



Climate-associated shifts in color and body size for a tropical bee pollinator

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Abstract – Habitat degradation and climatic changes are causing declines in bee populations, which in turn threaten wild plant reproductive success and the global food supply. We examined spatial and temporal variation in traits that may influence the way bees respond to environmental changes. For a color polymorphic species, we characterized proportions of three morphs and measured body size of individuals within sites of varying elevation over an 11-year sampling period. We found climate-associated variation in both color and body size, as well as temporal shifts in these traits that were associated with climatic conditions of sites. The proportion of bees that were red-orange increased relative to two other color morphs. Body size increased over time, and it increased more at drier sites. These results suggest that precipitation may be an important driver of trait shifts in tropical bees and motivate investigations of natural selection on color and body size due to differential climatic tolerances.

color / body size / climate / habitat degradation / pollinator / tolerance

1. INTRODUCTION

Pollinators are essential to the reproduction of almost 90% of flowering plants (Ollerton et al. 2011), and they increase seed set in at least two-thirds of crops (Klein et al. 2007). Both land-use and climatic changes drive declines in pollinator populations (Bates et al. 2011; Forister et al. 2019). These declines have been linked to declines in wild plant populations (Biesmeijer et al. 2006), as well as increases in the vulnerability of food systems (Gallai et al. 2009).

Bee pollinators may be particularly likely to suffer negative effects of future land-use and climatic changes because insect flight muscle activity can increase body temperature well beyond ambient air temperature (Heinrich and Buchmann 1986). This can force bees to either forage near their critical thermal limits (Chappell

1982, 1984) or cease food collection in high ambient temperatures (Willmer and Stone, 2004). Increasing climatic extremes and deforestation are eliminating cooler microclimates (Mantyka-pringle et al. 2012), so identifying phenotypic traits that mediate the way bees respond to environmental changes and determining drivers of phenotypic variation in those traits is important.

Color and body size are likely key traits that mediate responses of bees to environmental changes, but predicting which phenotypes may be favored in a warming world with less natural habitat is not straightforward. Color influences thermal tolerance, such that darker colored morphs prefer cooler areas in areas that are heterogeneous for temperature, presumably because this reduces heat absorption (Ahnesjö and Forsman 2006). Avoidance of heat gain may also explain why dark-colored bees forage preferentially during cooler times of the day (Chappell 1982; de Farias-Silva and Freitas 2020). These observations lead to the prediction that in a

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warming world, natural selection should favor lighter body colors. However, darker colors may instead be favored because they have greater amounts of melanin pigments that protect against UV radiation (Bastide et al. 2014) or provide resistance to pathogens (Roulin 2014). In addition to the shade of body color, the specific hue is often strongly associated with risk of predation (Hines and Williams 2012). Therefore, tradeoffs may exist between hues that reduce heat and those that provide camouflage (Gómez et al. 2016).

Regarding body size, smaller individuals have higher surface area to volume ratios that can release heat more quickly (Brans et al. 2017). In addition, smaller body sizes are favored when resources are scarce (Brown and Maurer 1989). Indeed, larger bees seem to be more vulnerable to negative effects of habitat destruction (Bartomeus et al. 2013; Oliveira et al. 2016; Scheper et al. 2014), likely because they require more resources to successfully raise brood (Müller et al. 2006). However, smaller body sizes are also less desiccation tolerant (Brans et al. 2017). Water loss can have profound, negative fitness consequences (Benoit et al. 2010; Bujan et al. 2016), so the way that body size changes with increasing temperature should depend not only on temperature but also on moisture availability.

We examine trait variation, shifts, and possible abiotic drivers for the Euglossine bee, *Euglossa championi* Cheesman 1929, over an 11-year period across southern Costa Rica. *Euglossa championi* exhibits substantial morphological variation throughout Costa Rica, with cuticular colors among individuals within sites ranging from reddish orange to bluish green (Roubik and Hanson 2004; Figure 1). It is unknown if the variation in color is associated with abiotic factors for *E. championi*, but other Euglossine species show intraspecific color variation that is associated with geography (Ferrari and Melo 2014). Color in Euglossine bees is structural, such that spacing among grooves of the outer surface of the body (integument) determines the wavelengths of light that are reflected and thus seen (Land 1972). In bees of the genus *Euglossa*, structural coloration causes iridescence, which reflects light (Seago et al. 2009) and has been hypothesized to reduce heat gain (Mossakowski 1979). Work on how

