

Morphological shifts in orchid bees linked to urbanization compromise pollination services

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Abstract

Urbanization creates novel environmental conditions that challenge individual survival. The expansion of building areas, along with habitat loss and rising temperatures in urban areas, not only affect species diversity and composition, but often drive morphological, physiological, and functional changes either as adaptative responses or as outcomes of environmental stress. Such individual-level shifts in key traits can compromise critical ecosystem services like pollination. In this sense, orchid bees (Apidae: Euglossini) are essential pollinators in Neotropical ecosystems and could serve as excellent model organisms for studying whether potential effects of urbanization on morphology compromise specialized pollination services. In this study, we sampled orchid bee communities across 14 sites representing an urbanization gradient in a Neotropical city surrounded by cloud forest in Mexico. We estimated urbanization using satellite imagery, assessed a set of morphometric measurements in the five most abundant orchid bee species, and quantified pollination of *Gongora galeata* (Orchidaceae), a specialized orchid that is exclusively pollinated by *Euglossa obrima*. At the assemblage level (all species together), urbanization was associated with smaller body sizes (i.e. head width) and higher wing asymmetry, revealing developmental stress. In the case of *E. obrima*, wing asymmetry was associated with lower pollination probability of *G. galeata*. These findings suggest that urbanization promotes morphological changes in orchid bees, and such changes at the individual level are compromising pollination, a fundamental ecosystem service provided by these specialized Neotropical bees.

Introduction

Urbanization is driving profound global environmental change by transforming natural landscapes, degrading habitats, and disrupting ecosystem functioning and biodiversity (Alberti, 2008; Grimm et al., 2008). These transformations are associated with elevated temperatures (Oke, 1973), climate instability (Kuttler, 2008), pollution (MdMeftaul et al., 2020), and shifts in resource availability (Wilson & Jamieson, 2019), which act as selective forces and drive contemporary evolution (Johnson & Munshi-South, 2017). Thus, elucidating how organisms cope with rapid environmental shifts is fundamental for predicting biodiversity trajectories and maintaining the stability of ecosystem functions in a rapidly urbanizing world.

Body size is a fundamental life-history trait that in insects influences fecundity, longevity, sexual dominance and attractiveness, thermoregulation, foraging, home range, and energy expenditure (Blanckenhorn, 2000). Previous studies have shown that bees tend to be smaller in human-modified habitats such as cities (Renauld et al., 2016). This pattern may result from two non-exclusive mechanisms. On one hand, urban warming can favor smaller body sizes through faster development in ectotherms (Atkinson, 1995), enhanced flight performance for foraging (Ferrari et al., 2024), and improved evaporative cooling efficiency from a higher surface area-to-volume ratio (Verberk et al., 2021). Second, reduced number of floral resources in urban areas may act as an environmental filter, favoring smaller species or individuals (Grab et al., 2019). Reduced body size in urban environments has also been reported in other arthropods (Weller & Ganzhorn, 2004), but see (Merckx et al., 2018). Species' responses to urbanization vary depending on their ecological and life-history traits (Wenzel et al., 2020), highlighting the need to study multiple species when evaluating urban impacts on wildlife.

Among morphological traits, body symmetry is especially sensitive to environmental stress and can therefore reveal subtle effects of urbanization on insect development (Beasley et al., 2013). In many insect species, urban-related factors such as land use, pollution, or increased impervious surfaces have been linked to changes in fluctuating asymmetry (Rech et al., 2022). This type of asymmetry occurs when there is no consistent directional bias (i.e., sometimes the left side is larger, and other times the right side is larger). Because it reflects developmental instability, it is the most commonly used metric for estimating asymmetry (Leamy & Klingenberg, 2005). Environmental stressors during development, particularly temperature instability, appear to be key drivers of these changes (Beasley et al., 2013). Despite this, the effects of urbanization on insect symmetry remain poorly studied, even though they may have important consequences for ecosystem services such as pollination.

