we examine the variation of climatic lag amongst 80 amphibian assemblages from the Hylidae family across America. For our analyses, we calculated the climatic lag for each assemblage as the difference between community temperature indices (CTI) and average historical temperatures for both maximum and minimum values. Using generalized linear mixed models, we evaluated a potential set of variables driving climatic debt. Trends in assemblage responses were visible and varied across sites. Higher lag values were concentrated in southern provinces of America, suggesting that assemblages in these areas may face difficulty in adapting to increasing temperatures, hence lower thermal ranges. Tropical assemblages seemed to be adapting quicker, displaying less lag or, in some cases, climatic credit. However, out of all the tested variables, only changes in evenness and heterogeneity may have an impact on lag. These results could suggest that the scale of our investigation was too large, encouraging further analyses at a regional scale as well as additional research into the complex nature of climatic lag and the variables that shape the lag dynamics effect.

Keywords.– Anura, climate change, climatic debt, conservation, Hylidae.

INTRODUCTION

The scientific literature has widely documented the impacts of climate change across different organizational levels, from genes to ecosystems (Scheffers et al., 2016; Pecl et al., 2017). Diverse responses suggest that contemporary climate change does not impact local assemblages equally (Fei et al., 2017). For instance, local assemblages may react in an idiosyncratic fashion, either benefiting from rapid environmental changes or showing an inability for local adaptation (Stewart, 2009; Barbet-Massin & Jetz, 2015; Bonachela et al., 2021). Many studies have documented how local assemblages have responded to increases in temperature during the last century (Antão et al., 2020; Lenoir et al., 2020; Pacheco-Riaño et al., 2023).

Local assemblages may change through different processes, including changes in species composition, relative abundance, population declines, and local extirpation (Devictor et al., 2008; Bonachela et al., 2021). For instance, it has been detected that enhanced temperatures turn warm-adapted species more common in assemblages relative to cool-adapted counterparts (Devictor et al., 2008; Bertrand et al., 2011; Blonder et al., 2017; Bonachela et al., 2021). This phenomenon is known as thermophilization, and it is strongly linked with the observed thermal niche traits of species in each site (Stevens et al., 2015; Govaert et al., 2021; Rosenblad et al., 2023; Borderieux et al., 2024).

The average thermal niche breadth for species in a given locality can be used as a proxy for the community thermal index (CTI), defined as the community-weighted mean of species' temperature preferences (Bowler & Böhning-Gaese, 2017). Therefore, this approach may provide helpful information about how local assemblage matches historical local climate conditions (Blonder et al., 2017; Bonachela et al., 2021; Duchenne et al., 2021). For instance, local communities can exhibit substantial departures from their CTI values in relation to local temperatures, therefore suggesting climatic mismatches. Climatic mismatches are measured as the differences between the average of thermal niche breadths for all species inhabiting a site (CTI) and the historical local climatic conditions (Svenning & Sandel, 2013; Blonder et al., 2017; Bonachela et al., 2021).

When differences in climatic mismatches return negative values, local assemblages may be lagging in response to observed local climatic changes, and species so exposed may face higher extinction risk (i.e., climatic debts). By contrast, positive values indicate that local assemblages are keeping in pace with observed local climatic changes and therefore, the extinction risk may be low (i.e., climatic credit) (Svenning & Sandel, 2013; Sunday et al., 2014; Bonachela et al., 2021). The lagged or climatic debts have been commonly reported in the literature in different taxa (Bertrand et al., 2011; Feeley et al., 2020; Zellweger et al., 2020; Richard et al., 2021; He et al., 2023; Pacheco-Riaño et al., 2023). In general, it has been found that landscape heterogeneity, topographical complexity, past climatic velocity, and the degree of temperature increase can explain relatively well the climatic mismatches of many local assemblages (Devictor et al., 2012; Bertrand et al., 2016; Alexander et al., 2018; Feeley et al., 2020; Zellweger et al., 2020; Pacheco-Riaño et al., 2023).

Understanding the dominant factors underlying climatic mismatches, including species traits, environmental conditions, and past climate dynamics, is crucial in anticipating which local assemblages can be more at risk (He et al., 2023). However, many past studies have focused on a subset of taxa on temperate biomes, so that enhanced understanding is needed about how climatic mismatches emerge in other taxonomic groups and the spatial drivers across tropical and subtropical regions. Recent studies have shown that several species are particularly at risk of ongoing climate warming due to life history traits and narrow ecological requirements (Luedtke et al., 2023). Despite increasing assessments of climate change and its effects on amphibian distribution, only about 4% of the 7,477 species of Anura have been assessed to date (Alves-Ferreira et al., 2022). Some species of amphibians are sensitive indicators of climate repercussions due to their ectotherm condition and link to both terrestrial and aquatic environments (Stuart et al., 2008; Duan et al., 2016). Their highly water-permeable skin means amphibian activity, and migration is vastly dependent on the abiotic factors of their surroundings (Lawler et al., 2010). Physiologically, even minute changes in temperature and moisture may impact negatively amphibians, reinforced by their limited thermal tolerance and restricted dispersal abilities (Smith & Green 2005; Mitchell & Bergmann, 2016). Therefore, this taxon is ideal for investigating whether climatic mismatches may be prevalent amongst local assemblages across different regions (Villaseñor et al., 2017).

Here, we evaluated the presence of climate mismatches within a set of hylid frog communities across the American continent. We used the difference between the community temperature index (CTI) and historical temperature records for each locality to establish whether a local assemblage is lagged or ahead of historical temperature records from 1961-2018. In addition, we tested how different predictor variables, including species traits (e.g., body size), habitat heterogeneity, topography, and past climatic velocity, are associated with climate mismatches across geography. These predictor variables have been used to explain climate mismatches across different taxa and regions (Bertrand et al., 2016; Alexander et al., 2018; Zellweger et al., 2020; Pacheco-Riaño et al., 2023).

MATERIALS AND METHODS

Study area and species

Hylidae is a speciose family of Anura comprising over 1,049 recognized species that are commonly known as treefrogs (Araujo-Vieira et al., 2023).This family is widely distributed across the globe from the Australo-Papuan region to the American continent. The area of interest for our work includes both the Nearctic and Neotropical region, encompassing South and Central America and the Caribbean Islands, which covers a diverse range of habitats, from forest to deserts and montane ecosystems.