color variation of insect integuments influences their thermal properties is scant, but some iridescent insect integuments have been observed to substantial heat gain (Schultz and Hadley 1987). Previous work on intraspecific variation in body size in Euglossine bees revealed seasonal and habitat-associated differences that are suggestive of climate influences on traits, but this work did not include direct quantification of how traits vary with climate (Silva et al. 2009; Pinto et al. 2015). Here, our specific aims were to determine (a) if the distribution of trait variation among sites is associated with climatic conditions; (b) if traits change temporally; and (c) if the way that traits change temporally depends on climatic conditions. We document climate-associated morphological variation in both color and body size, and we find that the way traits shift temporally depends on climatic conditions. Our analysis of shifts in multiple functional traits together provides insights into synergistic effects of trait values on responses of organisms to global changes.

2. MATERIALS AND METHODS

2.1. Species, sampling, and trait measurements

Euglossa championi is found from Mexico to Ecuador at elevations from sea level to around 2000 m, is about 13 mm in length, and pollinates orchids in at least 10 genera as well as many other tropical plants (Roubik and Hanson 2004). *Euglossa championi* can be distinguished from other sympatric species by facial markings and a fuzzy tuft on the middle leg (Roubik and Hanson 2004). We sampled a total of 647 male *E. championi* bees across 18 sites throughout southern Costa Rica in 2009, 2010, 2017, 2018, and 2019 (Figure 2; Online Resource 1–Tables S1 and S2). Sites were located in Puntarenas province, which is predicted to experience the most extreme deforestation of the Costa Rican provinces (Stan and Sanchez-Azofeifa 2019). Within five sites, we sampled at more than one location (average distance among locations 0.45 km; Online Resource 1–Table S1). The nearest location in any site was separated from a location in another site by 2.5–96 km. We note that not all sites were



Figure 1 Color variation in *E. championi*: blue-green (left), green-orange (middle), and red-orange (right).

sampled in all years but the climatic conditions sampled were largely balanced across years (Fig. S1). In addition to forest fragments, the sampling area is comprised of agricultural areas, towns, and pastureland. At each site, we sampled between the hours of 9am and 12pm on sunny days using the chemical baits cineole and methyl salicylate. We placed baits in forest fragments between zero and 93 m of forest edges, approximately 1.5 m off the ground on tree trunks, and netted bees as they arrived. We stopped sampling when no bees arrived for more than 15 min. Bees were killed using ethyl acetate, placed in vials with 95% ethanol for transfer back to the laboratory, and then pinned.

We assessed the color of the samples visually and binned bees into three categories: blue-green, green-orange, or red-orange (Figure 1). We considered bees blue-green if they had an abdomen that was entirely green or blue, without orange or reddish markings. We considered bees green-orange, and not red-orange, if the dorsal side of their thorax had distinctive orange coloration surrounding a red streak in the middle of the surface, and if abdominal segment T1 was greenish and not golden. We considered specimens to be red-orange if they had large red areas on the dorsal surface of their thorax, as well as golden coloration on abdominal segment T1, rather than greenish coloration. To characterize body size, we measured the intertegular span, which is the space between where the wings attach (Cane 1987), as well as body length, using digital calipers (Blue-Point®, 0.01-mm precision). We chose these traits

because they are correlated with resource use, metabolism, dispersal, and pollination effectiveness in bees (Biesmeijer et al. 1999; Peters et al. 2016; López-Urbe et al. 2019). Specimens are vouchered at the University of San Francisco, San Francisco, CA.

2.2. Assessing climatic variation

We extracted data from the WorldClim database v1.4 at a 30-s resolution (www.worldclim.org) corresponding to each location's geographic coordinates using the raster (Hijmans 2020) and sp (Pebesma et al. 2017) packages in R. We included the 19 bioclimatic variables into a principle component analysis (PCA) using the factoextra package (Kassambara and Mundt 2017), and we used the first and second principle components (PC1 and PC2, respectively) in models (described below). The PCs used in models were therefore from climatic data from only the sites in which we sampled. At one of the sites in which three locations were sampled, the WorldClim database placed one location in a different climatic grid cell than the other two locations (Site 12, Online Resource 1–Table S1). In this case, we used the WorldClim data from the center location, which was 0.63 and 0.64 km from the other locations, in models.