Orchid bees (Apidae: Euglossini) play a critical role as long distance pollinators in tropical America (Janzen, 1971; Roubik, 1989) and are known to be sensitive to urbanization (Allen et al., 2019; Nemésio et al., 2015). These bees pollinate over 800 species of Neotropical orchids, many of which depend exclusively on them for reproduction (Ramírez, 2019). Their interactions with orchids are highly specialized and often require precise morphological traits, such as specific body size, to achieve pollination (Dressler, 1967). Urbanization not only reshapes community structure (da Rocha-Filho et al., 2020), but may also impose selective pressures that affect key functional traits that could have implications in pollination. Previous studies have highlighted the influence of urbanization on orchid bee morphological traits (Añino et al., 2024; Garlin et al., 2022), but the consequences on their pollination function are still poorly understood (Hernández-Rivera et al., 2024). Therefore, we investigated how the urban landscape, specifically the percentage of built area, influences orchid bee body size and fluctuating wing asymmetry, and the consequences of these traits on pollination function. As a result of the stressful conditions generated by urban habitats, we predict that: (i) Orchid bees from areas with higher urbanization will have smaller body sizes than in less urbanized areas. (ii) Fluctuating asymmetry in wings will be positively correlated with urbanization. Finally, (iii) changes in morphological traits, smaller body size and increased wing asymmetry, will have a negative impact on specialized orchid fruit production.

Methods

Study area, sampling and measurements

We conducted fieldwork in the city of Xalapa, Mexico, which is a medium-sized city (~ 600,000 inhabitants; INEGI, 2010) immersed in remnants of cloud forest. Xalapa green areas include gardens, urban parks and cloud forest patches (Capitanachi et al., 2004; García-Campos, 1993), covering ~ 20% of the city with woody vegetation (Lemoine-Rodríguez et al., 2019). Towards the city center, biotic and abiotic changes occur, such as reduction in abundance and diversity of native epiphytes (Aoki-Gonçalves et al., 2023) and an increase of about 5°C in ambient temperature compared to surrounding forested areas (Lemoine-Rodríguez et al., 2019). We established 14 sampling sites along an urbanization gradient, spanning from fully urbanized areas to adjacent conserved cloud forest zones. Each site was separated by at least 400 m and was distributed across two transects, each approximately 7 km in length

(Fig. 1). In these sites, urbanization is clearly associated with a loss of species diversity and pollination services (Hernández-Rivera et al. 2024), but the effects on individual morphology and associated pollination remains unknown.

At each site, we monitored orchid bees from May to July 2023, when bee activity peaks, using two generalist aromatic attractants: eucalyptol and eugenol. Eight traps (four per attractant) were deployed, made from 2.5 L plastic bottles with entrance holes and a cotton wick infused with the attractant. Traps were set for four hours (9:00–13:00), spaced ~ 5 m apart in a straight line. Additionally, bees attempting but failing to enter the trap were captured with entomological nets. Each site was sampled seven times, spaced about a week apart, alternating visits across the 14 sites. Sampling occurred only on sunny or partly sunny days to ensure consistency. To avoid killing the bees, we used a capture-mark-release method. Collected bees were cooled on ice for 3 minutes, marked, photographed, and identified to species level with identification keys for Mexican Euglossini before releasing them (Juárez-Ramos & Hinojosa-Díaz, 2021). Small species (*Euglossa*) were marked on the right wing with a permanent marker and bigger ones (*Eufriesea*, *Eulaema* and *Exaerete*) were marked with tags glued in the scutellum. For the photographs, we placed graph paper on the lid of a Petri dish. Upon capturing the bees, we carefully positioned them in this area to ensure that both the bee and the reference scale were clearly visible in the image.

We analyzed the five most abundant species (Fig. 1C; Supplementary material S1). Body size was estimated from head width (HW; maximum distance between the external lateral margins of the compound eyes) and intertegular distance (IT; distance between tegulae), both measured in ImageJ (Fig. 2D). While intertegular distance is primarily associated with flight capacity (e.g., muscle mass and load-bearing ability), head width is often linked to functional traits, brain volume (Gowda & Gronenberg, 2019) and mechanosensory adaptations (e.g., setae size; Peat et al., 2005). Despite their distinct biological implications, both metrics are strongly correlated with overall body size (e.g., body mass) and can provide complementary insights into ecological traits (Añino et al., 2024).