Hylidae distribution data

Data on hylid species composition across America was acquired from a compilation created by Wiens et al. (2011) which included literature and museum records from the late 1800s to the early 2000s. We excluded sites with only one species as this was likely due to poor sampling or human impacts. Hence, we have confidence in using their data for our study, selecting 80 sites from the original 123.

Our study used the biogeographic regionalisation of the American continent by Escalante et al. (2021) and Morrone et al. (2022). The selected sites corresponded to 49 different provinces. We compiled the list of all hylid species found at the sites and their species richness. We standardized scientific names to avoid species synonyms, and therefore, species with taxonomic uncertainty were excluded from the analyses (n = 270).

Occurrence species records and estimates of climatic thermal tolerance proxies

We gathered occurrence records from the Global Biodiversity Information Facility website (GBIF; https://doi.org/10.15468/dl.ucqfaw) for each 270 species at the 80 sites. Any essential climatic data such as latitude and longitude, species name, and occurrence ID was extracted. To improve the accuracy of the created dataset, any records outside the designated area or with geographical ambiguity were removed using different R packages (R Core Team, 2024). Resulting in a compilation of 358,864 unique species locality records.

To calculate thermal tolerance for each species, we acquired bioclimatic data from the WorldClim database version 2 (Fick & Hijmans, 2017), which included the maximum temperature of the warmest month (BIO5) and the minimum temperature of the coldest month (BIO6) for all occurrence records. Average values for each temperature variable (mean BIO5 and mean BIO6) were calculated based on all occurrence records for each hylid species, creating a comprehensive dataset with average temperature values for each of the 270 species. The distribution dataset was then filtered to determine which species were present at each of the 80 sites, thus establishing the species assemblages for each one. The complete procedure is schematized in Fig. 1.

Community Temperature Index and Climate Mismatch

The community temperature index (CTI) was calculated by taking an average of maximum temperatures (mean BIO5) and an average of the average minimum temperatures (mean BIO6) for all the hylid species inhabiting each one of the 80 localities previously refined. To examine the presence of climate mismatches across localities, we subtracted the values of minimum and maximum community temperatures (CTI) from the minimum and maximum local historical temperature values. The historical temperature records for 1961-2018 were extracted for each locality from the CRU-TS database (Harris et al., 2020). Climate mismatches with negative values indicated that local assemblages showed lagged responses to historical temperatures (i.e., climate debts), whereas climate mismatches with positive values indicate that local assemblages showed ahead responses to historical temperatures (i.e., climate credits).

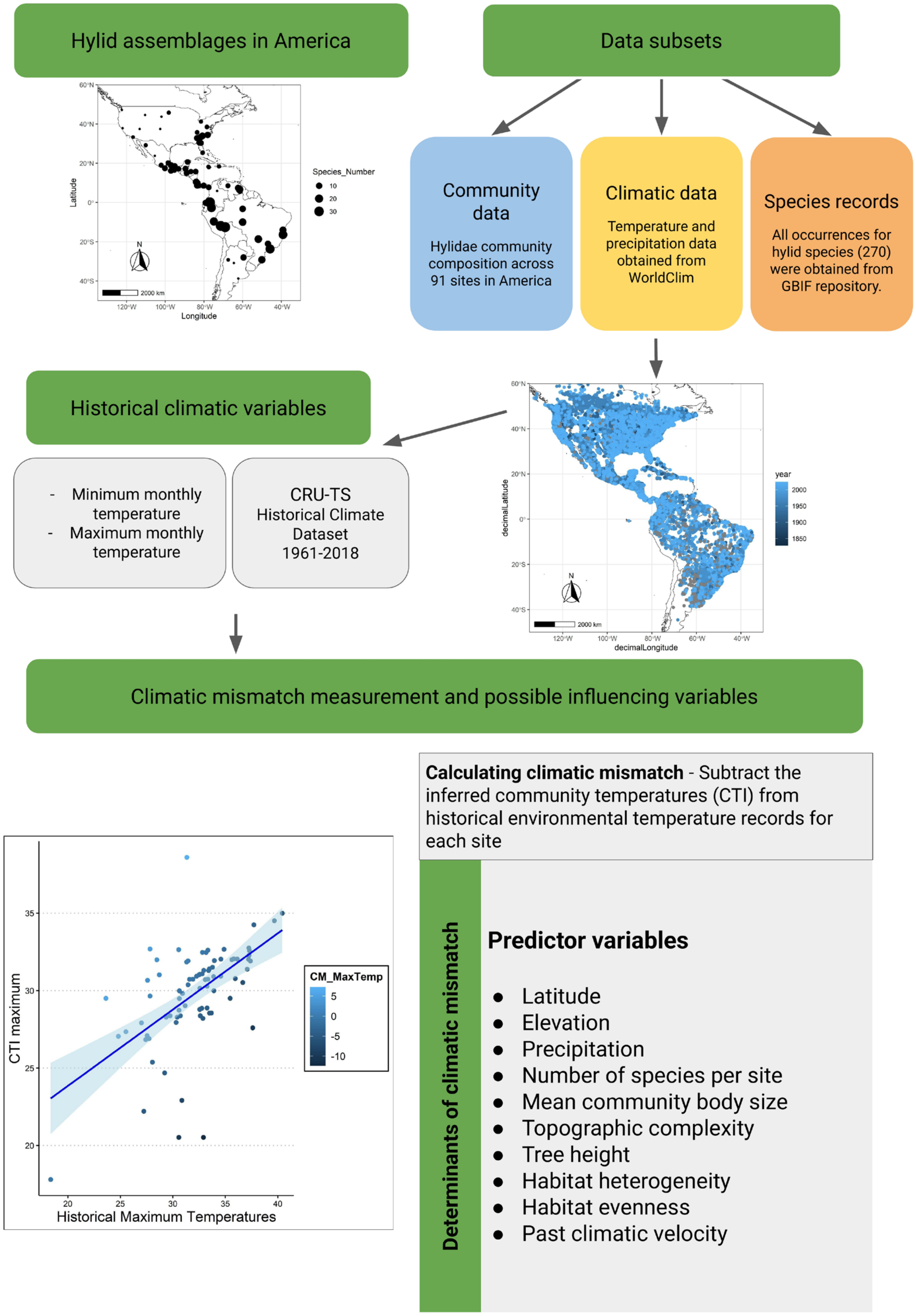

Figura 1. Flujo de trabajo de la metodología de estudio que resume el proceso mediante el cual se obtuvieron los resultados del rezago climático.

