Thermal flexibility and a generalist life history promote urban tolerance in butterflies

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ABSTRACT

Urban expansion poses a serious threat to biodiversity. Given that the expected area of urban land cover is predicted to increase by 2-3 million km^2 by 2050, urban environments are one of the most widespread human-dominated land-uses affecting biodiversity. Responses to urbanization differ greatly among species. Some species are unable to tolerate urban environments (i.e., urban avoiders), others are able to adapt and use areas with moderate levels of urbanization (i.e., urban adapters), and yet others are able to colonize and even thrive in urban environments (i.e., urban exploiters). Quantifying species-specific responses to urbanization remains an important goal, but our current understanding of urban tolerance is heavily biased towards traditionally well-studied taxa (e.g., mammals and birds). We integrated a continuous measure of urbanization — VIIRS night-time lights — with over 900,000 species' observations from GBIF to derive a comprehensive analysis of species-specific (N=158 species) responses of butterflies to urbanization across Europe. The majority of butterfly species included in our analysis avoided urban areas, regardless of whether species' urban tolerances were quantified as a mean score of urban tolerance across all occurrences (79%) or as a species' response curve to the whole urbanization gradient (55%). We then used the species-specific responses to urbanization to assess which life history strategies promote urban tolerance in butterflies. These trait-based analyses found strong evidence that the average number of flight months, likely associated with thermal niche breath, and number of adult food types were positively associated with urban tolerance, while hostplant specialism was negatively associated with urban tolerance. Overall, our results demonstrate that specialist butterflies, both in terms of thermal and diet preferences, are most at risk from increasing urbanization, and should thus be considered in urban planning and prioritized for conservation.

Keywords: GBIF; butterflies; lepidoptera; trait-based ecology; climate change; generalism

INTRODUCTION

Anthropogenic habitat modification is, and will continue to be, one of the most significant drivers of biodiversity declines (Pereira et al. 2010; Barlow et al. 2016; Matuoka et al. 2020). Of the various anthropogenic stressors, urbanization is one of the most widespread near-term threats to biodiversity assemblages (McDonald et al. 2019). Urbanization directly leads to habitat loss, fragmentation, and degradation (Liu et al. 2016). Moreover, urbanization is associated with increased noise (Francis et al. 2011), light (Hopkins et al. 2018), and chemical (Kabir et al. 2014) pollution, which also adversely impacts biodiversity (McKinney 2006). With the expected amount of urban land cover to increase by 2-3 million km^2 by 2050 (Huang et al. 2019), it is critical to understand how biodiversity responds to urbanization.

While the evidence is clear that urbanization can significantly alter biological communities (Fenoglio et al. 2020), in many cases leading to biotic homogenization (McKinney 2006), there is a large range of responses among species (Threlfall et al. 2012; Lintott et al. 2016; Gippet et al. 2017). Some species have adapted to (Homola et al. 2019), and are even thriving in, urban environments (Evans and Gawlik 2020), while others have been extirpated by urbanization processes (Warren et al. 2019). In general, species can be placed along a continuum according to their response to urban environments. On one end of this continuum, species preferentially avoid urban areas leading to displacement in the face of increasing urbanization. And on the other end of this continuum, species persist in, or even colonize, urban environments to take advantage of various aspects of the form and structure. Quantifying the extent to which a given species is able to tolerate urban environments is important for restoration prioritization and for incorporating biodiversity in future urban planning (e.g., Winchell et al. 2017).

A species' ability to tolerate urban environments is a result of that species' unique life history and circumstances, including the species it interacts with (Martin and Bonier 2018), its niche breadth (Bonier et al. 2007; Palacio 2020), various life history traits (Rodewald and Gehrt 2014; Lowe et al. 2017; Jung and Threlfall 2018; Callaghan et al. 2019), phylogenetic predisposition (Sol et al. 2017), or cultural influences (Clucas and Marzluff 2012). This body of previous research has highlighted the complexity of this question, and results have been largely inconclusive. However, ecological theory predicts that species traits may be useful predictors to describe generalities across species (Vallet et al. 2010; Barnum et al. 2017; Jung and Threlfall 2018). Identifying these general patterns in the types of species most at risk from increasing urbanization will also aid conservation decision-making.

Our current understanding of urban tolerance and the relationship between urban tolerance and ecological and life history traits is heavily biased towards traditionally well-studied taxa (e.g., mammals and birds). Much is known about the ability of traits to predict urban tolerance in birds (Callaghan et al. 2019; Palacio 2020), mammals (Santini et al. 2019; Uchida et al. 2020), and amphibians (Winchell et al. 2020; Martínez-Gómez 2020). For other taxa, such as insects, the response to urbanization remains poorly quantified, but there is evidence that some taxa are more affected than others (e.g., Fenoglio et al. 2020). It is increasingly important to better understand how insects are responding to increasing urbanization, given the potential declines of insects at various spatial scales (Wepprich et al. 2019; Piano et al. 2019; Didham 2020; Svenningsen et al. 2021).

Butterflies have large geographic ranges, occupy a number of different niches, are popular with the general public and hence citizen science monitoring, and can be used as indicators of environmental change due to their sensitivity to local environmental changes at small scales (Blair 1999; Essens et al. 2017). These attributes combine to make butterflies an excellent taxa to quantify responses to urbanization. Although butterflies are negatively impacted by urbanization (Mata et al. 2014; Tzortzakaki et al. 2019; Fenoglio et al. 2020; Kurlyo et al. 2020), minor changes in urban greenspace management (e.g., connectivity) can help foster and lead to an increase in butterfly diversity within urban environments, suggesting species are affected by the relative amount of urban surfaces compared to green surfaces (Mata et al. 2014; Dylewski et al. 2019; Nagase et al. 2019; Iserhard et al. 2019). But as with other more well-studied taxa, certain species are more likely to tolerate urban environments than other species and species-specific responses to urbanization still need to be quantified (Mata et al. 2014).

Our objective was to quantify species-specific measures of urban tolerance for European butterfly species at a macroecological scale (i.e., continental Europe) using a continuous measure of urbanization. First, we integrated these species-specific measures of urban tolerance with trait data to test which traits best predict urban tolerance in butterflies. We expected that certain life history and ecological traits would correlate with urban tolerance (see Table 1 for details on traits tested and predictions), including climate tolerance such as flight period and overwintering strategy (Pöyry et al. 2006), the degree of generalism (Bartanova et al. 2014), body size (Coulthard et al. 2019), microhabitat use (Essens et al. 2017), and general life history traits such as voltinism and egg laying type (Wepprich et al. 2019). Second, we applied a cluster analysis across all species to characterize the most typical species' response curves to urbanization and the complex of traits associated with each type of response. Ultimately, these analyses help to identify the species that are most at risk from increasing urbanization.

METHODS

Butterfly observation data from GBIF

We downloaded data from the Global Biodiversity Information Facility (GBIF) for butterfly occurrence throughout continental Europe (GBIF.org 2020). We downloaded data from 2010 to 2020 and only considered observations of butterflies in Europe (i.e., from Papilionidae, Hesperiidae, Pieridae, Riodinidae, Lycaenidae, and Nymphalidae). Only observations that had coordinates and did not have geospatial issues, as flagged by GBIF, were kept for potential analysis. We removed possible GBIF duplicates from analysis by removing any observations that had the same date, latitude, longitude, and species.

We defined a near-contiguous European region for analysis to account for geographic heterogeneity in the number of records (see Table S1 with the countries included in the analysis and the corresponding sample sizes). We trimmed the extent to exclude predominantly offshore islands and regions with disparate records from the analysis (see Figure S1 for the study extent).

Urban tolerance of butterflies

We estimated a measure of urban tolerance for each species along a continuum of urbanization. This approach is similar to what others have used to calculate species’ thermal tolerances (e.g., Devictor et al. 2012). We overlaid GBIF observations with a continuous measure of urbanization: VIIRS night-time lights (Elvidge et al. 2017). VIIRS night-time lights measure the radiance in the night-time sky, which strongly corresponds to urbanization processes such as human population density and urban form and function (Pandey et al. 2013; Zhang and Seto 2013; Stathakis et al. 2015). It has an added advantage that it is globally applicable, and open-source data, allowing for the applicability of our analysis in other parts of the world. We took the median values of all images from 2014-2020 at the native resolution of 15 arc-seconds (~ 500 m) (Evlidge et al. 2017). See Callaghan et al. 2020a for more details about this process. Spatial analyses were performed in Google Earth Engine (Gorelick et al. 2017). We acknowledge that butterflies can necessarily select habitat at spatial scales less than 500 m, but our analysis here was focused on landscape-level responses.

After each observation was assigned a measure of VIIRS night-time lights at a continuous scale, each species had a distribution of their frequency of use along an urbanization gradient (e.g., Figure S2). Only species with a minimum of 250 observations were considered for analyses as this has been shown previously to minimize the variance in response to urbanization among species and be applicable at localized spatial scales (Callaghan et al. 2020a; Callaghan et al. 2020b). Because each species differs in their geographic extent across Europe (Schweiger et al. 2014) we adjusted the distribution of VIIRS night-time light levels for each species by standardizing for (1) the available urban habitat in a species' range and (2) the bias in sampling observations in a species' range relative to urban habitat (Callaghan et al. 2020c, Liu et al. 2021). To do this, we created a concave hull around the observations for each species using the concaveman package in R (Gombin 2020). We then subtracted the mean of all VIIRS values for all observations within a species' range from the mean of all VIIRS observations for a given species. This provides a value that can be negative (species under-occupy urban areas suggesting they actively avoid them) or positive (species over-occupy urban areas suggesting they prefer them). This measure of urban tolerance was treated as our response variable in further analyses and referred to as an urban tolerance score. The urban tolerance score was strongly correlated with the breadth of urbanization used by a species as well, calculated by the interquartile range of species' distribution to VIIRS night-time lights (see Figure S3). In other words, species with higher mean urban tolerance scores also occupied areas with a large range of VIIRS values.

To confirm that our measure of urban tolerance captured the continuum in species-specific responses, and was not driven by detection bias of species towards urban areas, we ran an additional analysis using occupancy-detection models. We modelled relationships between species' occurrence patterns and the level of urbanization using species-specific occupancy models, also allowing urbanization to affect detection probabilities, in the unmarked package (Fiske and Chandler 2011). There was a strong correlation in the estimated urban tolerances between these two markedly different approaches, and we therefore focused our analyses on the urban tolerance score described above, which is a simpler and more generalizable approach (see details in Figure S4).

Life history and ecological traits

Based on known relationships in the published literature, we developed a trait framework that involved five broad categories of traits (i.e., extent of specialization, body size, microhabitat use, life history, and climate tolerance), each with one or more specific variables to represent these categories, with a total of 11 different traits (Table 1). The traits investigated were: (1) average number of flight months; (2) overwintering strategy; (3) mean temperature in a species' range;

(4) number of adult food types; (5) hostplant specificity; (6) hostplant specialism index; (7) wind index; (8) mean voltinism; (9) egg laying type; (10) hostplant growth forms; and (11) number of egg laying locations. Trait data were extracted from Middleton-Welling et al. 2020 for all traits besides the mean temperature of a species' range (a measure of thermal preference), which was extracted from Schweiger et al. 2014. After taxonomic matching (all names were matched to the taxonomy provided by Middleton-Welling et al. 2020), we were left with 159 species that had both an urban tolerance score and associated trait data (Table S2). One of these species, however, Geranium Bronze (*Cacyreus marshalli*) had an urban tolerance score 5x greater than any other species in our dataset because it is a known invasive pest that often relies on houseplants and has known synanthropy with novel anthropogenic environments (Quacchia et al. 2008). This was the only species in the dataset that was not native to our study region within Europe. This species was regarded as an atypical, outlier species, and thus excluded from our analyses.