In addition, to assess asymmetry, we measured the lengths of both the right and left wings and calculated standardized fluctuating asymmetry (FA) using the following formula: $FA = 1/2 (\text{left wing} - \text{right wing}) / (\text{left wing} + \text{right wing})$. Values of asymmetry could be positive (right-side wing larger) or negative (left-side wing larger), while values equal to zero indicate perfect symmetry. To visually assess how bee asymmetry varies across our study sites along the urbanization gradient, we used ridge plots generated with the “ridgeplot” function from the ggplot2 package. Because our main objective was to evaluate asymmetry as an indicator of developmental instability or developmental stress (Vaca-Sánchez et al., 2025), for the statistical analyses we used the absolute value of the asymmetry, discarding variation linked to the direction of the asymmetry (i.e., whether it is skewed to the right or left) (Brito et al., 2021). All bee measurements were made using ImageJ software.

Urbanization metric

Urbanization was quantified using Sentinel-3 satellite imagery, calculating the Normalized Difference Built-up Index (NDBI; Zheng et al., 2021). This index ranges from -1 to 1, where positive values indicate built-up areas and negative values are typically associated with vegetation or water bodies. All satellite images used for urbanization assessments were taken on August 1, 2023. To ensure appropriate scaling for each response variable, where effects are most evident, we applied a series of buffers (radii of 50, 100, 200, 300, 400, 500, and 600 m) to each sampling site. The strength of the association between urban habitat predictors and ecological responses was assessed using the correlation coefficient in models where urbanization metric (NDBI) as predictors, and each ecological trait (HW, IT and FA) as a response variable (Jackson & Fahrig, 2015). We selected the buffer size that provided the best prediction for each response variable (i.e., the highest correlation coefficient), ensuring an optimal spatial scale (Dáttilo et al., 2022; Hernández-Rivera et al., 2024).

Pollination experiment

We used *Gongora galeata* orchid (Orchidaceae: Stanhopeinae) as a model of specialized pollination because it is exclusively pollinated by *E. ohrima* in our study area (Hernández-Rivera et al., 2024). The orchids of *Gongora* genus (subtribe Stanhopeinae) are obligately pollinated by male euglossine bees and are incapable of produce fruits without their pollination service, thus constituting an exemplary model for the study of specialized pollination mechanisms (Liu et al., 2025). We cultivated 56 plants and deployed ~ 3 per site during the flowering season, with a mean of 24 flowers per site. We recorded the initial number of flowers at the time plants were installed, and fruit set (i.e., the number of pollinated flowers that developed into fruits) was assessed two weeks later. In order assess whether bee morphological traits influenced pollination success, we restricted pollination analyses only to seven sites, which were sites with confirmed *E. ohrima* presence.

Statistical analysis

Statistical analyses were conducted in R (R Core Team, 2023). To assess general patterns across species we used generalized linear mixed models to test the effect of NDBI on HW, IT, and FA, with species ID as a random effect with *lme4* package (Bates, 2010). For FA models, head width was included as a covariate to account for size-dependent variation in asymmetry detection. To assess species-specific effects of urbanization on body traits we fitted general linear models for each species separately, testing the effect of NDBI on HW, IT and FA.

To evaluate whether body size or asymmetry of *Euglossa ohrima* influenced pollination probability of *Gongora galeata* across our urbanization gradient we fitted beta-binomial mixed models using the function *glmmTMB* (Brooks et al., 2017). The number of pollinated flowers out of the total flowers per plant was used as the response variable, body size (HW and IT analyzed separately due to high correlation; $r = 0.837$, $t = 7.9505$, $p = 0.03$), FA, and NDBI as fixed effects. Plant ID was included as a random intercept, and we use the mean values of both body size and FA measurements of *E. ohrima* per site as predictor variables. Magnitude of both fixed and random effects can be observed in Table S5.