Figure 1. Workflow of the methodology, which summarises the process through which climatic lag results were obtained.

Body size data assemblage

Body size data for each hylid species was gathered from various literature sources (see Appendix SI for Supplementary Materials). We used the maximum snout-to-vent length for males (SVL, in mm) for each species; if not possible, we used adult sizes when there was no distinction between sexes. In some cases, we completed the missing species data with an average of maximum SVL of other species in the same genus. The average hylid assemblage size calculation followed the same process as the one used to calculate the bioclimatic indices data.

Environmental variables across local sites

The predictor variables for each site were obtained from a range of different public repositories. Precipitation data were obtained from CHELSA database (Karger et al., 2017). Elevation and roughness were obtained from Amatulli et al. (2018), based on the 250 m GMTED (Global Multi-resolution Terrain Elevation Data) due to their appropriateness for large-scale environmental analyses. Habitat evenness and habitat heterogeneity were obtained from Tuanmu and Jetz (2015) based on the enhanced vegetation index (EVI) at 1-km resolution layers. Past climatic velocity was calculated using Loarie's method (Loarie et al., 2009) with paleoclimatic data at 1.5-minute resolution from Paleoclim database (Brown et al., 2018). Tree height data was extracted from Potapov et al. (2021) which collected information from the Global Ecosystem Dynamics Investigation (GEDI) on canopy height measurements, creating a 30m2 spatial resolution global map.

Statistical analysis

We employed a generalised linear mixed model (GLMM) using the *lmer* function from the *lme4* R package (Bates et al., 2015), with the residual error of the linear function following a Gaussian distribution, to assess which factors drive the geographical variation in climatic mismatch. The minimum and maximum climatic mismatch per community were treated as the response variables in GLMM, and predictors such as absolute latitude, elevation, precipitation, number of hylid species, mean community body size, topography roughness, tree height, habitat heterogeneity, habitat evenness, past climatic velocity were treated as fixed responses. Biogeographic provinces were treated as a random effect. All variables were scaled to mean = 0 and SD = 1 to enable direct comparison of the predictor importance. We checked residuals from models to evaluate whether they adjusted to normality. We plotted the effect size for each predictor to identify key factors that have larger marginal effects on the climatic mismatch across sites. Kruskal-Wallis tests were run to investigate whether the differences in the response amongst provinces differed significantly. We also conducted GLMM analysis with a few regions using the original classification from Wiens et al. (2011) as a random effect, but the results were highly similar (Fig. S1 and S2), so we only reported results and discussion from the first analyses.

RESULTS

Geographical patterns of climate mismatches for local hylid assemblages

We found that for minimum historical temperatures local hylid assemblages exhibited high positive values for climate mismatches (i.e., climatic credits) especially in North America, north of Argentina and south of Brazil (Fig. 2a). By contrast, negative values for climate mismatches (i.e., climate debts) were mainly distributed across Mexico, Central America, the Andes region in Ecuador and Peru, the Atlantic Forest and Amazonia in Brazil. Negative values for climate mismatches indicate that these assemblages may have been unable to keep up with fast increases in environmental temperatures in the last decade. For maximum local temperatures, we found that most assemblages across the continent showed high climate mismatches (i.e., climatic debts) with a few exceptions in Central America and the east of South America (Fig. 2b).

For minimum temperature, most of the local hylid assemblages exhibited positive climate mismatches (i.e., climatic credits) across biogeographical provinces. Local assemblages in biogeographic provinces in Argentina (Monte, Chaco, and Pampean) and in the United States (Montanian and Saskatchewan) exhibited the highest values of climatic mismatches (above 10 °C) (Fig. 3a). For maximum temperature, the general pattern was opposite, with most assemblages across provinces exhibiting high negative values between 0 and -5 °C (i.e., climate debts) (Fig. 3b). The highest negative values (> 10 °C) were in the Chaco, Monte, and Pampean province located in the southern of South America (Fig. 3b). Most other assemblages maintained a consistent range of climate mismatch between 0 and -5 °C.

Overall, most assemblages were degrees ahead of the anticipated minimum temperature leading to the observed climatic credits. By contrast, with maximum temperatures, we found that many local assemblages were exhibiting negative values for climate mismatch leading to the observed climatic debt. Kruskal-Wallis tests revealed no significant differences in lagged response among the provinces ($p > 0.05$), indicating a general consistency of mismatch for maximum and minimum temperatures.