The WorldClim database provides climatic averages within 30-s grid cells from 1970 to 2000, which are useful for comparing among sites that vary climatically. We used WorldClim data in models that compared traits among sites (see the

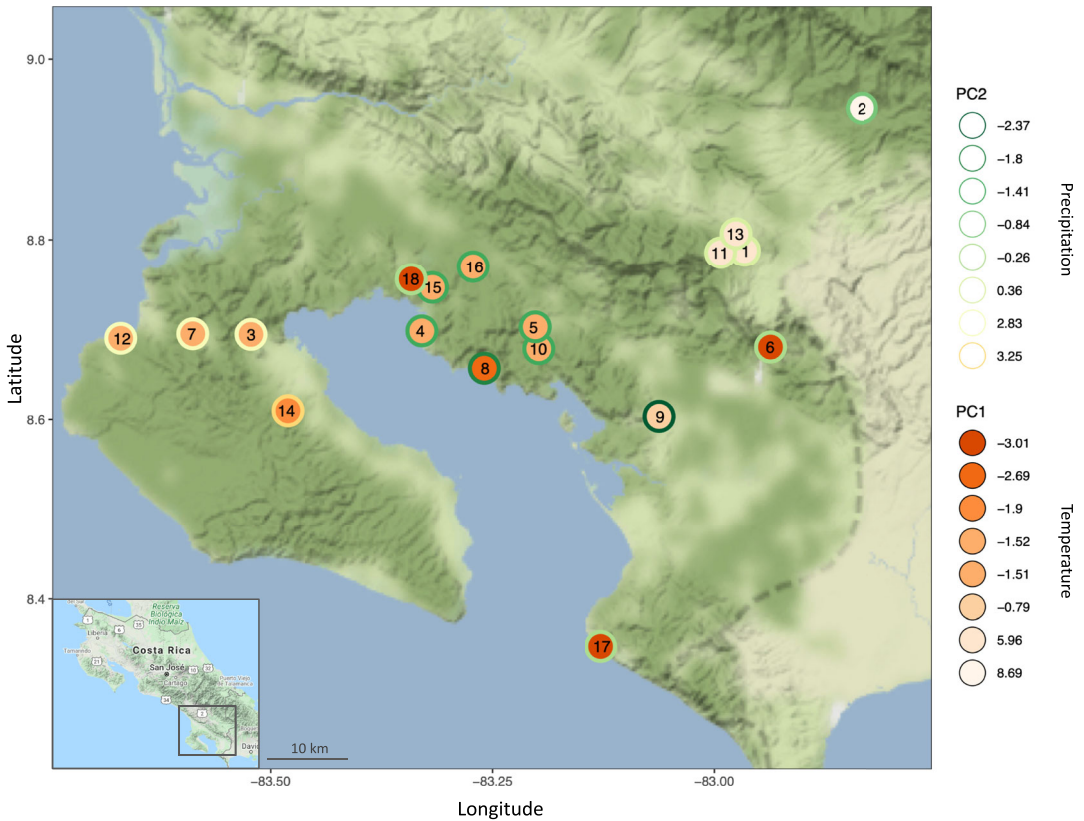


Figure 2 Map of sampling sites in southern Costa Rica. For each site, the interior color reflects the values of principle component 1 (PC1), and the outline color reflects the values of principle component 2 (PC2) from the analysis of WorldClim data. Lower PC1 values (darker colors) reflect higher temperature values of the bioclimatic variables incorporated into the principle component analysis. Lower PC2 values (darker colors) reflect greater precipitation and lower climatic variability of values of the bioclimatic variables.

“Modeling trait variation” section). We also directly assessed if traits change temporally and in response to climate by obtaining hourly climate for one site that has been experiencing rapid climatic warming (the Las Cruces Biological Station; Figure 3). We ran a separate set of models using samples only from the Las Cruces Station ($N = 156$ bees) to investigate how traits of bees varied with detailed climatic variables from the weather station at that site (see the “within-site analysis” below). Detailed hourly climatic data used to calculate climatic averages began midway through 2008 at the Las Cruces Station, so climatic averages that take all months into account were available starting in 2009. Therefore, trait measurements from only 2010 onward were used to

assess relationships between traits and climatic variables.