Results

FA was more heterogeneous in highly urbanized areas, with more pronounced extremes (Supplementary material S2). For the whole assemblage of euglossine bees, we found that more urbanized sites, with larger NDBI values, had bees with higher FA ($p < 0.001$; Fig. 2) and reduced HW ($p < 0.001$) but no differences in IT (Table 1). When analyzing species individually, urbanization was associated with increased FA ($F = 19.53$; $p < 0.001$; Supplementary material S3) and smaller HW ($F = -0.239$; $p < 0.001$) of *Euglossa viridissima*, but no significant effects in other species. Urbanization did not affect the IT of either species. Our analysis of *G. galeata* pollination revealed that sites with higher *E. ohrima* FA had lower pollination ($z = -2.42$, $p = 0.02$; Fig. 3; Table 1), as did sites with higher NDBI ($z = -2.01$, $p = 0.043$). In contrast, neither IT nor HW were associated with pollination.

Table 1

Model results of each response variable indicating buffer size as scale of effect. Significant results showed in bold. For morphometric response variables linear models with gaussian distribution and for pollination model binomial distribution.

	Head width (HW; 100mts)			Intertegular distance (IT; 200 mts)			Absolute asymmetry (100mts)			Pollination probability (300 mts)		
Predictors	Est	CI	p	Est	CI	p	Est	CI	p	Est	CI	p
NDBI	-0.203	-0.30 – -0.11	< 0.001	-0.006	-0.08 – 0.07	0.87	0.022	0.01 – 0.03	< 0.001	-41.42	-81.68 – -1.15	0.04
IT							0	-0.01 – 0	0.277			
HW										-4.45	-19.22 – 15.32	0.939
<i>E. ohrima</i> asymmetry										-219.44	-396.86 – -42.02	0.02
Random Effects												
σ^2	0.02			0.01			0			0.82		
τ_{00}	0.03 _{species}			0.07 _{species}			0.00 _{species}			0.00 _{ID}		
ICC	0.67			0.85			0.01					
N	5 _{species}			5 _{species}			5 _{species}			19 _{ID}		
Observations	423			429			397			29		

Discussion

In this study, we present evidence that urbanization is a driver of morphological variation in orchid bees, with consequences on orchid pollination. Consistent with our first prediction, HW decreased with increasing urbanization. This pattern may arise from anthropogenic stressors such as habitat fragmentation and reduced floral resources (Wray et al., 2014), which can lead to smaller body size through phenotypic plasticity (e.g., developmental constraints leading to smaller size) and/or natural selection (e.g., within a population, only smaller individuals survive). Elevated thermal stress may constrain growth (Atkinson, 1995; Oke, 1973). In this context, smaller orchid bees, such as *Euglossa*, are able to dissipate heat more efficiently than larger genera like *Eufriesea*, *Eulaema*, and *Exaerete*, owing to differences in body size and pubescence (May & Casey, 1983). Resource-limited conditions, where traits such as shorter development time and more efficient resource use confer advantages, despite potential trade-offs with fecundity or dominance (Goldenberg et al., 2022; Verberk et al., 2021). Similar reductions in body size have been found in other studies in bees in cities and agricultural lands (May-Itzá et al., 2021; Garlin et al., 2022) and these changes could have significant ecological consequences, potentially affecting bees' foraging range, pollination efficiency, and survival in thermally stressful urban environments (Jauker et al., 2016). Finally, the absence of urbanization effects on IT, trait linked to flight musculature (O'Neill, 1983), may indicate preserved flight capacity in these bees. This could be a response to the need for specialized species like *Euglossa* to forage over larger distances in fragmented urban landscapes (Ferrari et al., 2024; Tommasi et al., 2022) maintaining this trait under stabilizing selection (Buchholz & Egerer, 2020).