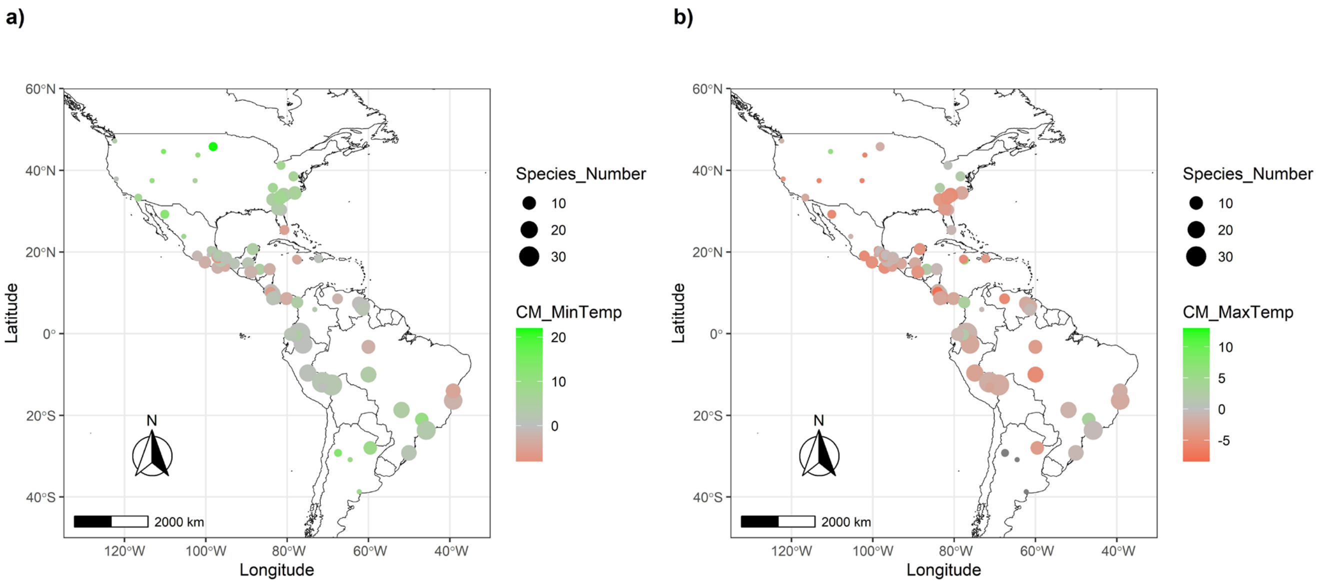

Figura 2. Mapa que muestra la distribución espacial de los desajustes climáticos para las comunidades locales de Hylidae incluidas en este estudio (a) en comparación con las temperaturas históricas máximas por sitio, (b) en comparación con las temperaturas mínimas históricas por sitio.

Figure 2. Map showing the spatial distribution of climate mismatches for the local Hylidae communities included in this study (a) compared to historical maximum temperatures per site, (b) compared to historical minimum temperatures per site.

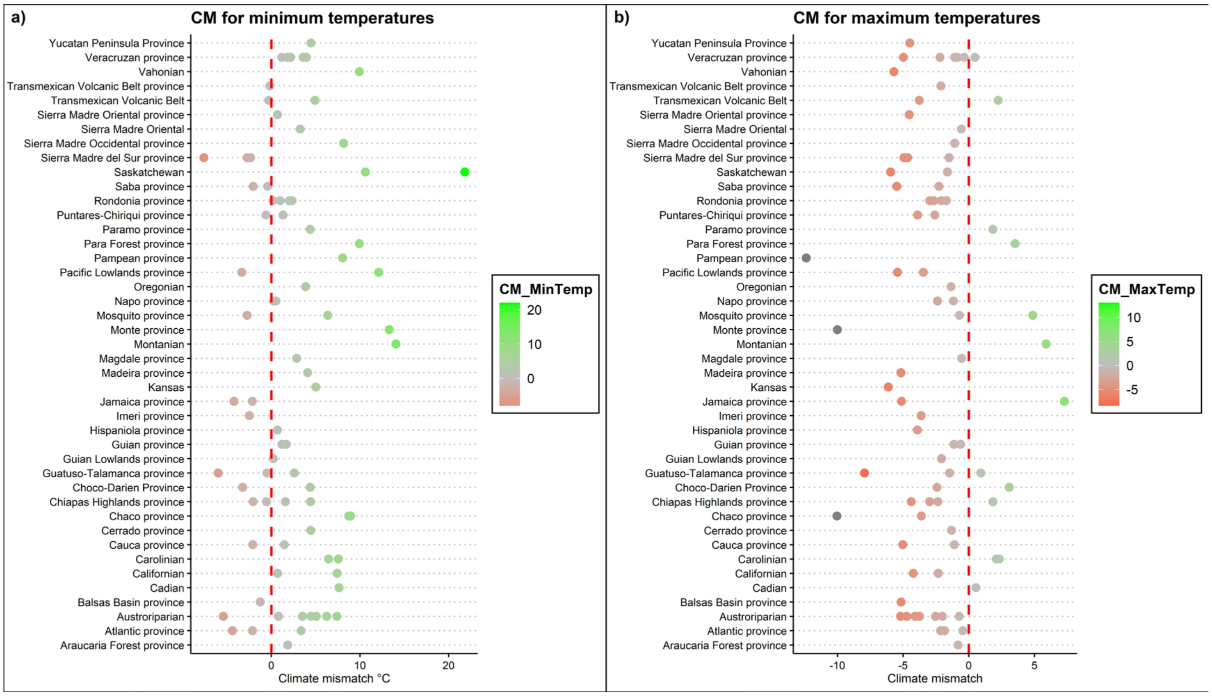

Figura 3. Tendencias del desajuste climático de ensambles locales de hílidos para (a) la temperatura mínima y (b) máxima en diferentes provincias biogeográficas en América. Cualquier valor inferior a cero representa deuda climática, mientras que cualquier valor superior a cero, muestra crédito climático.

Figure 3. Trends in climate mismatches for (a) minimum and (b) maximum temperature across different biogeographical provinces throughout America. Any value below zero demonstrates climatic debt whereas any value above zero shows climatic credit..

Drivers of climate mismatches from local hylid assemblages

Climate mismatches for minimum temperatures across local hylid assemblages were explained by absolute latitude, elevation, past climate velocity, and slightly for body size (Fig. 4a). By contrast, only a marginal effect of body size and precipitation was found for the climate mismatches for maximum temperatures (Fig. 4b). Higher values of climate mismatches, indicating climate debts, for minimum temperatures tend to increase toward extra-tropical sites and high elevations where have occurred rapid climate change since the Last Glacial Maximum (Fig. 4a and 5a). The average body size for hylid assemblages had a relatively mixed effect on the climate mismatches for minimum (positive effect) and maximum temperatures (negative effect) (Fig. 4 and 5).

DISCUSSION

Our study aimed to assess the observed current response of hylid assemblages in the face of increased temperatures in the last four decades across a comprehensive set of localities in the Americas. We quantified climate mismatches for 80 local hylid assemblages, which indicate whether these assemblages are lagged (positive values) or ahead (negative values) of current historical trends of temperatures. We found a substantial variation across geography and biogeographical provinces of climatic mismatches (Fig. 2 and 3). We detected a positive significant effect of some variables on climate mismatches for minimum temperatures but not for maximum temperatures including absolute latitude, elevation, past climate velocity, and body size (Fig. 4). Other variables were independent of climate mismatches. These results align with previous research on other taxa in tropical areas (Feeley et al., 2020), and suggest that local hylid assemblages increase the ahead response to extratropical areas and most assemblages in tropical ecosystems are in climatic disequilibrium with the current trend in warming.