2.3. Modeling trait variation

In general, we determined how traits varied with time, with climatic conditions of sites, and with each other using linear mixed models implemented with the lme4 package in R (Bates et al. 2014). The trait of interest was the dependent variable, year sampled was a fixed factor, and site was a random factor. We evaluated if fixed factors and their interactions improved models using likelihood ratio tests (LR tests) comparing nested models with and without the factor or interaction of interest (Zeileis and Hothorn 2002). The P-

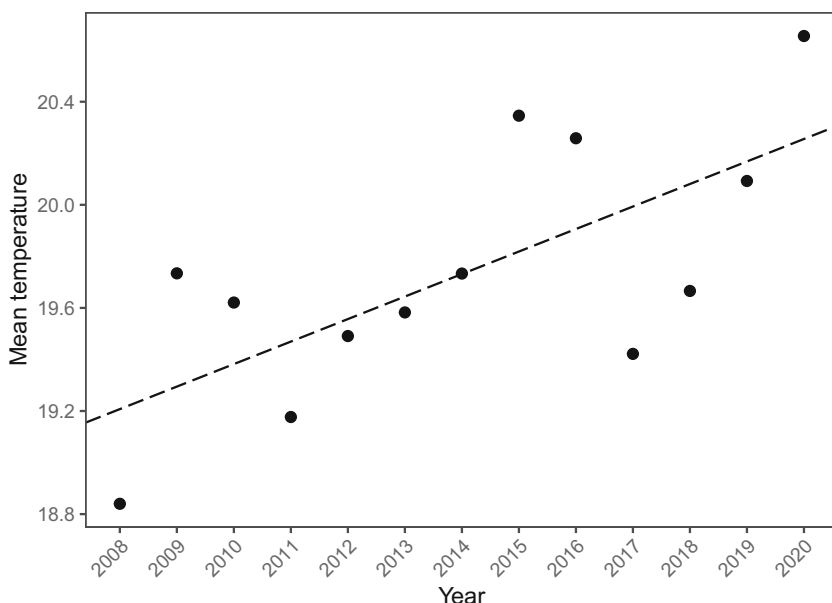


Figure 3 Mean yearly ambient air temperature at the Las Cruces Biological Station. Temperature increased on average by 0.09 °C per year from 2008 to 2020.

values reported reflect LR tests, and estimates reflect coefficients of the best model chosen via backward model selection. We visualized predicted values of traits over time for sites that fell into different climatic groups using the sjPlot R package (Lüdecke 2017).

To explore environmental determinants of body color variation, we assessed if the proportion of bees of each color varied with climate or changed over the sampling period. We used proportions as dependent variables in mixed models that included PC1 and PC2 from the analysis of WorldClim data as independent variables and site as a random effect. We included only sites that had at least ten samples to mitigate against lower sample sizes biasing estimates, and we examined model residuals and verified that Gaussian error distributions were appropriate. The reduced dataset contained a total of 574 samples from ten sites with an average number of specimens used per site per year of 26 ± 2.9 (SE) (Online Resource 1–Table S2). To explore environmental determinants of variation in body size, we used the full dataset ($N = 647$ bees). We ran separate models with IT span and body length as the dependent variable when determining if body size shifted

temporally and with climate and body color. The independent variables were PC1 and PC2 from the analysis of WorldClim data, color, and site was a random effect. We included color when modeling possible changes in body size for two reasons. First, this allowed us to determine if color was associated with body size. Second, this allowed us to control for possible effects of color on body size when determining if body size changed with climate and time.

To assess how color and body size of bees at the Las Cruces Station varied over time (hereafter, “within-site analysis”), we used linear models to model body color proportions and linear mixed models with color as a random effect to model body size. The respective trait was the dependent variable, and for each trait, we ran six models each with a climatic variable measured in the year prior to the year in which bees were sampled at the Las Cruces Station as the independent variable. The six climatic variables included average temperature, minimum temperature, maximum temperature, average total millimeters of monthly precipitation, minimum total monthly precipitation, and maximum total monthly precipitation. We estimated the overall statistical significance of the

multiple comparisons of climatic variables using a method that controls the level of falsely rejected null hypotheses while correcting for increase typed I error (Benjamini and Yekutieli 2001), and we used a false discovery rate of 0.05.

In addition to determining how color and body size changed over time, we also asked whether there was any evidence for resource partitioning among bees of different colors or body sizes. We collected with cineole and methyl salicylate simultaneously so we evaluated if there were associations of phenotype and whether bees foraged at one type of bait over the other. We ran a generalized linear mixed model with a binary dependent variable that reflected the bait at which each bee was caught, color and IT span as independent variables, site and year as random effects, and a binomial error structure.

3. RESULTS

Both color and body size varied over time and with climate, which differed substantially among sites. Examining contributions to the first and second principle components (PC1 and PC2) from the analysis of WorldClim data revealed that the first principle component (PC1) explained 74% of the variance among sites and was negatively associated with temperature. The second principle component (PC2) explained 17% of the variance among sites and was positively associated with climatic variability and negatively associated with precipitation (Online Resource 2–Fig. S2).