Regarding our second prediction, as expected, wing FA was positively correlated with urbanization. Urban ecosystems are often characterized by unstable microclimates (Chapman et al., 2017) and heterogeneous resource availability (Baude et al., 2016), factors that may disrupt normal developmental processes, leading to greater morphological deviations (Vanderplanck et al., 2019). Our results suggest that *Euglossa viridissima* responds strongly increasing asymmetry with urbanization. We propose for future studies to investigate the effects of body asymmetry on orchid bee reproduction, pollination, and flight capacity and to explore the long-term consequences of developmental instability, especially in changing urban climates.

According to our third prediction, we found that high wing FA in *Euglossa ohrima* negatively affected fruit production of *Gongora galeata*. To our knowledge, no previous studies have directly linked pollinator symmetry to pollination, although floral symmetry is well known to mediate plant–pollinator interactions (Kooi et al., 2021). By analogy, asymmetry in traits critical for flower handling (e.g., wings, legs) may disrupt contact with reproductive structures, reducing pollen transfer and plant fitness (Møller, 2000). Despite this, mechanistic studies on native species are needed to evaluate how urbanization-induced asymmetry may destabilize specialized mutualisms, particularly in native species where knowledge remains limited (Liang et al., 2023).

Although bee body size is a key determinant of pollination type (for example, larger bees typically perform buzz pollination whereas smaller bees can access narrow flowers; De Luca & Vallejo-Marín, 2013; Fenster et al., 2004), the absence of a body size related pattern in pollination observed in this study may reflect either the generalized foraging strategies of the pollinator (Cane & Schiffhauer, 2003) or the limited size variation dependence in this species (Gérard

et al., 2020). However, orchid pollination by euglossine bees is known to be highly sensitive to morphology, as orchids such as *Gongora* rely on precise pollen placement (Hetherington-Rauth & Ramírez, 2015). Even minor deviations in symmetry or size could impair pollen attachment or transfer. This suggests pollinator asymmetry may represent an overlooked factor in the stability and coevolution of specialized mutualisms.

In conclusion, urbanization appears to exert multifaceted pressures that not only affect key morphological traits but also pollination services provided by bees, potentially limiting flight performance and foraging efficiency. Future research should aim to disentangle the relative contributions of specific urban stressors such as chemical pollution, thermal stress and nutrient availability to the morphological changes and their effects on orchid pollination. Understanding and investigating the effects of urban landscape characteristics on multiple traits of species could provide insights about conservation management strategies for native pollinator species and their specialized services in the context of global environmental change.

Declarations

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Competing interests

The authors declare no conflicts of interest related to this work.

Author contributions

A.H.R. Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **D.I.D.P.** Writing, Methodology, Data curation. **P.H.O.R.** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization, Visualization. **W.D.** Writing, Methodology, Writing – review & editing. Validation, Investigation. **B.M.** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Conceptualization. **D.G.T.** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Formal analysis, Conceptualization, Project administration.