Climate mismatch variation across geography

Treefrog assemblages had a noticeably lower thermal tolerance for maximum temperatures in sub-tropical regions, which could be attributed to the thermal sensitivity of local assemblages in these areas. While studies have demonstrated the sensitivities of both regions, our results indicate that hylid assemblages in sub-tropical areas may be more susceptible than previously considered. This is evident from their noticeably lower thermal tolerance, reflected in their negative climate mismatch values,

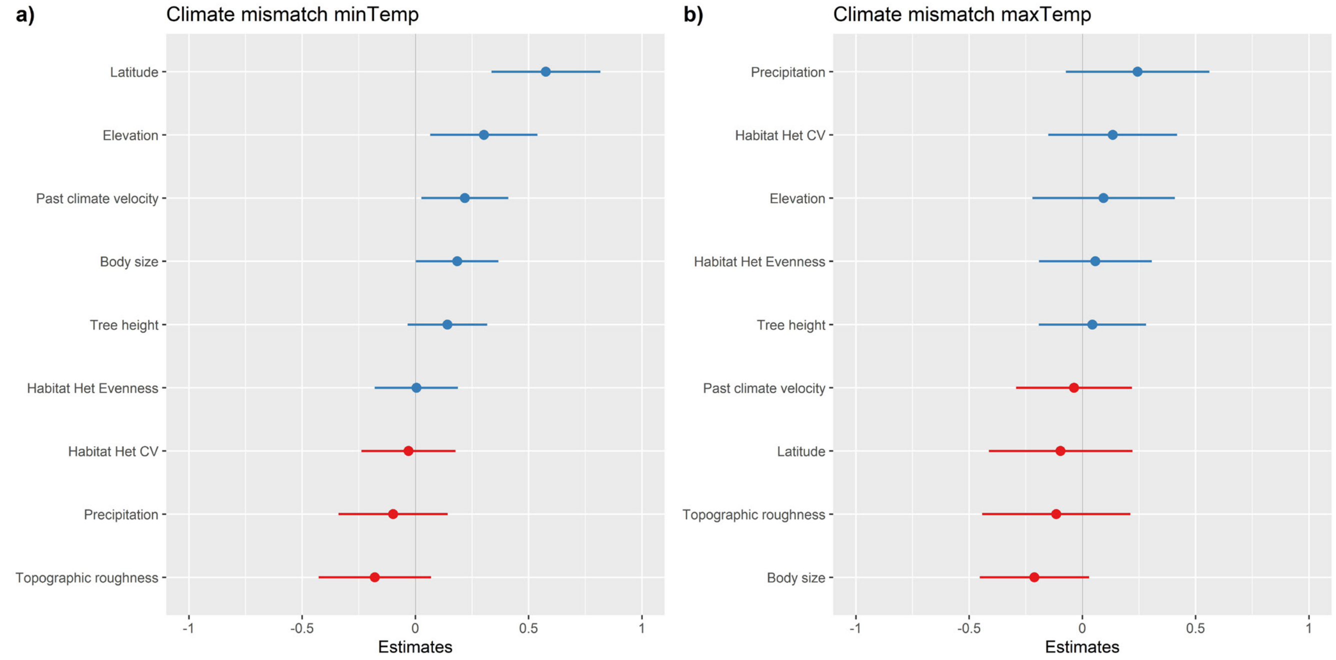

Figura 4. Diagrama de bosque de los tamaños del efecto con intervalos de confianza para cada variable predictiva frente al desajuste climático para (a) temperaturas mínimas y (b) máximas. Los tamaños de efecto fueron estimados usando un modelo linear generalizado mixto (GLMM). El azul representa un efecto positivo y el rojo es un efecto negativo..

Figure 4. Forest plot of effect sizes with confidence intervals for each predictor variable against climate mismatches for minimum (a) and maximum (b) temperatures estimated from a generalized linear mixed model (GLMM). Blue represents a positive effect, and red represents a negative effect.