Statistical analysis

We approached our analysis from different angles, using different statistical tools, to provide complementary evidence and visualizations on how urban tolerance was associated with species' traits. In brief, this involved: (1) correlation analysis to examine simple correlations among all traits; (2) multiple regression analysis to focus on understanding variation in urban tolerance and partial effects of other traits; (3) boosted regression trees to examine non-linearity and account for interactions among traits; and (4) clustering analysis to visualize the dominant trait clusters associated with an urbanization gradient.

Correlation and Regression modelling. First, for all numeric predictor variables (N=10), we assessed the pairwise relationships between urban tolerance and the predictor variables using Pearson correlation coefficients. Second, to assess the strength of the relationship between a given predictor variable and urban tolerance, accounting for the relationship of all other predictor variables, we used multiple linear regression with a Gaussian distribution. The response variable was urban tolerance, and the predictor variables (N=11) were: the average number of flight months, wing index, mean temperature in range, the number of adult food types (log10 transformed), mean voltinism, the number of hostplant growth forms, the number of egg laying locations, hostplant specificity, egg laying type, hostplant index (log10 transformed), and overwintering stage. Egg laying type was a categorical variable with three levels (single, small, and large batches) but was dummy-coded in the multiple linear regression because it showed little correlation with the response variable in exploratory analyses; we therefore did not assess differences among the levels of egg laying type. Parameter estimates from the model were standardized by centering and dividing 2 standard deviations (Gelman 2008). In addition to the large model with all the traits, we ran two separate linear regressions between urban tolerance and overwintering stage and hostplant growth form, respectively (see Table 1). These two traits were treated separately as each trait was associated with multiple binomial levels, and we wanted to avoid over-inflating the number of predictor variables in a single multiple linear regression. In each instance, the possible overwintering stages (i.e., egg, larval, pupal, adult) and possible hostplant growth forms (i.e., shrub, tall herb/grass, short herb/grass, and tree) were treated as binomial predictor variables in separate multiple linear regressions. For all three multiple linear regression models, we used weights in the model-fitting procedure where more weight was given to a species based on the number of observations of that species used to derive its urban tolerance score, but the number of observations was capped at 1000 to ensure that our results were not driven by a few species with high weights.

Boosted regression trees. We also performed a third analysis, using boosted regression trees (Elith et al. 2008). This analysis is advantageous because it allows for both linear and nonlinear relationships between urban tolerance and the ecological and life history traits of butterflies, as well as complex interactions among the predictor variables themselves. Because of the robustness of this analysis, we included all possible predictor variables from the three multiple linear regressions mentioned above (N=19), testing our entire suite of different predictions (Table 1). Although predictor variables do not need to be transformed for boosted regression trees (Elith et al. 2008), we kept the log10-transformed versions of hostplant index and the number of adult food types for consistency with the multiple linear regression modelling. First, we extracted the relative influence for each predictor variable, which shows the effect of each predictor variable on the response variable normalized to sum to 100 (Friedman 2001; Elith et al. 2008). Second, for any variable that explained >5% of the total relative influence, we produced partial dependency plots that illustrate the influence of a given predictor variable accounting for the average effects of other predictor variables (e.g., Vilmi et al. 2019). The boosted regression tree analysis was performed using the dismo package in R (Hijmans et al. 2017). We used a tree complexity of 5, a learning rate of 0.001, and a bag fraction of 0.5 (e.g., Elith et al. 2008; Buston and Elith 2011; Vilmi et al. 2019). Exploratory analyses varying the level of tree complexity, learning rate, and bag fraction showed no difference in the quantitative or qualitative results.

Clustering analysis. To characterize the trait values associated with the most typical patterns of species' urban tolerance, we used Generalized Additive Models (gams) in combination with clustering analysis. We used gams to model the presence/absence of species in 5 x 5 km grids within their distributional extent (delineated by the convex hull of their occurrence records) with urban cover in each grid as the predictor, as a spline term. A gam was fit to each species separately, assuming a binomial error distribution, and VIIRS within each species range was logged (to the base 10) and scaled between 0 and 1 for each species' gam. We used a spline to allow a non-linear relationship between species occupancy and VIIRS, and hence accommodate the diversity of possible species' urban response curves. However, we constrained the spline to a low number of knots (k=5) to minimize biologically unrealistic multi-modal response curves from being fit. Using the fitted gam, we then predicted the occupancy probability of each species within grid cells of varying VIIRS values between 0 and 1 (in sequential steps of 0.05). Once we had characterized the response curve of each species to varying urban cover amounts (VIIRS), we then identified the most typical response curves using a clustering analysis. We first calculated a dissimilarity matrix among species' response curves. Since we were not interested in differences in the mean occupancy of species but rather relative differences in occupancy according to urban cover, we used a correlation-based dissimilarity metric (Pearson correlation coefficient). We then used hierarchical partitioning to split the dissimilarity matrix into discrete groups (i.e., clusters) of species sharing the most similar urban' response curves. To identify the most appropriate number of clusters, we compared several cluster metrics including Dunn's index, silhouette widths, and minimum cluster size and meaningful biological interpretation. For each cluster, we calculated the mean occupancy of species at each VIIRS value and bootstrapped the species values to provide 95% confidence intervals. Finally, we visualized the distribution of species traits in each cluster to identify the suite of traits values associated with each.

Data analysis and availability

All data analysis was conducted in R statistical software and relied heavily on the tidyverse (Wickham et al. 2019). Statistical significance, in the case of multiple linear regressions, was concluded at alpha <0.05. Code and data to reproduce these analyses are currently available here (https://github.com/coreytcallaghan/butterfly_urbanness) and will be permanently archived in a Zenodo repository upon acceptance of this article.

RESULTS

We used a total of 922,687 observations for 158 species to position each species' urban tolerance along an urbanization-tolerance continuum. The mean number of observations per species was 5840 (± 9748 SD). A total of 125 species (79%) had an urban tolerance score < 0, suggesting that they disproportionately use less urbanized habitat in comparison with that available within their range. The mean urban tolerance score was -0.73 (+/- 1.60) (Figure 1). The most urban tolerant species was *Polygonia egea* (urban score=5.97), followed by *Satyrium w-album* (urban score=4.29), *Thecla betulae* (urban score=3.56), and *Pieris rapae* (urban score=3.44). In contrast, the least urban tolerant species were *Euphydryas maturna* (urban score=-4.37), *Muschampia proto* (urban score=-3.84), *Hipparchia fidia* (urban score=-3.77), and *Glaucopsyche melanops* (urban score=-3.63) (Figure 1). For an interactive version, showing the urban tolerance scores for the 158 species included in analysis, see here.

Pairwise relationships between the urban tolerance score and ecological and life history traits (Figure 2; Figure 3) showed that urban tolerance was positively correlated with all variables aside from hostplant specialism index. In particular, urban tolerance was strongly correlated with the average number of flight months (r=0.53) and mean voltinism (r=0.45), and less weakly correlated with the number of adult food types (r=0.28). There was weak positive correlation between mean temperature in range (r=0.11) and urban tolerance, and there was a negative relationship between urban tolerance and hostplant specialism index (r=-0.24). Overall, our predictions matched the expected relationship for our numeric variables (cf Table 1 and Figure 3a).

Our multiple linear regression explained the variance in urban tolerance reasonably well (R^2=0.38), showing that there was strong evidence (i.e., confidence intervals did not overlap zero) that the average number of flight months and the number of adult food types were the most important traits associated with urban tolerance (Figure 3b). The other traits were not significantly associated after accounting for the effects of these two traits. However, weak evidence was found for a positive relationship between mean voltinism, wing index, and number of hostplant growth forms and urban tolerance. A separate multiple linear regression for binomial traits of hostplant growth forms showed that species associated with all four types of hostplant growth forms were more likely to be tolerant of urban environments, but there was strong evidence for species that associated with shrub hostplant and tall herb/grass (Figure S5). For the overwintering stage, a separate multiple linear regression showed that species overwintering as adults and pupae showed a positive relationship with urban tolerance, whereas species that overwinter as larvae or eggs showed a negative relationship with urban tolerance. There was strong evidence that species that overwinter in the larval stage are negatively associated with urban tolerance (Figure S6).

Boosted regression tree analysis showed that our predictor variables explained 23.8% of deviances in urban tolerance of butterflies. The most important predictor variables — those that explained >5% of relative influence — were the average number of flight months (35.5%), mean temperature in a species range (14.5%), hostplant specialism index (11.4%), wing index (10.7%), overwintering stage as larvae (7.1%), and the number of adult food types (6.3%) (Figure 3c; Figure 3d). The boosted regression tree analysis showed the non-linear patterns in these predictor variables. For the average number of flight months, there were marginal gains in urban tolerance from ~ 4–6 flying months per year, but then from ~6–8 there was a strong increase in the relationship with urban tolerance. Hostplant specialism index showed a generally smooth decline in its association with urban tolerance, and wing index showed a non-linear positive response with urban tolerance. In contrast, mean temperature in a species range showed a non-linear response with a positive association from about 0 degrees Celsius to 10 degrees Celsius, followed by a negative association with urban tolerance from about 10 degrees Celsius to 15 degrees Celsius (Figure 3d; Figure 2).

Our cluster analysis of responses to urbanization supported an ecological interpretation of three main clusters generalizing the diversity of species-specific responses to urbanization along a gradient of urbanization (Figure 4a), showing relatively strong agreement with our urban tolerance scores (Figure S7). Cluster 1 (N=25 species) grouped together species most common in high urban areas — i.e., urban exploiters; cluster 2 (N=46 species) grouped together species most common at intermediate levels of urbanization — urban adapters; and cluster 3 (N=87 species) grouped together species that were most common at low urban areas and rarely occurred outside of low urban areas — i.e., urban avoiders (Figure 4a; Table S2). When these clusters were mapped onto species-specific traits, we found a general increase from cluster 3 (least urban tolerant) to cluster 1 (most urban tolerant) in the number of average food types eaten by adults (Figure 4b) and the number of average flight months (Figure 4e). Typically, species in cluster 1 had a flight period of ~ 7 months, while species in clusters 2 and 3 were flying ~ 3–5 months during the year, on average. Also, the number of adult food types was typically 3 for species in cluster 1, but fewer than 3 types in the other clusters. We also found a general decrease from cluster 3 to cluster 1 in the hostplant specialism index values (Figure 4c). There were no apparent differences among clusters for the mean temperature in range, yet the most warm-adapted species tended to be captured in cluster 1 (Figure 4d).

DISCUSSION

We integrated a continuous measure of urbanization — VIIRS night-time lights — with over 900,000 species' observations from GBIF to derive a comprehensive analysis of species-specific (N=158 species) responses of butterflies to urbanization across continental Europe. The majority of butterfly species included in our analysis were shown to avoid urban areas (Figure 1; Figure S7), regardless of whether species' tolerances were quantified as a single mean score (79% of species avoided urban areas) or as a species' response curve to the whole urbanization gradient (55% of species). Together, these results help to explain the reduced taxonomic diversity of butterflies in urban ecosystems (e.g., Pignataro et al. 2020; Fenoglio et al. 2020; Kurlyo et al. 2020) and highlight which species should be the focus of active conservation in urban areas (see

Table S2). Still, a reasonable number of species (25 species) were shown to be more common in urban areas than elsewhere (Figure 4a), hinting at which species might be the winners of anthropogenic change as urban areas continue to expand. Overall, our results demonstrate that generalist life histories enable butterfly species to tolerate urban areas, whether generalism is defined in terms of climate or diet preferences.