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Figures

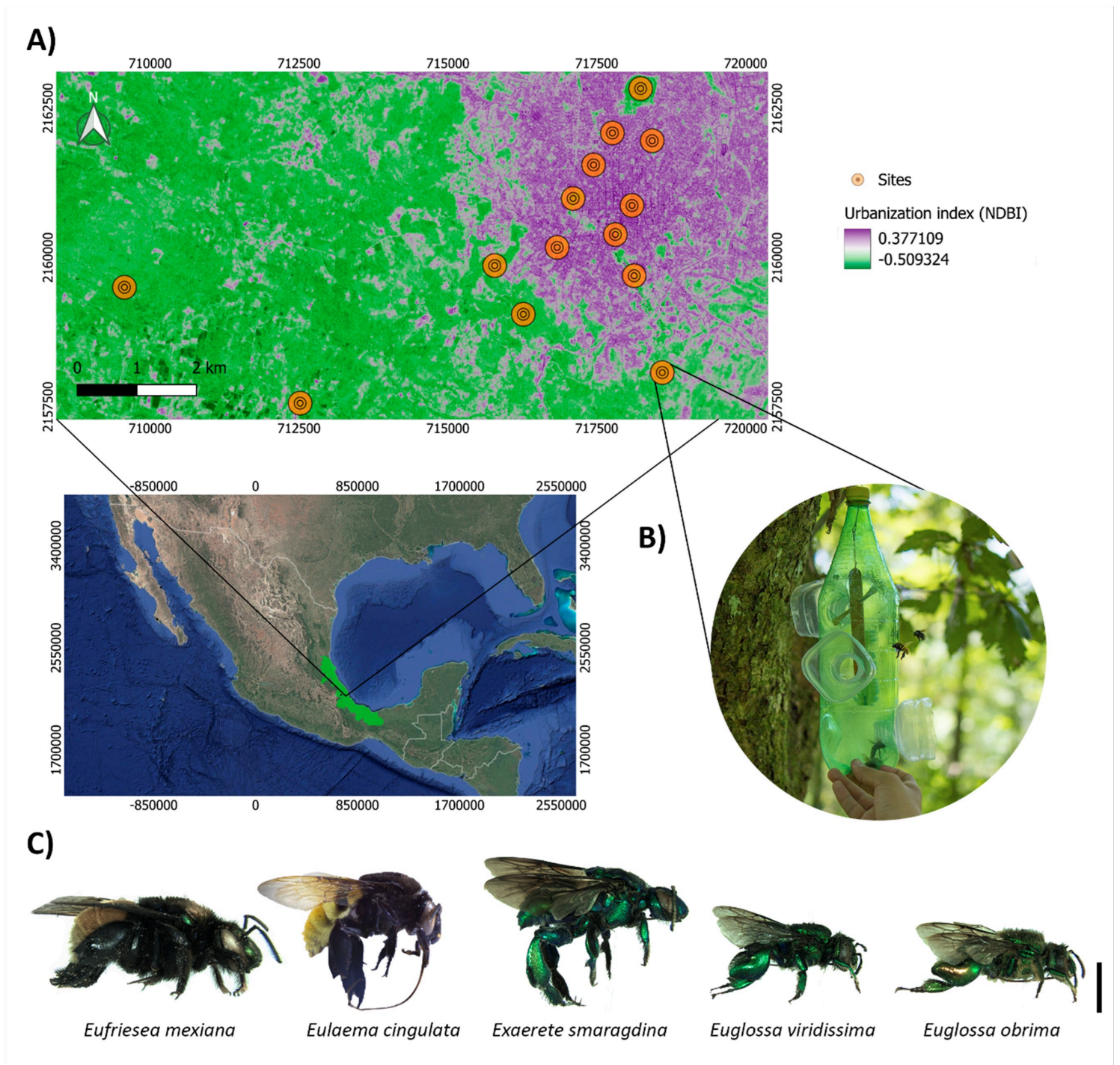


Figure 1

(A) Map of the study sites evaluating the effects of urbanization on orchid bee morphometry and pollination. Colors represent normalized difference built-up index (NDBI) as urbanization index with a gradient between purple (urban) and green (vegetated) sites. Circles represent different buffer sizes (50, 100 and 200 m of radii). (B) Attractive traps made from 2.5 L plastic bottles with entrance holes and a cotton wick infused with the attractant. (C) Bee species studied; the black bar indicates 5 mm scale.