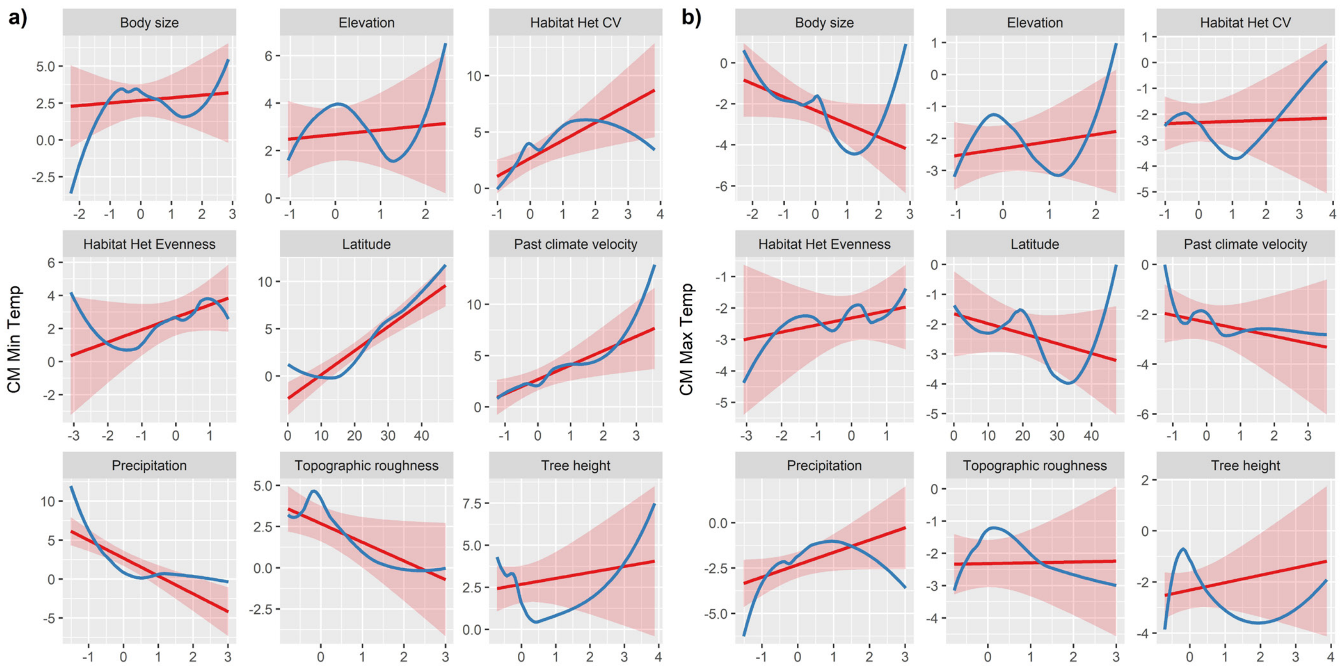

Figura 5. Diagrama de diagnóstico de cada variable predictora sobre el desajuste climático para (a) temperaturas mínimas y (b) máximas obtenidos del ajuste del modelo linear generalizado mixto (GLMM). La línea roja corresponde a los valores ajustados y el área roja corresponde al intervalo de confianza. La línea azul corresponde a una línea suavizada de un modelo de regresión local (loess). Ver texto principal para mayor información.

Figure 5. Diagnostic-plots of each predictor variable on the climate mismatch for (a) minimum and (b) maximum temperatures obtained from a fitted generalized linear mixed model (GLMM). Red line corresponds to fitted values and the shaded red area correspond to the interval confidence. Blue line corresponds to a loess-smoothed line. See text for further information..

suggesting lagged responses for maximum local temperatures. Another possibility is a potential decrease in the margin of tolerance for heat and stress, which could have long-term impacts on hylid populations and their performance (Pottier et al., 2022). These findings support the hypothesis that local amphibian assemblages are likely not showing fast responses to contemporary climate change (Subba et al., 2018). Prior research proposes that thermal tolerances for tropical ectotherms correspond more closely with the temperature conditions they experience, unlike sub-tropical species. This may imply that there is a greater degree of local adaptation to contemporary temperature in the tropics (Feder & Lynch, 1982; Navas-Martín et al., 2022), which could clarify why tropical assemblages in our results show less drastic temperature mismatches than those in sub-tropical zones, particularly for maximum local temperatures. However, it is important to note that both tropical and sub-tropical assemblages are experiencing changes and suffering from the impacts of ongoing climate change (Polato et al., 2018). These findings contrast with certain other studies, suggesting that tropical ectotherms face greater risk due to narrower thermal safety margins, meaning a lower tolerance to changing temperatures (Dillon et al., 2010; Deutsch et al., 2018; Kitudom et al., 2022). Some studies also propose that sub-tropical species may have a greater response-ability to shift the timing of seasonal life process (Sunday et al., 2011). These hypotheses regarding the sensitivity of tropical and sub-tropical species to climate change are still under debate, and further studies are necessary before a conclusion can be reached.

The biological consequences of climate change are expected to increase with latitude, corresponding to high-temperature increases (Deutsch et al., 2018). We found that sub-tropical provinces such as Monte, Chaco, and Pampean exhibited negative climate mismatch values consistent with the assumption that these assemblages are exposed to the most under changing climatic conditions. Our findings support the hypothesis that latitudinal factors (e.g., seasonality) may play a role in shaping the responses of local assemblages to ongoing temperature increases, at least for minimum temperatures (Sinai et al., 2022). These regions, known for agriculture and livestock production, have some of the driest grasslands in the country and are known to be particularly threatened globally (Namkhan et al., 2021). Since the early 2000s, they have been hotspots for agricultural land–use change (Piquer-Rodríguez et al., 2018) and these modifications in land use and cover may continue to affect the ability for hylids to adapt to increasing temperatures by posing limitations to their dispersal abilities, increasing the possibility of population bottlenecks occurring (Schivo et al., 2020). Furthermore, although tree frogs in tropical regions are susceptible to habitat destruction, studies indicate an expansion in their ranges, which may help them evade rising temperatures to a greater extent than their sub-tropical counterparts (Zumbado-Ulate et al., 2021), or there is a possibility that they are more plastic in terms of adaptability than previously thought.

Despite the varying environmental challenges faced by different assemblages, one of the most significant concerns associated with rising temperatures is evaporative water loss (Withers et al., 1984; Lertzman-Lepofsky et al., 2020). Ectotherms' performance is closely linked to temperature tolerance and evaporative water loss is the primary mechanism for thermal regulation (Le Galliard et al., 2021). Consequently, dehydrated individuals become more sensitive to temperature increases and lose their ability to thermoregulate. Almost all assemblages investigated in this study displayed a lower thermal tolerance margin than expected due to conditions becoming hotter and possibly drier (Greenberg & Palen, 2021), which could explain their lower thermal tolerances and compromise their reproductive abilities and other essential physiological functions (Hoffmann et al., 2021). Furthermore, amphibians tend to seek environments that facilitate hydration, which may be reflected in the debt distribution amongst the investigated assemblages. But there are fantastic exceptions, and amphibians in very dry or seasonal environments show some remarkable adaptations. There is a probability that the local hylid assemblages with the lowest thermal tolerance are simultaneously affected by critical water loss, limited dispersal abilities, and narrow thermal niche breadth.

Predictors of climate mismatches across local assemblages

Prior research has demonstrated a significant effect of predictor variables on the observed climate mismatches of an area, as evidenced by broader confidence intervals (Richard et al., 2021). However, these investigations have been performed mostly on plant communities within more specific regions, potentially minimizing the chance of error. Given this context, it is essential to recognise that studies on plant communities and their results might not be directly comparable to species communities' studies on other taxonomic groups. We found a strong effect of latitude, as previously discussed, and a lesser effect for elevation, past climate velocity, and body size for climate mismatches for minimum temperatures. The body size and precipitation had a small effect on maximum temperatures, suggesting that it is possible that additional variables related to microclimatic conditions can play a role in controlling how amphibian assemblages respond to different climate axes (minimum and maximum temperatures). For instance, the topographic and habitat variables we included as predictors likely are operating at larger spatial scales and are not able to explain climate mismatches across hylid species assemblages (Bertrand et al., 2011; Devictor et al., 2012; Auffret & Svenning, 2022). The choice of large-scale predictor variables in our study and the lack of consideration of additional functional traits (beyond body size) likely helps to explain why these factors had a minor or non-significant effect in explaining the variation in climate mismatches across local hylid assemblages.