The analysis that included all sites revealed that proportions of red-orange bees increased and proportions of blue-green and green-orange bees decreased over time (Table I, Figure 4, Online Resource 2–Fig. S3). The red-orange morph increased more, and the blue-green morph decreased more, at sites with high temperatures (Table I; Online Resource 2–Fig. S4). Greater climatic variability and lower precipitation were associated with stronger increases in the red-orange morph and stronger decreases in the green-orange morph, while the blue-green morph decreased more at sites with lower climatic variability and higher precipitation (Table I; Online Resource 2–Fig. S4).

The analysis that included specimens only from the Las Cruces site (within-site analysis) revealed that over time, the proportion of green-orange bees decreased (Est = -0.01 ; $P = 0.005$), the proportion of blue-green bees did not change (Est = -0.01 ; $P = 0.20$), and the proportion of red-orange bees increased (Est = 0.23 ; $P = 0.038$). Body color proportions were not associated with climatic conditions in the previous year (Online Resource 1–Table S3). The color morphs differed in their IT span, with the red-orange morph being largest, followed by the blue-green morph, and with the green-orange morph being smallest (Table I; Fig. S5). Body length did not differ among colors (Table I).

When considering all sites, there was substantial variation in both measures of body size within years and climatic regimes (Online Resource 2–Figs. S6 & S7). When controlling for color, both measures of body size varied with climate such that individuals were larger at colder sites (Table I). Greater climatic variability and lower precipitation were negatively associated with IT span and positively associated with length (Table I). Both measures of body size increased over time but depended on climatic conditions of sites in different ways. Both IT span and length increased more at sites that were less hot, but IT span increased more at sites with greater climatic variability and less precipitation, while length increased less at sites with greater climatic variability and less precipitation (Table I; Online Resource 2–Fig. S8).

The within-site analysis from the Las Cruces Station revealed similar increases in body size over time (IT span Est = 0.0063 ; $P = 0.01$; length Est = 0.007 ; $P = 0.011$), and associations with precipitation. IT span was larger, and length was shorter following years with less precipitation, regardless of body color (Figure 5; Online Resource 1–Table S3). Temperature in the previous year was associated neither with IT span nor with length (Online Resource 1–Table S3).

There was some evidence for resource partitioning among color morphs. Relative to blue-green bees, red-orange and green-orange bees were more likely to be caught while

Table I. Results of linear mixed models assessing shifts in the proportion of bees of each color and two measures of body size (IT span and length) over time and in relation to climatic conditions of sites. Columns include trait of interest, variable or interaction examined, chi-square value and P-value from likelihood ratio tests, and estimates pertaining to each variable that was included in the final model for each trait. Dashes indicate the trait of interest did not improve the model and no estimate was obtained. Contrasts between the three colors (blue-green (BG), green-orange (GO), and red-orange (RO)) in their effects on body size are shown in the estimate column in the row pertaining to color. Independent variables include year, principle components one and two from an analysis of climate differences among sites (PC1 PC2), and body color for models where a measure of body size was the dependent variable. PC1 was negatively associated with temperature. PC2 was positively associated with climatic variability and negatively associated with precipitation

Dependent variable	Independent variable	χ^2	P-value	Est
Proportion blue-green	Year			-0.012
	PC1			-0.002
	PC2			-0.093
	Year \times PC1	10.9	< 0.001	0.0009
	Year \times PC2	5.3	0.022	0.011
Proportion green-orange	Year			-0.015
	PC1			-0.019
	PC2			0.14
	Year \times PC1	9.8	0.0018	0.0019
	Year \times PC2	5.5	0.019	-0.013
Proportion red-orange	Year			0.029
	PC1			0.025
	PC2			-0.07
	Year \times PC1	8.7	0.0033	-0.0031
	Year \times PC2	7.5	0.0061	0.0033
IT span (mm)	Year			0.0059
	PC1			0.0089
	PC2			-0.0018
	Color	10.2	0.006	GO, BG: 0.018 GO, RO: 0.026 BG, RO: 0.008
	Year \times PC1	13.0	< 0.001	0.00025
Length (mm)	Year			0.033
	PC1			0.024
	PC2			0.061
	Color	5.5	0.063	-
	Year \times PC1	10.6	0.0011	0.00022
Year \times PC2	8.1	0.0044	-0.0024	

collecting from cineole than methyl salicylate (red-orange est. = 0.81, $P = 0.033$; green-orange est. = 0.45, $P = 0.033$). There was no difference between red-orange and green-

orange bees in their propensity to collect from one bait or the other (Est. = -0.17, $P = 0.63$), and there was no association of IT span and bait preference (Est. = -1.4; $P = 0.08$).