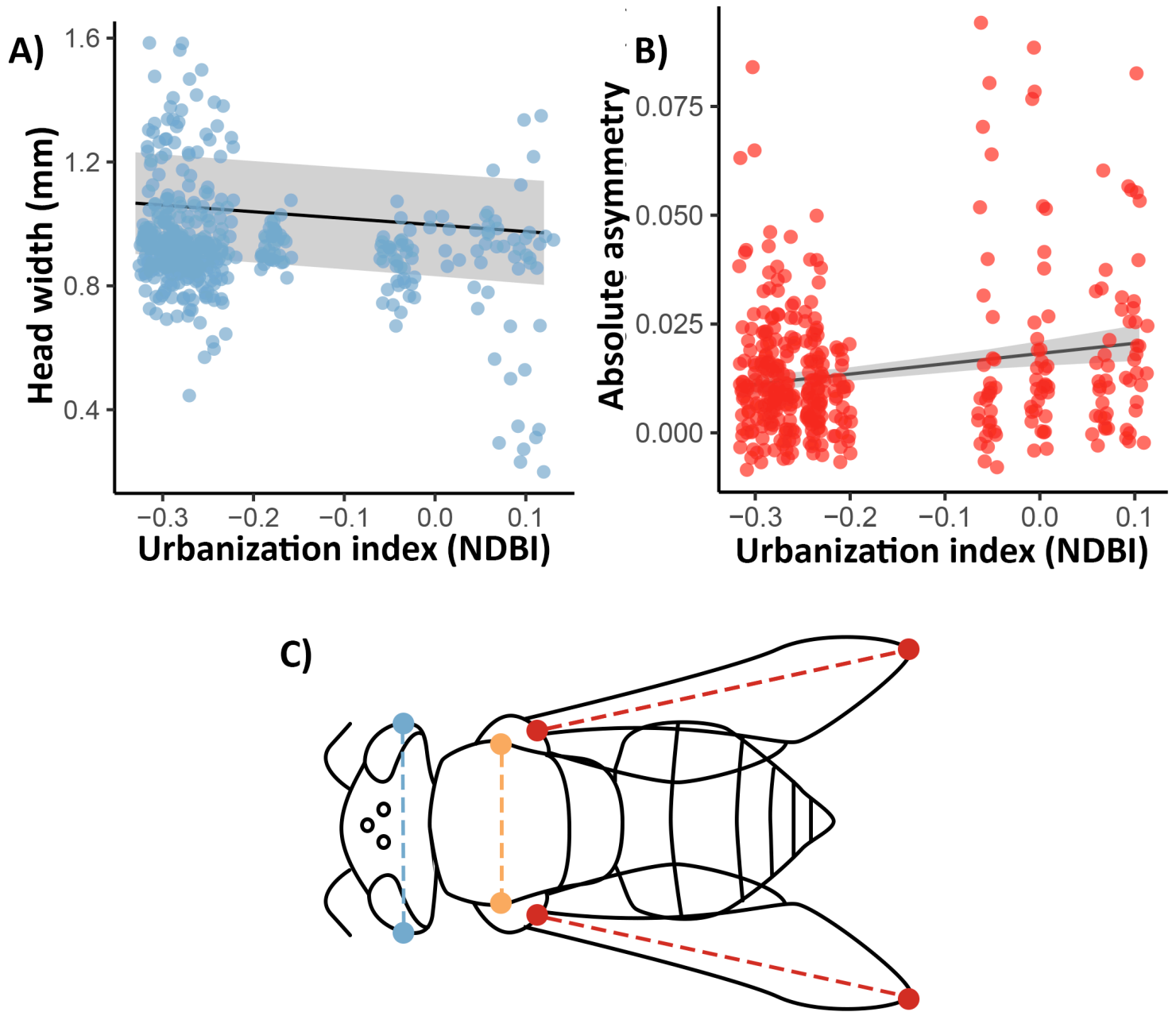


Figure 2

Head width (A) and asymmetry (B) of whole assemblage of euglossine bees in 14 sites representing an urbanization gradient. NDBI values are higher in more urbanized areas and lower in vegetated areas. Lines show model results and grey shadows 95% CI. Measurements for intertegular space, head width and wing asymmetry (C).