Past climatic velocity, which estimates the speed at which species must move over the surface of Earth to maintain constant climatic conditions since the Last Glacial Maximum (~21,000 years before present; Loarie et al., 2009), serves as a proxy measure of the exposure of an assemblage to climate change rather than a reflection of the impact (Corlett & Westcott, 2013). Amphibians, including hylids, are considered, in general, poor dispersers due to various physiological factors, such as susceptibility to desiccation and their relatively small size, affecting their ability to keep up with environmental temperatures and rendering them particularly vulnerable to the speed of climate change. A significant positive effect of past climatic velocity on climate mismatch trends would be expected, given that amphibian species tend to exhibit lower adaptation rates to climate change and require more time to evolve (Diniz-Filho et al., 2019). Areas that experience extreme climate changes are likely to be those that consequently suffer from increasing past climatic velocities. As a result, the assemblages show lower thermal tolerances and higher debt values. Our results correspond to sub-tropical regions, which undergo greater climatic variation than tropical assemblages. This could be reinforced by fragmentation of natural vegetation cover, further limiting essential functions such as dispersal and adaptation abilities.

LIMITATIONS

Using an extensive dataset, our study is one of the first to analyse climate mismatch in local amphibian assemblages across the American continent. We found significant evidence supporting climatic lagged responses in several localities consistent with previous findings amongst other taxonomic assemblages across the continental region (Kerr et al., 2015; Stephens et al., 2016; Feeley et al., 2020). However, we acknowledge several methodological limitations associated with the data used in our study, limiting our results and the subsequent conclusions we came to. The lack of statistical significance for several predictor variables in our results may be partially attributed to the scale of our study and the extent of our studied local hylid assemblages. Although we aimed to examine a wide representative area encompassing the entire American continent, further studies at local scales may have been more appropriate for identifying the factors influencing the presence of climatic lagged or ahead responses, for instance, including hylid species abundances and critical thermal traits (CTmin/CTmax).

Additional factors, both evolutionary and physiological, were not considered in this study, and those could influence the accumulation of debt or credit (e.g., the ability of individual species to adapt to ongoing increases in local temperatures; He et al., 2023). While a few studies have provided positive evidence of multiple predictor variables contributing to debt results, these studies were primarily conducted on a regional scale; in sub-tropical regions (Bertrand et al., 2011; Auffret & Svenning, 2022). Long-term monitoring of the effect of climate change on amphibian populations in tropical areas is crucial, as, without it, accurate future projections of climate change impacts on species populations cannot be made.

Despite efforts to limit the scope of our study by investigating only one widely distributed amphibian family, relying on external literature and historical records, hylid data could have introduced inaccuracies into our hylid datasets. Overall, comprehensive data are absent for ectotherms regarding heat-tolerance data and body size. This may be due to poor sampling, particularly in boreal and tropical regions. Additionally, there has been a neglect in considering the interaction between environmental temperatures and water availability (Herrando-Pérez et al., 2023). Regarding body size, shrinking is a typical species response to climate warming. Therefore, if this response applies to hylids, variation amongst the continent would be expected to be seen as smaller body sizes tend to mean a lower metabolic rate and lower energy demands. In a broader perspective, this could be deemed a more effective adaptation mechanism to a warming world. It can be reasonably anticipated that this response could become pervasive, thereby being termed the third universal response to warming (Daufresne et al., 2009; Gardner et al., 2011). However, the limited availability of body size data impeded our ability to analyse any trends in body size as a response to climate change in different localities. Therefore, future investigations or reanalyses should incorporate more accurate body size data in relation to climatic debt.

While this temporal mismatch is undeniable, it is necessary to identify the specific bioclimatic variables that hinder assemblages' ability to cope with increasing temperatures to project the impact of climate change accurately. Future studies could adopt a similar methodology to understand climatic debt and its contributing factors and formulate possible solutions, focusing on the interaction between local and regional scales.

CONCLUSIONS

Our study provides evidence supporting the hypothesis of climate disequilibrium across local assemblages of hylid frogs in America. The climate disequilibrium is reflected in the considerable variation of climate mismatch values, suggesting that many local assemblages show a mix of responses to contemporary climate change. We found that hylid assemblages in sub-tropical areas exhibit a lag response for maximum temperatures, suggesting a restricted thermal safety margin for these species. We recommend that future studies continue to develop realistic reflections of community responses to climate change, addressing the limitations that currently exist in data that may have constrained our study. With growing concerns regarding how species will respond to climate change, it is necessary to start detangling the complex web of factors that impact a species' response. Our research hopefully sheds light on how there is a requirement to prioritize research on climate mismatch, with particular emphasis on tropical regions of the planet. Highlighting the importance of continued species data collection in the field for enhanced accuracy in similar future projects. Such records could provide invaluable insights into biotic responses to climate change and aid in predicting future responses while also comparing them to historical records. After all, by recognising and understanding what communities need prioritizing and the underlying reasons why, we can help create future guidelines for global biodiversity conservation.

Acknowledgments.- The authors thank the funding from a DGAPA-PAPIIT project IA206523.

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APPENDICES

Appendix 1. Datasets and R codes used in this manuscript are available at the following link: https://figshare.com/s/352a0e0485f35723f6df
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Apéndice 1. Los conjuntos de datos y códigos R utilizados en este manuscrito están disponibles en el siguiente enlace: https://figshare.com/s/352a0e0485f35723f6df .