We found support that climate, or thermal, flexibility was linked with urban tolerance among European butterflies. The average number of flying months was consistently the strongest and most important predictor of urban tolerance across our different analyses. In temperate Europe, species with long flight periods during the year, typically over multiple seasons, have to cope with a range of climatic conditions and hence may have a broader thermal niche breadth. The relationship between urban tolerance and thermal preferences or flexibility has been found in other taxa as well, including ants (Diamond et al. 2017), trees (Kendal et al. 2018), lizards (Campbell-Staton et al. 2020) and birds (Deutsch et al. 2008; Clavero et al. 2011; Barnagaud et al. 2012). Our results, combined with previous literature, support the general notion that species with broad environmental tolerance may prosper in urban environments (Bonier et al. 2007): those species have the necessary flexibility to succeed in the unique and novel environmental, physiological, and/or ecological attributes of urban environments. We also found that species with longer flight periods were likely to be bi- or multi-voltine, explaining why voltinism was also somewhat associated with urbanization in our analysis. More generally, our results support the hypothesis that human-dominated habitats may pose a thermal challenge for much of biodiversity (Daily and Ehrlich 1996).

The mean temperature within a species' range, previously used as a measure of thermal preference in butterflies (Devictor et al. 2012), explained some variability in urban tolerance among species. Urban areas are typically warmer than their surroundings because of the urban heat island effect. Hence, species that tolerate the negative effects of urbanization also have to tolerate the warmer mean temperatures within urban areas. But because urban areas, as measured in our analysis, can include urban cold islands as well, thermal flexibility may be more important than the mean temperature in a species' range. In our clusters of species responses to urbanization, cluster 1, comprising the most urban tolerant species, also included some of the most warm-adapted species in our analysis such as *Euchloe belemia*, *Polygonia egea*, and *Lampides boeticus* (Figure 4). However, the relationship between the mean temperature within a species' range and urban tolerance was non-linear and inconsistent across our other analyses. This might be because butterflies can respond to local microclimatic variation (Horner-Devine et al. 2003), and some species that are warm-adapted but not urban tolerant (e.g., *Charaxes jasius*, *Aricia cramera*, and *Pseudophilotes panoptes*) are using habitat at a scale not captured by our analysis. Because small invertebrates are more susceptible to local climatic conditions than larger-sized taxa, such as birds and mammals, the urban heat island effect may moderate some of the negative impacts of urbanization (Kaiser et al. 2016), especially in temperate regions where invertebrates are predicted to commonly experience temperatures below their thermal optimums (Deutsch et al. 2008). As climate change continues, species living in urban areas will have to tolerate even warmer temperatures, including heatwave events and summer droughts in Europe. As a result, voltinism and advances in phenology in butterflies are favored by climate change (Altermatt 2009). Therefore, associations between climate and urban tolerance suggest that selection pressures from climate warming may also foster urban tolerant species. Further disentangling the relationship between urban tolerance and thermal tolerance and flexibility will remain an important goal for understanding the influence of urbanization on butterflies and identifying the winners and losers of increasing urbanization.

In addition to the importance of thermal flexibility, we found that urban tolerance in butterflies was positively associated with diet generalism, confirming previous research that has demonstrated the link between diet and phenology in butterflies (Altermatt 2010). Diet generalism at both adult (i.e., the number of adult food types) and larval (i.e., hostplant generalism) life stages were important for tolerating urban ecosystems (Figure 3, Figure 4). This suggests that considering the influence of different life history stages (e.g., egg, larval, pupal, or adult) in how species adapt to urban environments may be important in future work. For most butterfly species, the larval stage is longer than the adult stage, and often larval food resources are thus more important in the butterfly life cycle (Altermatt and Pearse 2011). In support of this general pattern, we found that larval resources (i.e., hostplant specialism) were marginally more important than adult resources (Figure 3) in predicting urban tolerance. Tolerance to urbanization may be especially challenging for species that use different resources and habitats during their life cycle, including holometabolous insects, compared with other taxa with more uniform resource requirements during their lifespan. These differences among life history strategies could be linked to the differential impacts of thermal tolerance and local climatic events among life history strategies (Long et al. 2016). Alternatively, because urban environments can sometimes have greater species richness in plants, due in part to the prevalence of non-native plant species, species with diet generalism across life stages may be able to take advantage of this unique attribute of urban ecosystems.

Overwintering strategy and dispersal ability played more minor roles in a species' ability to use urban environments. Butterfly species' responses to climate has been previously shown to depend on their overwintering strategy (Long et al. 2016). We found that species overwintering as adults were more urban-tolerant than species overwintering as eggs (Figure 3b). And a separate analysis showed that species overwintering as adults or pupae were positively associated with urban tolerance whereas overwintering as eggs and larvae were negatively associated with urban tolerance (Figure S6). Species that overwinter as adults are typically those able to begin reproducing earlier in the season, whereas those overwintering as larvae must first undergo metamorphosis. Hence, this result is also consistent with the positive effect of the number of flight months on species tolerance to urbanization. Our results also showed that body size, as measured by wing index, was somewhat positively associated with urban tolerance. Body size in butterflies is linked to dispersal ability (Stevens et al. 2011; Sekar et al. 2011; Middleton-Welling et al. 2020) and climate tolerance (Klockmann et al. 2016), suggesting that both these traits probably interact to explain the moderate evidence we found that body size predicts urban tolerance among butterflies.

Our analysis was focused on butterfly responses to urbanization at a macro-ecological scale, using a globally-applicable remotely-sensed product of urbanization at a native resolution of ~500 meters (Elvidge et al. 2017). However, urbanization processes happen at multiple spatial scales, ranging from local to landscape levels (Concepción et al. 2015; Piano et al. 2019), and biodiversity responses to urbanization may differ among these spatial scales (Merckx and Van Dyck 2019). Butterflies can select habitat at fine-grained spatial scales within urban ecosystems smaller than 500 meters (e.g., Kaiser et al. 2016), such as urban meadows (Dylewski et al. 2019) or revegetated road verges (Saarinen et al. 2005; Valtonen et al. 2007). Indeed, the spatial resolution of our analysis likely explains why we found weak support for micro-scale habitat predictors such as the habitat of hostplant types or egg-laying location types. These traits may be important for predicting space use within urban areas, but not urban tolerance as measured in our current analysis. Future work should formally test how species-specific responses to urbanization varies among spatial scales in butterflies (e.g., Moll et al. 2020; Callaghan et al. 2020). In addition to our limitations in the spatial resolution, we highlight that we only looked at urban preferences in butterflies averaged across the full annual cycle, but some species may increase their use of urban areas during certain times of the year. For example, some species may move into urban areas during late fall when the surrounding temperatures drop, taking advantage of the urban heat island effect (Kaiser et al. 2016). Future work should investigate patterns in urban tolerance of butterflies across the full annual cycle (Marra et al. 2015). Finally, we treated phenology as a fixed trait in our analysis but in reality, species' phenology can vary among years and places. Indeed, phenology might also vary with urbanization, with warmer temperatures within urban areas allowing some butterflies to appear earlier in the year (but see Diamond et al. 2014).

Butterflies are popular with the non-scientific public and provide many cultural ecosystem services (e.g., McGinlay et al. 2017), particularly within urban ecosystems where they are most likely to be encountered even by casual observers. Butterflies, therefore, might play important roles in minimizing 'extinction of experience' for humans who are becoming increasingly concentrated in urban areas (Soga and Gaston 2016). Conserving urban biodiversity, including butterflies, is increasingly important in urban conservation planning. An important first step in this process is understanding the species that are tolerant and intolerant of urban ecosystems. We provide a method to efficiently quantify the urban tolerance of butterflies at a macro-ecological scale and accomplished this for 158 species of European butterflies. As data in GBIF continues to grow, largely due to citizen science efforts (Chandler et al. 2017), our analysis here can be updated for the remaining European butterfly species. Nonetheless, we provide strong evidence that generalism, in terms of both climate and diet, is inherently linked with urban tolerance and that generalist species are best-adapted to urban ecosystems. Our findings suggest that the majority of European butterfly species avoid highly urbanized areas, highlighting the need to include greening strategies in urban planning and conservation decisions (Ramírez-Restrepo and MacGregor-Fors 2017).

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REFREFERENCES

Altermatt, F. (2010a) Climatic warming increases voltinism in european butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1281–1287.

Altermatt, F. (2010b) Tell me what you eat and i'll tell you when you fly: Diet can predict phenological changes in response to climate change. *Ecology Letters*, **13**, 1475–1484.

Altermatt, F. & Pearse, I.S. (2011) Similarity and specialization of the larval versus adult diet of european butterflies and moths. *The American Naturalist*, **178**, 372–382.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Mac Nally, R., Thomson, J.R., Barros Ferraz, S.F. de, Louzada, J., Oliveira, V.H.F. & others (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, **535**, 144–147.

Barnagaud, J.-Y., Devictor, V., Jiguet, F., Barbet-Massin, M., Le Viol, I. & Archaux, F. (2012) Relating habitat and climatic niches in birds. *PloS one*, **7**, e32819.

Barnum, T.R., Weller, D.E. & Williams, M. (2017) Urbanization reduces and homogenizes trait diversity in stream macroinvertebrate communities. *Ecological Applications*, **27**, 2428–2442.

Bartonova, A., Benes, J. & Konvicka, M. (2014) Generalist-specialist continuum and life history traits of central european butterflies (lepidoptera)-are we missing a part of the picture? *European Journal of Entomology*, **111**, 543.

Blair, R.B. (1999) Birds and butterflies along an urban gradient: Surrogate taxa for assessing biodiversity? *Ecological applications*, **9**, 164–170.

Bonier, F., Martin, P.R. & Wingfield, J.C. (2007) Urban birds have broader environmental tolerance. *Biology letters*, **3**, 670–673.

Buston, P.M. & Elith, J. (2011) Determinants of reproductive success in dominant pairs of clownfish: A boosted regression tree analysis. *Journal of Animal Ecology*, **80**, 528–538.

Callaghan, C.T., Benedetti, Y., Wilshire, J.H. & Morelli, F. (2020a) Avian trait specialization is negatively associated with urban tolerance. *Oikos*, **129**, 1541–1551.

Callaghan, C.T., Major, R.E., Cornwell, W.K., Poore, A.G., Wilshire, J.H. & Lyons, M.B. (2020b) A continental measure of urbanness predicts avian response to local urbanization. *Ecography*, **43**, 528–538.

Callaghan, C.T., Major, R.E., Wilshire, J.H., Martin, J.M., Kingsford, R.T. & Cornwell, W.K. (2019) Generalists are the most urban-tolerant of birds: A phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos*, **128**, 845–858.

Callaghan, C.T., Ozeroff, I., Hitchcock, C. & Chandler, M. (2020c) Capitalizing on opportunistic citizen science data to monitor urban biodiversity: A multi-taxa framework. *Biological Conservation*, **251**, 108753.

Campbell-Staton, S.C., Winchell, K.M., Rochette, N.C., Fredette, J., Maayan, I., Schweizer, R.M. & Catchen, J. (2020) Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nature Ecology & Evolution*, **4**, 652–658.

Chandler, M., See, L., Copas, K., Bonde, A.M., López, B.C., Danielsen, F., Legind, J.K., Masinde, S., Miller-Rushing, A.J., Newman, G. & others (2017) Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*, **213**, 280–294.

Clavero, M., Villero, D. & Brotons, L. (2011) Climate change or land use dynamics: Do we know what climate change indicators indicate? *PLoS One*, **6**, e18581.

Clucas, B. & Marzluff, J.M. (2012) Attitudes and actions toward birds in urban areas: Human cultural differences influence bird behavior. *The Auk*, **129**, 8–16.