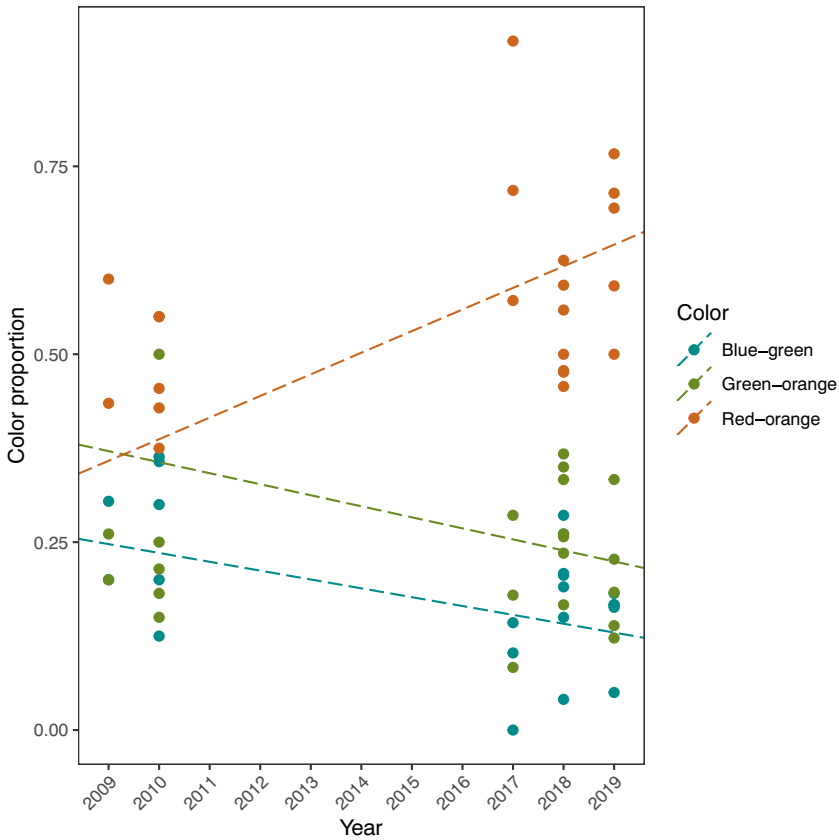


Figure 4 Proportions of bees of each color over the 11-year sampling period for each site sampled in that year. Regression lines reflect coefficients from mixed models used to determine if color proportions change temporally and with climatic conditions of site.

4. DISCUSSION/CONCLUSION

Intraspecific phenotypic variation can enhance species' resilience to environmental changes (Ducatez et al. 2017). Phenotypically distinct individuals often exploit different ecological niches (Forsman and Åberg 2008), so polymorphic species may be buffered from extinction by having some morphs that can withstand the changes (Takahashi and Noriyuki 2019). This study quantified temporal and climate-associated shifts in color and body size for a tropical bee pollinator over a geographic area that has been experiencing continued deforestation and climatic warming. We found increases in a red-orange morph and decreases in blue-green and green-orange morphs over an 11-year sampling period. Body size

increased over time and shifts in both color and body size were associated with temperature and climatic variability.

What drove variation in color among climatic regimes and over time? The disproportional increases in the red-orange morph at sites with higher temperatures would be consistent with this morph having higher temperature tolerance. Studies on whether structural color influences the thermal properties of the insect cuticle are scant, but there is evidence that the thickness of the cuticle can influence the extent to which heat can be lost (Clusella-Trullas and Nielsen 2020). It is also possible that developmental plasticity in response to climatic factors that governs integumental groove size could be responsible for variation in the frequencies of colors along climatic clines. In