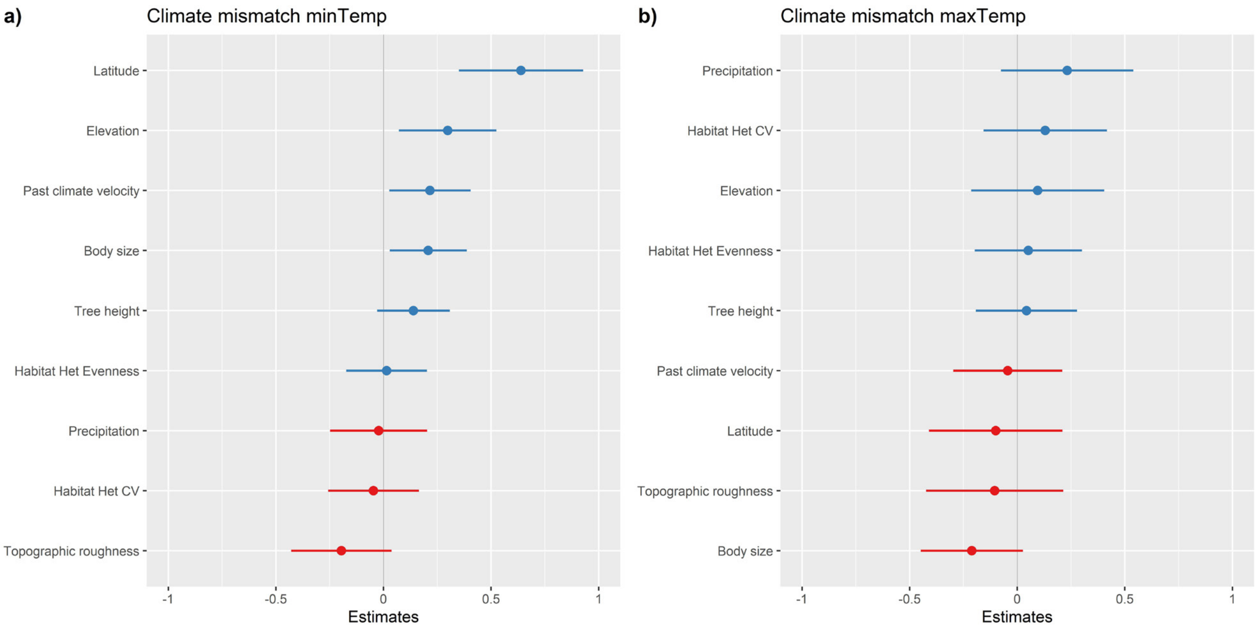

Figura S1. Diagrama de bosque de los tamaños del efecto con intervalos de confianza para cada variable predictiva frente al desajuste climático para (a) temperaturas mínimas y (b) máximas. Los tamaños de efecto fueron estimados usando un modelo linear generalizado mixto (GLMM). El azul representa un efecto positivo y el rojo es un efecto negativo.

Figure S1. Forest plot of effect sizes with confidence intervals for each predictor variable against climate mismatches for minimum (a) and maximum (b) temperatures estimated from a generalized linear mixed model (GLMM). Blue represents a positive effect, and red represents a negative effect.

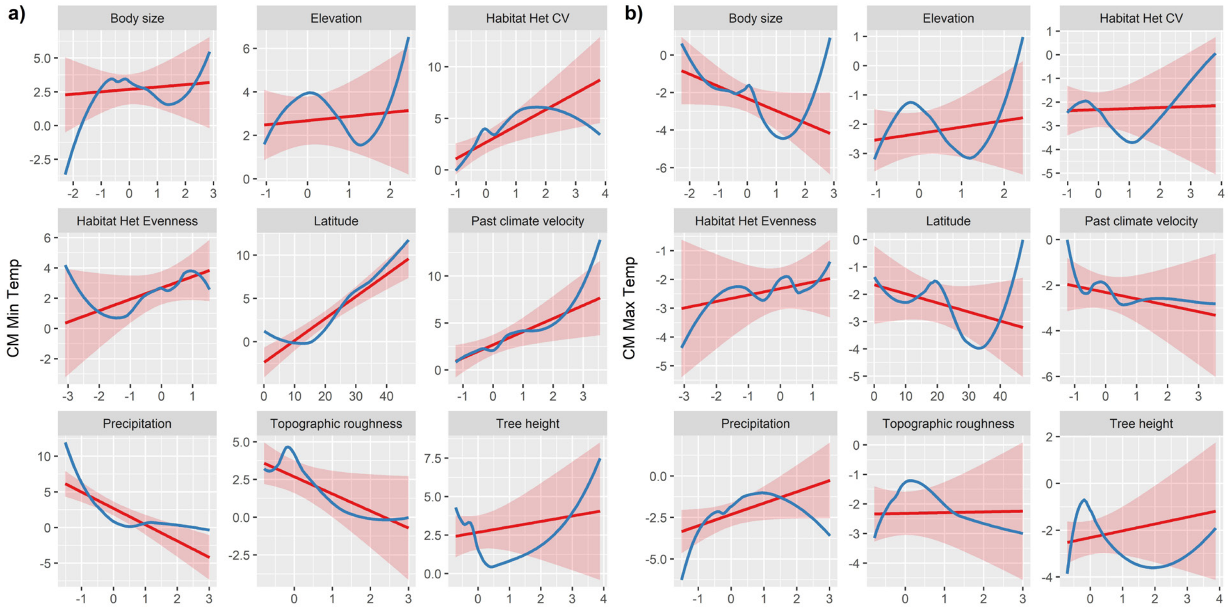

Figura S2. Diagrama de diagnóstico de cada variable predictora sobre el desajuste climático para (a) temperaturas mínimas y (b) máximas obtenidos del ajuste del modelo linear generalizado mixto (GLMM). La línea roja corresponde a los valores ajustados y el área roja corresponde al intervalo de confianza. La línea azul corresponde a una línea suavizada de un modelo de regresión local (loess). Ver texto principal para mayor información.

Figure S2. Diagnostic-plots of each predictor variable on the climate mismatch for (a) minimum and (b) maximum temperatures obtained from a fitted generalized linear mixed model (GLMM). Red line corresponds to fitted values and the shaded red area correspond to the interval confidence. Blue line corresponds to a loess-smoothed line. See text for further information.