Concepción, E.D., Moretti, M., Altermatt, F., Nobis, M.P. & Obrist, M.K. (2015) Impacts of urbanisation on biodiversity: The role of species mobility, degree of specialisation and spatial scale. *Oikos*, **124**, 1571–1582.

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

Daily, G.C. & Ehrlich, P.R. (1996) Nocturnality and species survival. *Proceedings of the National Academy of Sciences*, **93**, 11709–11712.

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

Devictor, V., Van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å. & others (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature climate change*, **2**, 121–124.

Diamond, S.E., Cayton, H., Wepprich, T., Jenkins, C.N., Dunn, R.R., Haddad, N.M. & Ries, L. (2014) Unexpected phenological responses of butterflies to the interaction of urbanization and geographic temperature. *Ecology*, **95**, 2613–2621.

Diamond, S.E., Chick, L., Perez, A., Strickler, S.A. & Martin, R.A. (2017) Rapid evolution of ant thermal tolerance across an urban-rural temperature cline. *Biological Journal of the Linnean Society*, **121**, 248–257.

Didham, R.K., Basset, Y., Collins, C.M., Leather, S.R., Littlewood, N.A., Menz, M.H., Müller, J., Packer, L., Saunders, M.E., Schönrogge, K. & others (2020) Interpreting insect declines: Seven challenges and a way forward. *Insect Conservation and Diversity*, **13**, 103–114.

Dylewski, Ł., Maćkowiak, Ł. & Banaszak-Cibicka, W. (2019) Are all urban green spaces a favourable habitat for pollinator communities? Bees, butterflies and hoverflies in different urban green areas. *Ecological Entomology*, **44**, 678–689.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.

Elvidge, C.D., Baugh, K., Zhizhin, M., Hsu, F.C. & Ghosh, T. (2017) VIIRS night-time lights. *International Journal of Remote Sensing*, **38**, 5860–5879.

Essens, T., Langevelde, F. van, Vos, R.A., Van Swaay, C.A. & WallisDeVries, M.F. (2017) Ecological determinants of butterfly vulnerability across the european continent. *Journal of Insect Conservation*, **21**, 439–450.

Evans, B.A. & Gawlik, D.E. (2020) Urban food subsidies reduce natural food limitations and reproductive costs for a wetland bird. *Scientific reports*, **10**, 1–12.

Fenoglio, M.S., Rossetti, M.R. & Videla, M. (2020) Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Global Ecology and Biogeography*, **29**, 1412–1429.

Fenoglio, M.S., Rossetti, M.R. & Videla, M. (2020) Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Global Ecology and Biogeography*, **29**, 1412–1429.

Fiske, I., Chandler, R. & others (2011) Unmarked: An r package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of statistical software*, **43**, 1–23.

Francis, C.D., Ortega, C.P. & Cruz, A. (2011) Noise pollution filters bird communities based on vocal frequency. *PLoS one*, **6**, e27052.

Friedman, J.H. (2001) Greedy function approximation: A gradient boosting machine. *Annals of statistics*, 1189–1232.

GBIF.org (2020). GBIF Occurrence Download. https://doi.org/10.15468/dl.p5nhwh

Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistics in medicine*, **27**, 2865–2873.

Gippet, J.M., Mondy, N., Diallo-Dudek, J., Bellec, A., Dumet, A., Mistler, L. & Kaufmann, B. (2017) I'm not like everybody else: Urbanization factors shaping spatial distribution of native and invasive ants are species-specific. *Urban Ecosystems*, **20**, 157–169.

Gombin, J., Vaidyanathan, R. & Agafonkin, V. (2020) *Concaveman: A very fast 2D concave hull algorithm*,.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D. & Moore, R. (2017) Google earth engine: Planetary-scale geospatial analysis for everyone. *Remote sensing of Environment*, **202**, 18–27.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2020) *Dismo: Species distribution modeling*,.

Homola, J.J., Loftin, C.S., Cammen, K.M., Helbing, C.C., Birol, I., Schultz, T.F. & Kinnison, M.T. (2019) Replicated landscape genomics identifies evidence of local adaptation to urbanization in wood frogs. *Journal of Heredity*, **110**, 707–719.

Hopkins, G.R., Gaston, K.J., Visser, M.E., Elgar, M.A. & Jones, T.M. (2018) Artificial light at night as a driver of evolution across urban–rural landscapes. *Frontiers in Ecology and the Environment*, **16**, 472–479.

Horner-Devine, M.C., Daily, G.C., Ehrlich, P.R. & Boggs, C.L. (2003) Countryside biogeography of tropical butterflies. *Conservation Biology*, **17**, 168–177.

Huang, K., Li, X., Liu, X. & Seto, K.C. (2019) Projecting global urban land expansion and heat island intensification through 2050. *Environmental Research Letters*, **14**, 114037.

Iserhard, C.A., Duarte, L., Seraphim, N. & Freitas, A.V.L. (2019) How urbanization affects multiple dimensions of biodiversity in tropical butterfly assemblages. *Biodiversity and conservation*, **28**, 621–638.

Jung, K. & Threlfall, C.G. (2018) Trait-dependent tolerance of bats to urbanization: A global meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, **285**, 20181222.

Kabir, M.I., Daly, E. & Maggi, F. (2014) A review of ion and metal pollutants in urban green water infrastructures. *Science of the total environment*, **470**, 695–706.

Kaiser, A., Merckx, T. & Van Dyck, H. (2016) The urban heat island and its spatial scale dependent impact on survival and development in butterflies of different thermal sensitivity. *Ecology and Evolution*, **6**, 4129–4140.

Kendal, D., Dobbs, C., Gallagher, R., Beaumont, L., Baumann, J., Williams, N. & Livesley, S. (2018) A global comparison of the climatic niches of urban and native tree populations. *Global Ecology and Biogeography*, **27**, 629–637.

Klockmann, M., Günter, F. & Fischer, K. (2017) Heat resistance throughout ontogeny: Body size constrains thermal tolerance. *Global Change Biology*, **23**, 686–696.

Kurylo, J., Threlfall, C., Parris, K., Ossola, A., Williams, N. & Evans, K. (2020) Butterfly richness and abundance along a gradient of imperviousness and the importance of matrix quality. *Ecological Applications*.

Lintott, P.R., Barlow, K., Bunnefeld, N., Briggs, P., Gajas Roig, C. & Park, K.J. (2016) Differential responses of cryptic bat species to the urban landscape. *Ecology and Evolution*, **6**, 2044–2052.

Liu, Z., He, C. & Wu, J. (2016) The relationship between habitat loss and fragmentation during urbanization: An empirical evaluation from 16 world cities. *PLoS One*, **11**, e0154613.

Lowe, E., Wilder, S. & Hochuli, D. (2017) Life history of an urban-tolerant spider shows resilience to anthropogenic habitat disturbance. *Journal of Urban Ecology*, **3**, jux004.

Marra, P.P., Cohen, E.B., Loss, S.R., Rutter, J.E. & Tonra, C.M. (2015) A call for full annual cycle research in animal ecology. *Biology letters*, **11**, 20150552.

Martin, P.R. & Bonier, F. (2018) Species interactions limit the occurrence of urban-adapted birds in cities. *Proceedings of the National Academy of Sciences*, **115**, E11495–E11504.

Martínez-Gómez, J. (2020) Digest: Phylogenetic comparative methods identify traits associated with urbanization tolerance in anolis. *Evolution*.

Matuoka, M.A., Benchimol, M., Almeida-Rocha, J.M. de & Morante-Filho, J.C. (2020) Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. *Ecological Indicators*, **116**, 106471.

McDermott Long, O., Warren, R., Price, J., Brereton, T.M., Botham, M.S. & Franco, A.M. (2017) Sensitivity of UK butterflies to local climatic extremes: Which life stages are most at risk? *Journal of Animal Ecology*, **86**, 108–116.

McDonald, R.I., Mansur, A.V., Ascensão, F., Crossman, K., Elmqvist, T., Gonzalez, A., Güneralp, B., Haase, D., Hamann, M., Hillel, O. & others (2020) Research gaps in knowledge of the impact of urban growth on biodiversity. *Nature Sustainability*, **3**, 16–24.

McGinlay, J., Parsons, D.J., Morris, J., Hubatova, M., Graves, A., Bradbury, R.B. & Bullock, J.M. (2017) Do charismatic species groups generate more cultural ecosystem service benefits? *Ecosystem services*, **27**, 15–24.

McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological conservation*, **127**, 247–260.

Merckx, T. & Van Dyck, H. (2019) Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects. *Global Ecology and Biogeography*, **28**, 1440–1455.

Middleton-Welling, J., Dapporto, L., García-Barros, E., Wiemers, M., Nowicki, P., Plazio, E., Bonelli, S., Zaccagno, M., Šašić, M., Liparova, J. & others (2020) A new comprehensive trait database of european and maghreb butterflies, papilionoidea. *Scientific Data*, **7**, 1–10.

Moll, R.J., Cepek, J.D., Lorch, P.D., Dennis, P.M., Robison, T. & Montgomery, R.A. (2020) At what spatial scale (s) do mammals respond to urbanization? *Ecography*, **43**, 171–183.

Nagase, A., Kurashina, M., Nomura, M. & MacIvor, J.S. (2019) Patterns in urban butterflies and spontaneous plants across a university campus in japan. *The Pan-Pacific Entomologist*, **94**, 195–215.

Palacio, F.X. (2020) Urban exploiters have broader dietary niches than urban avoiders. *Ibis*, **162**, 42–49.

Pandey, B., Joshi, P. & Seto, K.C. (2013) Monitoring urbanization dynamics in india using DMSP/OLS night time lights and SPOT-VGT data. *International Journal of Applied Earth Observation and Geoinformation*, **23**, 49–61.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W. & others (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496–1501.

Piano, E., Souffreau, C., Merckx, T., Baardsen, L.F., Backeljau, T., Bonte, D., Brans, K.I., Cours, M., Dahirel, M., Debortoli, N. & others (2020) Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology,* **26**, 1196–1211.

Pignataro, T., Bressan, P., Santos, A.L. & Cornelissen, T. (2020) Urban gradients alter the diversity, specific composition and guild distribution in tropical butterfly communities. *Urban Ecosystems*, 1–8.

Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009) Species traits explain recent range shifts of finnish butterflies. *Global Change Biology*, **15**, 732–743.

Quacchia, A., Ferracini, C., Bonelli, S., Balletto, E. & Alma, A. (2008) Can the geranium bronze, cacyreus marshalli, become a threat for european biodiversity? *Biodiversity and Conservation*, **17**, 1429–1437.

Ramírez-Restrepo, L. & MacGregor-Fors, I. (2017) Butterflies in the city: A review of urban diurnal lepidoptera. *Urban Ecosystems*, **20**, 171–182.

Rodewald, A.D. & Gehrt, S.D. (2014) *Wildlife population dynamics in urban landscapes*. *Urban wildlife conservation*, pp. 117–147. Springer.

Saarinen, K., Valtonen, A., Jantunen, J. & Saarnio, S. (2005) Butterflies and diurnal moths along road verges: Does road type affect diversity and abundance? *Biological Conservation*, **123**, 403–412.

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., Hardenberg, A. von & Ancillotto, L. (2019) One strategy does not fit all: Determinants of urban adaptation in mammals. *Ecology letters*, **22**, 365–376.

Schweiger, O., Harpke, A., Wiemers, M. & Settele, J. (2014) CLIMBER: Climatic niche characteristics of the butterflies in europe. *ZooKeys*, 65.