Shifts in color and body size for a tropical bee

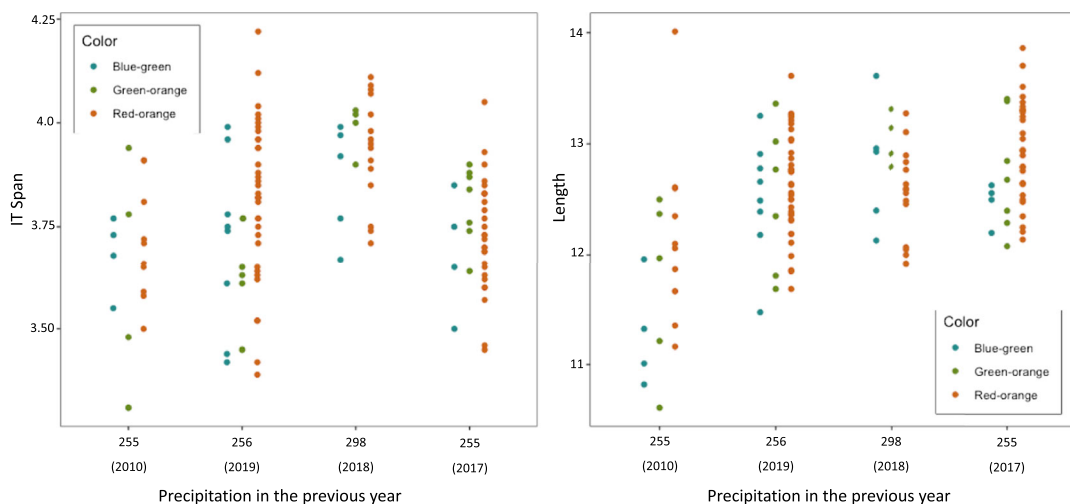


Figure 5 For samples obtained in the forest at the Las Cruces Station, the relationship between IT span and precipitation in the previous year (left panel), and length and precipitation in the previous year (right panel). Colors represent body colors and climatic data reflects values obtained using a weather station on the grounds of the station. Years on the x-axis reflect those in which the samples were obtained.

addition, disproportional heat gain of blue-green bees could be facilitated by their being darker than red-orange bees. Heat gain in insects has been studied in the context of the presence or amount of melanin pigments, with greater melanin leading to more heat gain (Trullas et al. 2007). The presence of melanin pigments was recently described for a Euglossine bee in the genus *Eulaema* (Nemésio and Martins 2013), but it has not been described in the genus *Euglossa*. Bees of the genus *Euglossa* tend to be brightly colored, rather than blackish like bees of the genus *Eulaema*, and may have melanin amounts that are similar among colors. Investigations of both how the spacing among groves influences the thermal properties of integuments and whether integuments of the color morphs differ in the amount of melanin pigments would be helpful to clarify these possibilities.

Shifts in body color proportions could also be driven by changes in the habitat matrix in which bees live. If habitat degradation is associated with habitat color changes, body colors that once provided camouflage may no longer reduce predation (Coker et al. 2009). Massive deforestation of Costa Rican forests is ongoing (Jha and Bawa 2006), and the habitat through which bees travel when

foraging or searching for mates is transitioning from primarily green to a composition of other colors. It is possible that predation on the greener color morphs is higher than that of the redder morph in deforested areas due to higher visibility of these morphs. The evidence we found for resource partitioning suggests that the color morphs could be specializing on different resources, which could be found in different geographic areas. It is also possible that selection for red coloration due to aposematic effects is contributing to the shifts in color proportions. Euglossine bees exist in Mullerian mimicry complexes whereby females of all species possess a powerful sting that predators learn to avoid (Dressler 1979; Dressler 1982), and males mimic females and are also thought to be avoided by predators (Janzen 1981). If Euglossine bees are at risk of predation in open areas, niche partitioning among color morphs could occur, and this could be accelerated by mimicry. We speculate that if the *E. championi* color morphs mimic different other Euglossine species, and bee community composition shifts to favor reddish bees in deforested areas, *E. championi* that mimic reddish species may have higher fitness because of greater predator experience with, and avoidance of, reddish

bees. Studies of the relative importance of aposematism and crypsis to intra and interspecific predation in open and forested areas would therefore be useful.

What do the temporal increases in body size suggest about the relative importance of temperature effects on development, resource availability, or climatic tolerance as possible drivers? Body size in insects is a phenotypically plastic trait that tends to be inversely correlated with developmental temperature (Atkinson 1994). We sampled in an area that is experiencing dramatic climatic warming (Figure 3). If shifts in body size were primarily due to plastic responses to temperature variability, we would expect body size to have decreased over the sampling period. Instead, we found increases in body size across sites over time, suggesting that temperature increases during development have not been the primary driver of trait shifts. The increases in body size also suggest that selection for smaller body sizes due to diminishing resources has not been the primary driver of trait shifts, as has been the case in other geographic areas such as the Netherlands (Oliveira et al. 2016). Instead, several lines of evidence suggest that desiccation tolerance may drive shifts in body size. First, the color morph that decreased the most in abundance at sites with lower precipitation (green-orange) was also the smallest color morph (Table 1; Fig. S5). Second, across the color morphs, the width (IT span) of bees increased during the 11-year sampling period, and it increased more at sites with lower precipitation. Third, at the Las Cruces site, body width increased and body length decreased following years with lower precipitation. While body length measurements have been deemed less reliable than other types of trait measurements in bees (Cane 1987), these data are suggestive of possible changes in shape. Greater width and lower length would increase volume relative to surface area, which could decrease water loss relative to more elongated body forms (Brans et al. 2017).