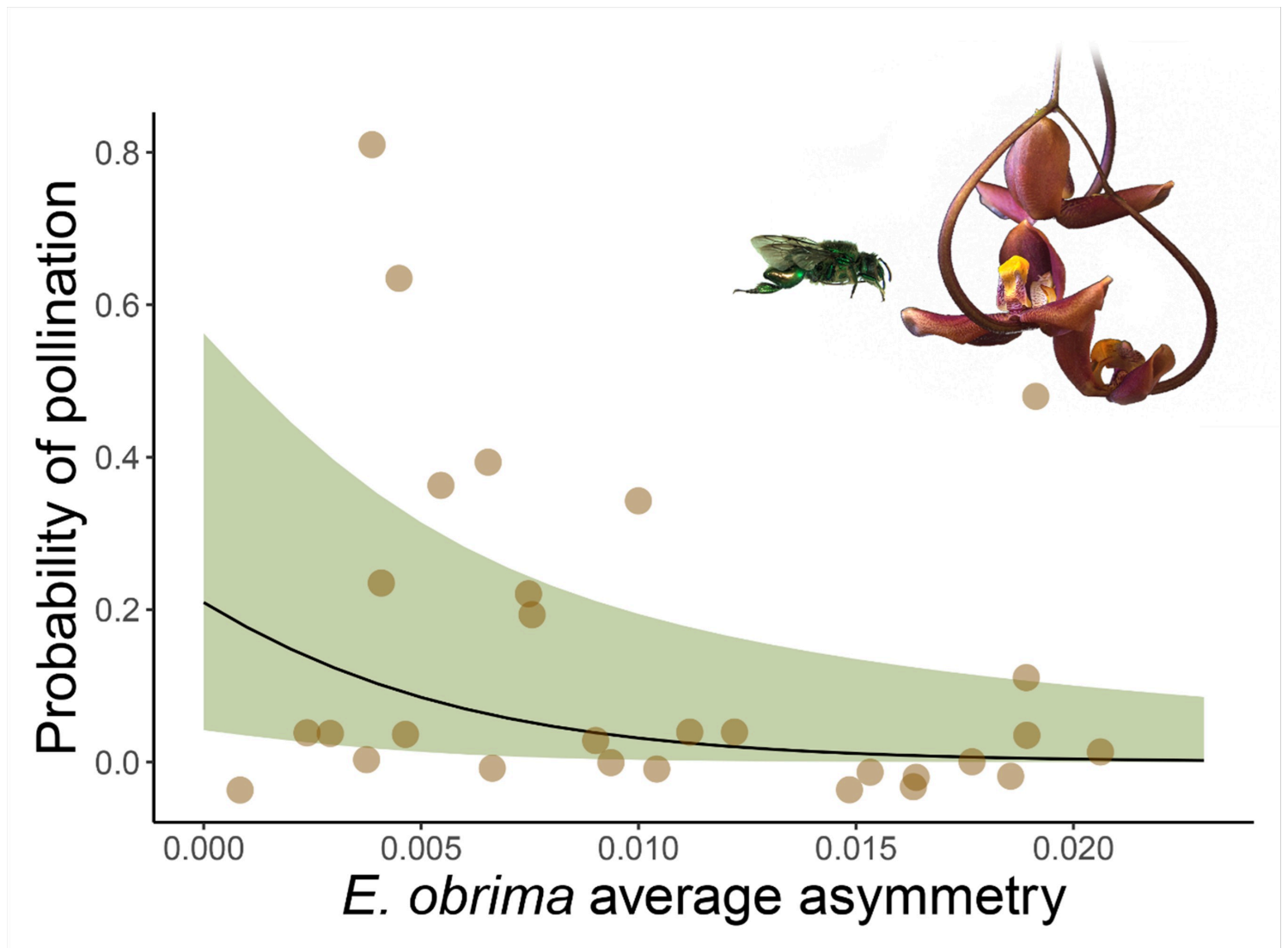


Figure 3

Gongora galeata probability of pollination (pollinated flowers out of the total flowers per plant) depending on *Euglossa obrima* asymmetry. Each point represents a floral spike ID; individual plants could flower multiple times, and each flower was treated as an independent observation of pollination probability ($n = 29$).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Scriptymatizeuglossini.rproj](#)
- [Gongorapollination1.csv](#)
- [scripteuglossiniasymmetry1.r](#)
- [matrix1.csv](#)