Sekar, S. (2012) A meta-analysis of the traits affecting dispersal ability in butterflies: Can wingspan be used as a proxy? *Journal of Animal Ecology*, **81**, 174–184.

Soga, M. & Gaston, K.J. (2016) Extinction of experience: The loss of human–nature interactions. *Frontiers in Ecology and the Environment*, **14**, 94–101.

Sol, D., Bartomeus, I., González-Lagos, C. & Pavoine, S. (2017) Urbanisation and the loss of phylogenetic diversity in birds. *Ecology letters*, **20**, 721–729.

Stathakis, D., Tselios, V. & Faraslis, I. (2015) Urbanization in european regions based on night lights. *Remote Sensing Applications: Society and Environment*, **2**, 26–34.

Stevens, V.M., Trochet, A., Van Dyck, H., Clobert, J. & Baguette, M. (2012) How is dispersal integrated in life histories: A quantitative analysis using butterflies. *Ecology letters*, **15**, 74–86.

Svenningsen, C.S., Bowler, D.E., Hecker, S., Bladt, J., Grescho, V., Dam, N.M. van, Dauber, J., Eichenberg, D., Ejrnæs, R., Fløjgaard, C. & others (2020) Contrasting impacts of urban and farmland cover on flying insect biomass. *bioRxiv*.

Threlfall, C.G., Law, B. & Banks, P.B. (2012) Sensitivity of insectivorous bats to urbanization: Implications for suburban conservation planning. *Biological Conservation*, **146**, 41–52.

Uchida, K., Shimamoto, T., Yanagawa, H. & Koizumi, I. (2020) Comparison of multiple behavioral traits between urban and rural squirrels. *Urban Ecosystems*, 1–10.

Vallet, J., Daniel, H., Beaujouan, V., Rozé, F. & Pavoine, S. (2010) Using biological traits to assess how urbanization filters plant species of small woodlands. *Applied Vegetation Science*, **13**, 412–424.

Valtonen, A., Saarinen, K. & Jantunen, J. (2007) Intersection reservations as habitats for meadow butterflies and diurnal moths: Guidelines for planning and management. *Landscape and Urban Planning*, **79**, 201–209.

Vilmi, A., Karjalainen, S.M., Wang, J. & Heino, J. (2019) Using traits to explain interspecific variation in diatom occupancy and abundance across lakes and streams. *Journal of Biogeography*, **46**, 1419–1428.

Warren, P.S., Lerman, S.B., Andrade, R., Larson, K.L. & Bateman, H.L. (2019) The more things change: Species losses detected in phoenix despite stability in bird–socioeconomic relationships. *Ecosphere*, **10**, e02624.

Wepprich, T., Adrion, J.R., Ries, L., Wiedmann, J. & Haddad, N.M. (2019) Butterfly abundance declines over 20 years of systematic monitoring in ohio, USA. *PLoS One*, **14**, e0216270.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J. & others (2019) Welcome to the tidyverse. *Journal of Open Source Software*, **4**, 1686.

Winchell, K.M., Carlen, E.J., Puente-Rolón, A.R. & Revell, L.J. (2018) Divergent habitat use of two urban lizard species. *Ecology and evolution*, **8**, 25–35.

Winchell, K.M., Schliep, K.P., Mahler, D.L. & Revell, L.J. (2020) Phylogenetic signal and evolutionary correlates of urban tolerance in a widespread neotropical lizard clade. *Evolution*.

Zhang, Q. & Seto, K.C. (2013) Can night-time light data identify typologies of urbanization? A global assessment of successes and failures. *Remote Sensing*, **5**, 3476–3494.

FIGURES

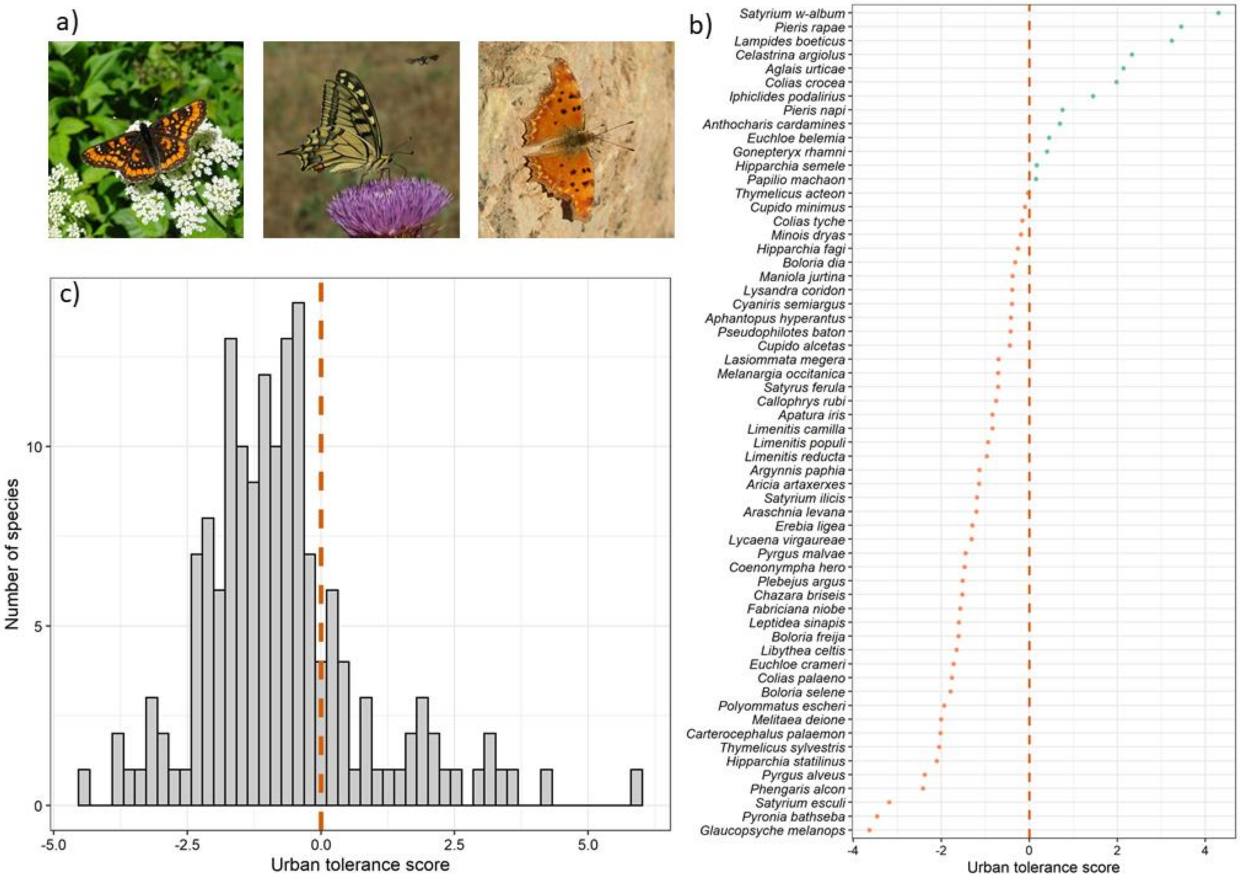

Figure 1. a) Three species included in our analysis, ordered from left to right in terms of their urban tolerance scores: Scarce Fritillary (*Euphydryas maturna*) with an urban tolerance score of -4.37; Old World Swallowtail (*Papilio machaon*) with an urban tolerance score of 0.15; Southern Comma (*Polygonia egea*) with an urban tolerance score of 5.97. All photos by Julia Wittman (@birdingjulia) and are CC-BY-NC. b) Example of the rankings for 60 randomly chosen butterflies, ranked from those that were found proportionately in more urbanized areas (above 0) to those found proportionately in less urbanized areas (below 0). For a full interactive figure showing all 158 species considered in analysis see here. c) A histogram of the urban tolerance scores for all 158 species included in the analysis.

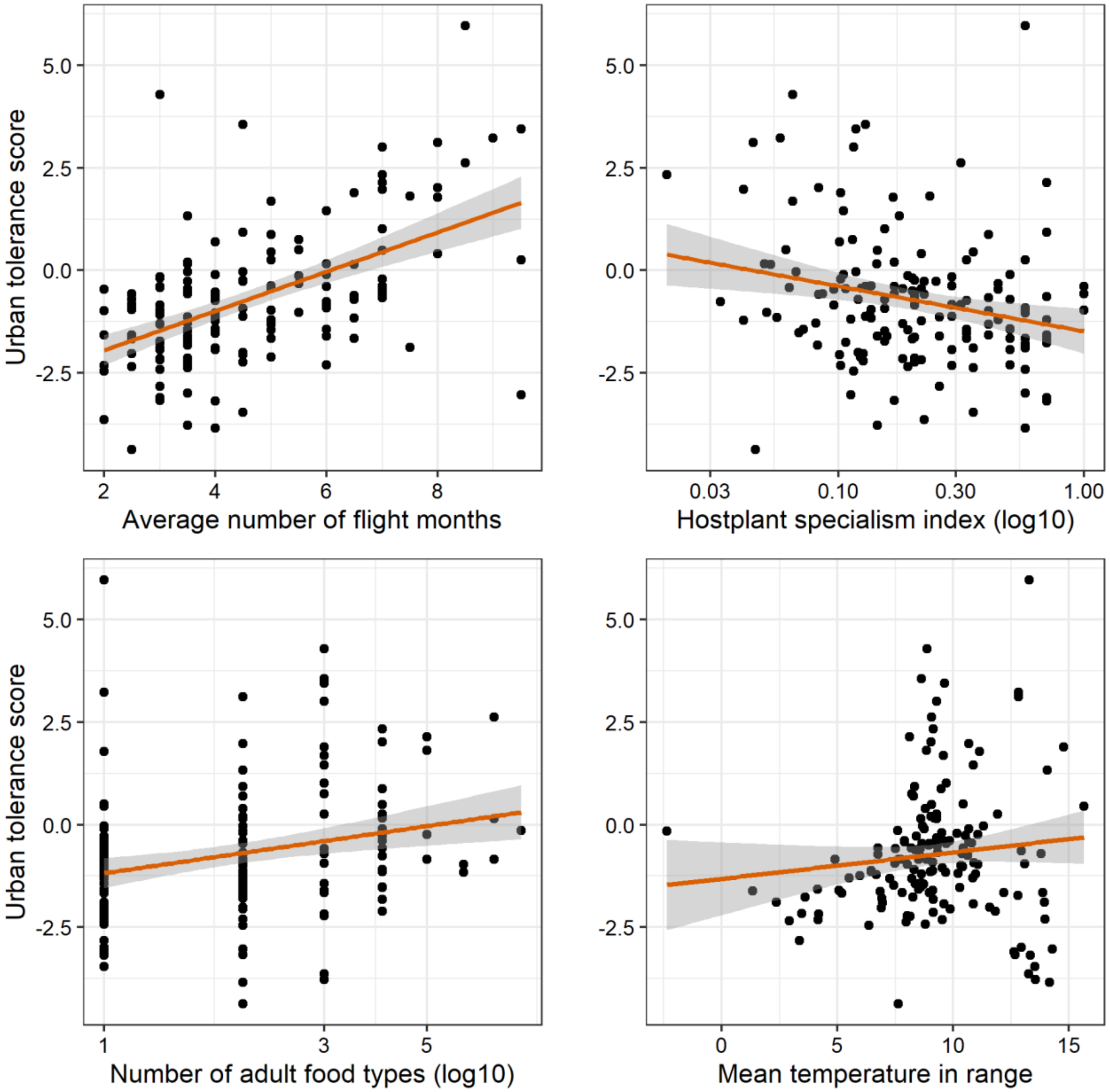

Figure 2. The relationship between our urban tolerance score for N=158 species of butterfly, and the average number of flight months (top left), hostplant specialism index (top right), number of adult food types (bottom left), and mean temperature in a species' range (bottom right). The orange line represents a simple linear model fit, and the shaded gray area represents a 95% confidence interval around the linear model fit.