Given the association of color and body size, to what extent might the changes we document in body size have been driven by selection on color, and vice versa? Regardless of color, body size increased over time, suggesting that changes in body size were not driven primarily by shifts in

color proportions. However, we cannot rule out that changes in color proportions were not driven by selection for larger body sizes. Body size increased over time, and red-orange bees were the largest, so it follows that if there were selection for larger body sizes, this could lead to increases in the proportion of red-orange bees merely because of their body size. Future work that explores thermal tolerances and predation risk of bees of different colors that are similar in body size is therefore warranted.

Previous work has documented variation in desiccation tolerance in insects across environmental gradients (Burdine and McCluney 2019), suggesting desiccation tolerance may mediate the way populations respond to climatic changes. However, adaptation to future environmental changes requires sufficient heritable genetic variation within populations. Hoffman et al (2013) found clinal variation in desiccation tolerance for *Drosophila birchii* across a moisture gradient in Australia, but heritability of desiccation tolerance within the most desiccation-resistant population was low, suggesting limited evolutionary potential. In our case, understanding if trait shifts reflect evolution of greater desiccation tolerance will require examination of how water loss varies with body size in controlled experimental settings, heritability estimates of desiccation tolerance, and evaluation of how variation in tolerance affects fitness across moisture regimes.

The association we found between morphology and climate is somewhat surprising given that Euglossines are capable of long-distance movement (Pokorny et al. 2015). There are also reports of more localized movement of Euglossines over time (Eltz et al. 1999; Wikelski et al. 2010). It may be that while males are capable of long-distance travel, dispersal distances of tens of kilometers may not be common in our study area. Previous work on *E. championi* found no evidence of restricted gene flow among most of the sites used in this study, no structure within sites, and significant genetic structuring only between two sites that are 22 km apart and are separated by deforested land (sites 1 and 2 from this study; Suni et al. 2014). Movement distances of Euglossine bees may be affected by how much heat they can tolerate (Roubik 1993), so it will be

worthwhile to examine if travel distances vary across continuously forested and deforested areas that vary in temperature.

Overall, our finding that color proportions and body size shifted temporally and with climate suggests that these traits may mediate responses of bee populations to environmental changes. Our findings also have potential implications for the plants that rely on Euglossine bees for sexual reproduction. Long-range flights of Euglossines promote gene flow in locally rare plant species (Williams and Dodson 1972). Our finding that traits shift with climate suggests that bees with particular trait combinations may be vulnerable to negative effects of warmer temperatures or lower humidity if they travel through hotter, deforested areas. Understanding how thermal tolerances of bees affect their propensity to travel through deforested landscapes will provide insight into the potential for gene flow in both bee and plant populations.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-021-00875-5>.

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AUTHOR CONTRIBUTION

SS collected the samples, SS and KDC designed the study, KDC performed the morphological measurements, and SS performed the statistical analyses and wrote the manuscript with input from KDC.

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DATA AVAILABILITY

The datasets that support the findings of this study are openly available in Zenodo Repository, DOI: 10.5281/zenodo.4099248. The hourly climatic data for the Las Cruces Biological Station was obtained from the Organization for Tropical Studies (accessed on 9 June 2020 for Station ID: 301; Lat: 8° 47' 7.27" N. Long: 82° 57' 32"; retrieved from: <http://www.tropicalstudies.org/meteoro>).

CODE AVAILABILITY

The R code that supports the findings of this study are openly available in Zenodo Repository, DOI: 10.5281/zenodo.4099248.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

Changements associés au climat dans la couleur et la taille du corps d'une abeille pollinisatrice tropicale.

Couleur / taille du corps / climat / dégradation de l'habitat / pollinisateur / tolérance.

Klima-assozierte Verschiebungen in Farbe und Körpergröße bei einem tropischen Bienenbestäuber.

Farbe / Körpergröße / Klima / Habitatdegradierung / Bestäuber / Toleranz.

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