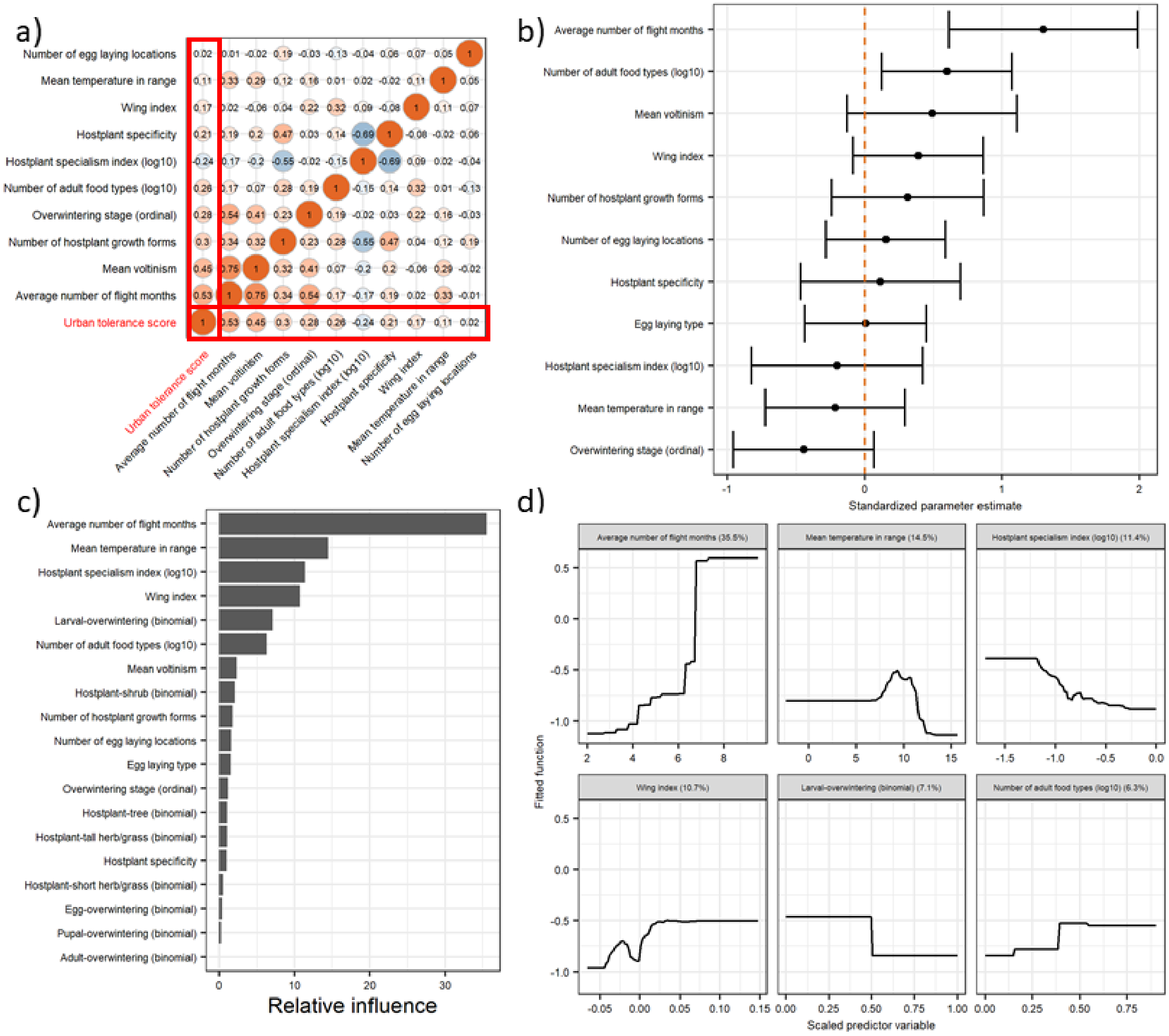

Figure 3. Results of our statistical analysis quantifying the relationship between urban tolerance score of butterflies (N=158) and various predictor variable (see Table 1). a) Correlation plot of all numeric predictor variables (N=10) and our response variable (in red text). Variables are ordered left to right by the strength of their pairwise relationship with the response variable. b) Results of our multiple linear regression and standardized parameter estimates with 95% confidence intervals. Variables to the right of the vertical orange line positively interacted with urban tolerance whereas variables to the left of the orange line negatively interacted with urban tolerance. c) and d) Results from our boosted regression tree analysis, with c) representing the relative influence of all predictor variables (N=19) included in the model, ordered from the variable with the most relative influence to the least, and d) shows the partial dependence plots for all predictor variables that had >5% relative influence on the urban tolerance of butterflies.

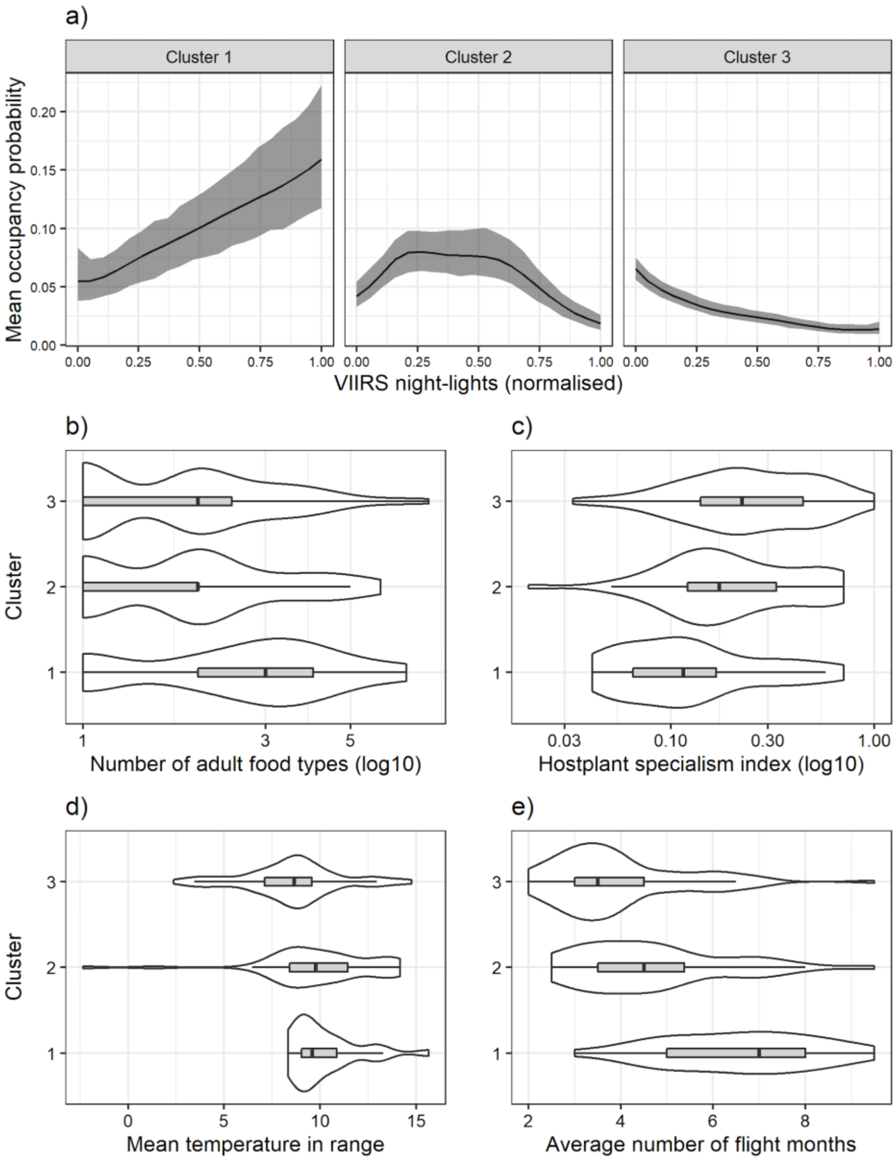

Figure 4. Results of our cluster analysis, and the three normalized responses to urbanization (a), for each cluster respectively. The clusters mapped to four traits (b-e), confirming the importance of these traits for urban tolerance among the species within each respective cluster. Cluster 1 (N=25 species) grouped together species most common in high urban areas — i.e., urban exploiters; cluster 2 (N=46 species) grouped together species most common at intermediate levels of urbanization — urban adapters; and cluster 3 (N=87 species) grouped together species that were most common at low urban areas and rarely occurred outside of low urban areas — i.e., urban avoiders (see Table S2 for the species corresponding to each cluster).

TABLES

Table 1. A summary of the traits included in analyses, as well as our prediction for each trait. All data were extracted from Middleton-Welling et al. 2020 except for the mean temperature in a species range which was extracted from Schweiger et al. 2014.

Category	Trait	Description	Prediction
Climate tolerance	Average number of flight months	The average number of months of the year a species is observed flying, taken as the average of the minimum and maximum number of flight months observed for each species.	We expected that species that had a greater number of flight months would be positive associated with urban tolerance.
	Overwintering stage (ordinal)	Originally a categorial variable, corresponding to the overwintering stage for a species, where the options are egg, larva, pupa, or adult. We converted the possible combinations of these categorical variables into an ordinal variable ranging from 1 (egg) to 4.5 (adult).	We expected that the ordinal overwintering stage variable would be positive associated with urban tolerance, as species that overwintered as adults would be more likely to be urban tolerant.
	Overwintering stage (binomial)	We also treated overwintering stage in a separate analysis where each categorical option was treated as a binomial predictor variable.	We expected that species which overwinter as adults would be the most urban tolerant, followed by species that overwinter as pupae, larvae, and eggs.
	Mean temperature in range	The mean temperature within a species range.	We expected that species with a higher mean temperature in their range would be positively associated with urban tolerance.
Extent of specialization	Number of adult food types	Eight possible adult food types were presented by Middleton-Welling et al. 2020: herbs, flowers, ergot, shrub/tree flower, honeydew, sap, decaying plant, animal, and mineral. We used the total number of categories an adult species feeds on, with a highest possible value of 8, and lowest of 1.	We expected a positive relationship between the number of adult food types and urban tolerance.
	Hostplant specificity	An ordinal variable corresponding with the range of host plants a species can use, ordered as monophagous species (1), narrow oligophagous	We expected a positive relationship between hostplant specificity and urban tolerance.

		(2), broad oligophagous (3), and polyphagous (4). See details in Middleton-Welling et al. 2020.	
	Hostplant index	An index ranging from 0 to 1, providing a quantitative measure of overall hostplant specificity, where 1 is most specific. See Middleton-Welling et al. 2020 for details of this calculation.	We expected a negative relationship between the hostplant index and urban tolerance: more specialized species would be least urban tolerant.
Body size	Wing index	A composite variable representing a single measurement of overall size for all butterfly species generated from forewing length and wingspan measures, for both males and females. See Middleton-Welling et al. 2020 for details of this calculation.	We expected a positive relationship between wing index and urban tolerance.
Life history	Mean voltinism	A measure of the number of generations a species has in a year. We took the mean value between the minimum and maximum voltinism measures provided by Middleton-Welling et al. 2020.	We expected a positive relationship between mean voltinism and urban tolerance.
	Egg laying type	A categorical variable representing three types of egg-laying strategies: single egg, small batch, and large batch. Some species may lay single eggs or small batches, and we used the largest possible category for each species.	We expected a positive relationship between the number of eggs a species lays with urban tolerance.
Microhabitat use	Number of hostplant growth forms	A variable representing the total number of growth forms of a species' hostplants, ranging from 1 to 5. The five categories of species' hostplants were short herb/grass (<1m), tall herb/grass (>1m), shrub, tree, and liana.	We expected a positive relationship between the number of hostplant growth forms and urban tolerance.
	Hostplant growth form (binomial)	We also treated hostplant growth form in a separate analysis where each categorical option was treated as a binomial predictor variable. But because so few species in our analysis used liana, this was not included as a variable.	We expected that species which use herbs/grass would be more positively associated with urban tolerance.

	Number of egg laying locations	A variable representing the total number of unique structures that eggs are laid on by a particular species, with a highest possible value of 7 for the most general, and 1 for the most specific. The 7 categories provided by Middleton-Welling et al. 2020 are bare ground, short turf/herbs/grass (<1m), tall herbs/grass (>1m), shrub, tree trunk, canopy, and liana.	We expected a positive relationship between the number of egg laying locations with urban tolerance.

SUPPLEMENTARY FIGURES

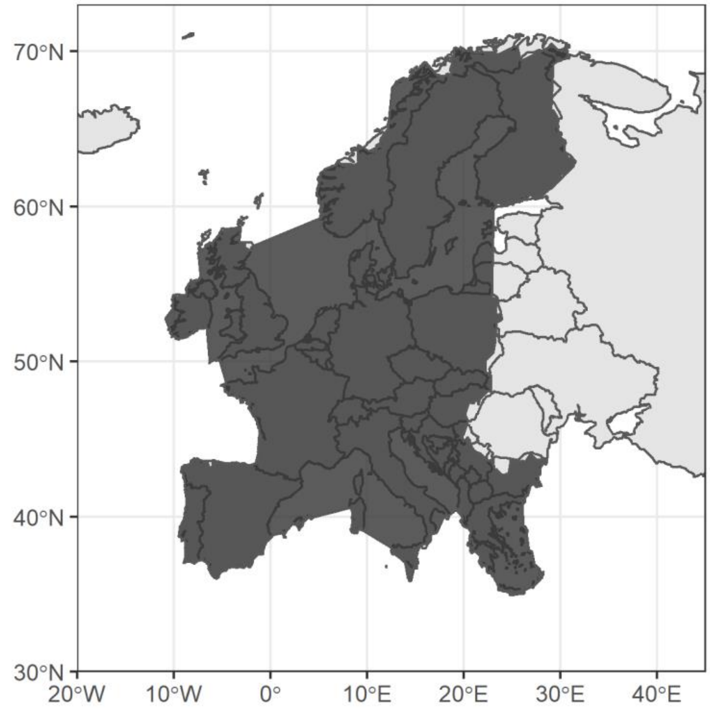

Figure S1. A map of the study extent that was manually delineated using the observations from GBIF. The concave map was made using the ‘concaveman’ package in R which is a R port for a mapbox library of the same name, and the default concavity of 2 was used to make a polygon surrounding our point observations from GBIF.

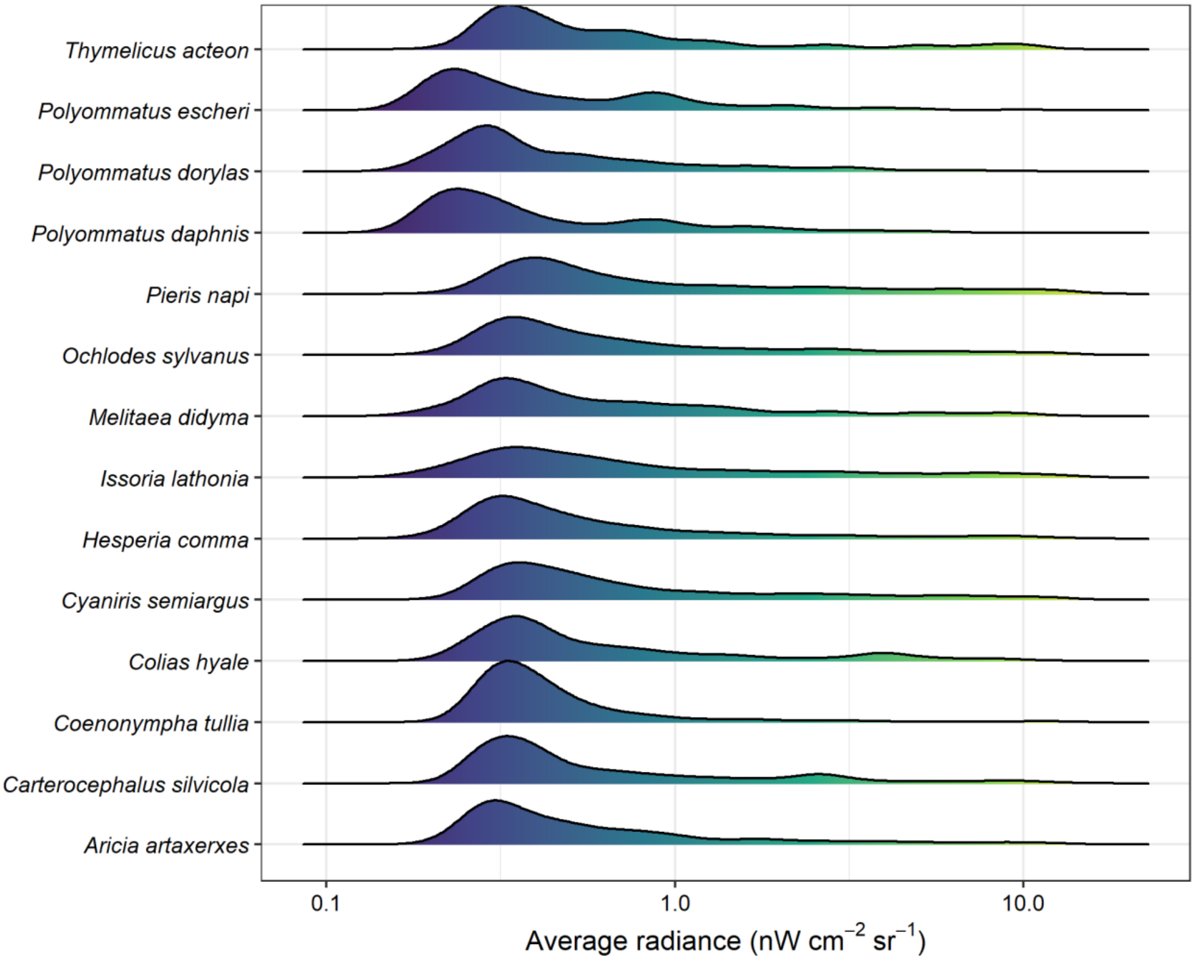

Figure S2. Fifteen example species, and their distribution in response to VIIRS night-time lights.

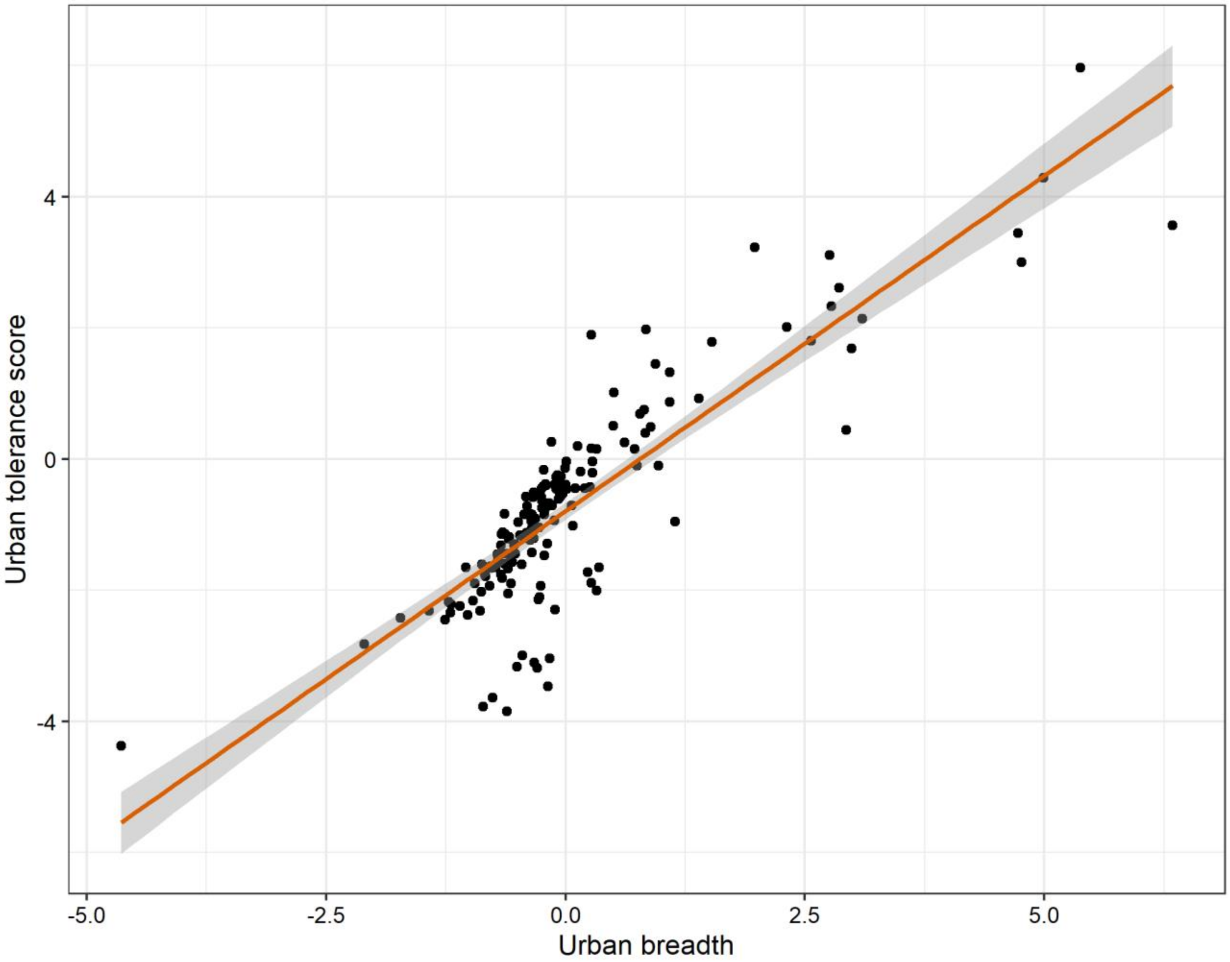

Figure S3. The relationship between urban tolerance (the difference between the mean of all observations within a species' range and the observations of each species within their range) and urban breadth (the difference between the interquartile range of all observations within a species' range and the observations of each species within their range) showed a strong positive relationship. Shown here are all species (N=158) included in analysis. Because of this relationship, our analysis focused on the urban tolerance score throughout.

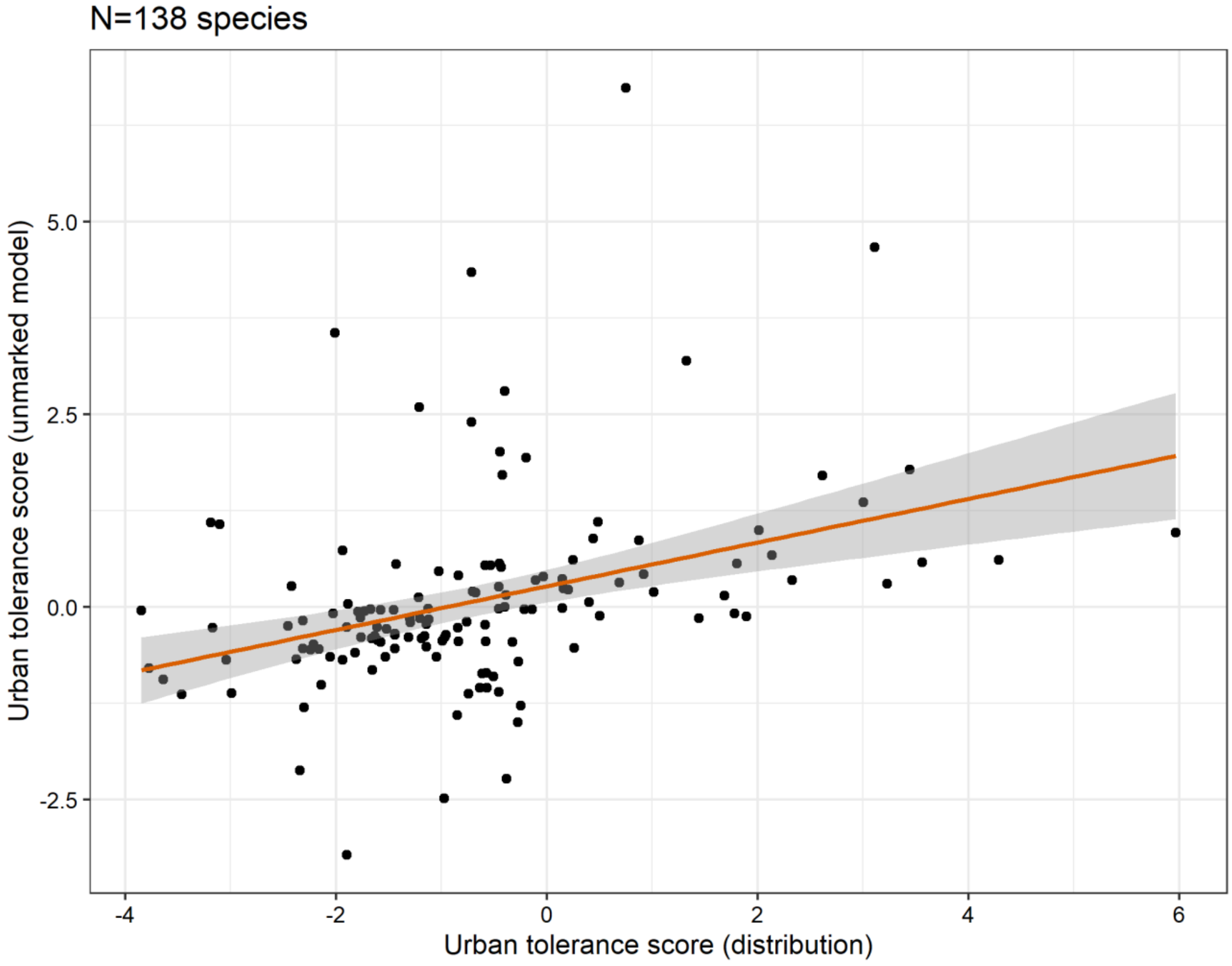

Figure S4. To confirm the reliability of our distributional approach, we performed a separate analysis to rank species along a continuum of urban tolerance/preference using unmarked models. For this analysis, species were grouped by 5km grid across Europe, and week of the year, into presence/absence, and each species was only calculated within its concave hull range. The mean VIIRS night-time lights level was also calculated within each 5km grid. An unmarked model was ran which accounted for the effects of urban cover (VIIRS) on the detection probability of species. Only species with a standard error of their modelled response to urbanization <2 was included in the comparison between the two approaches (N=138 species).

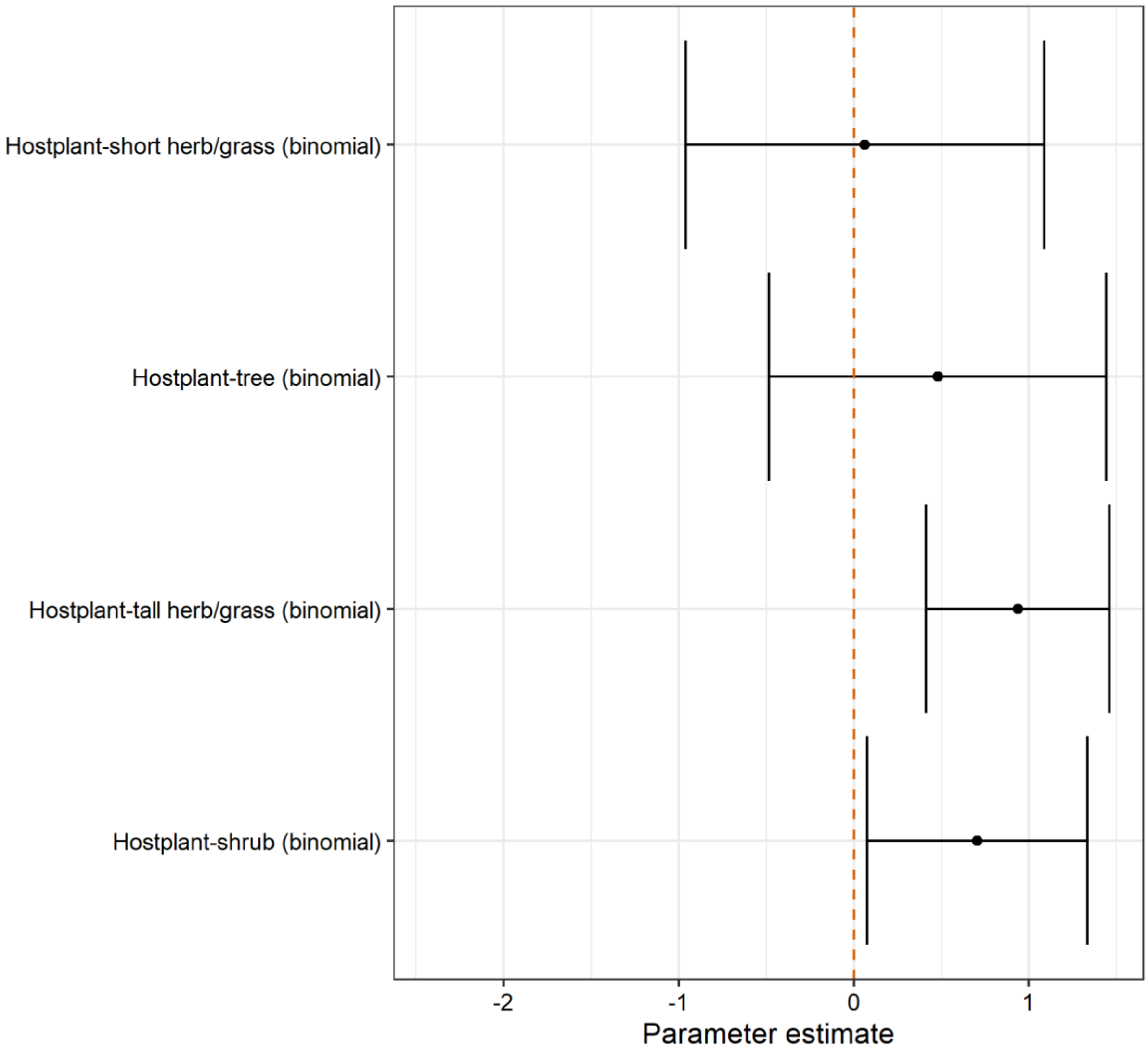

Figure S5. Results of a separate multiple linear regression which investigated the binomial predictor variables of hostplant growth form with the urban tolerance score response variable.

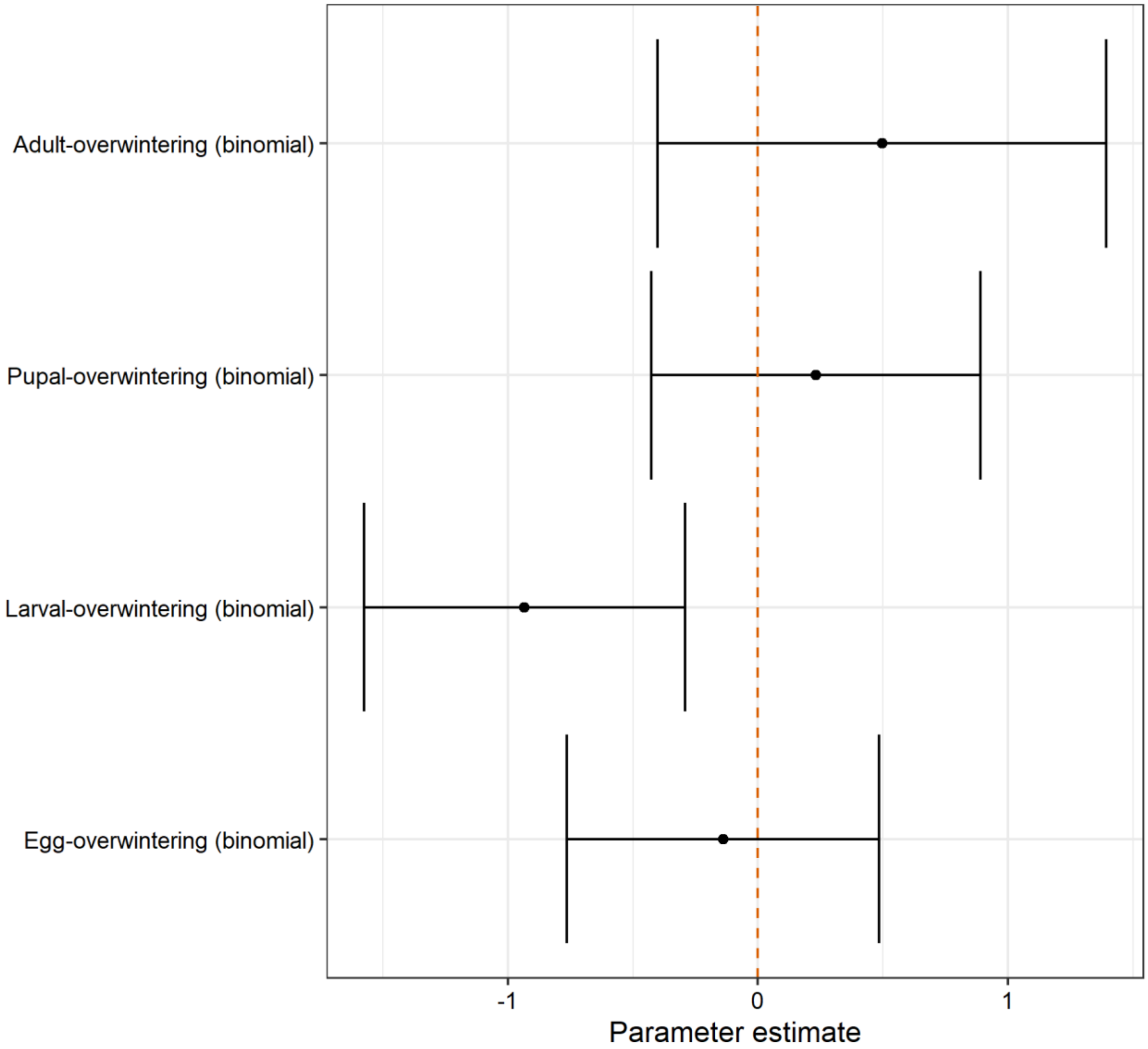

Figure S6. Results of a separate multiple linear regression which investigated the binomial predictor variables of overwintering stage form with the urban tolerance score response variable.

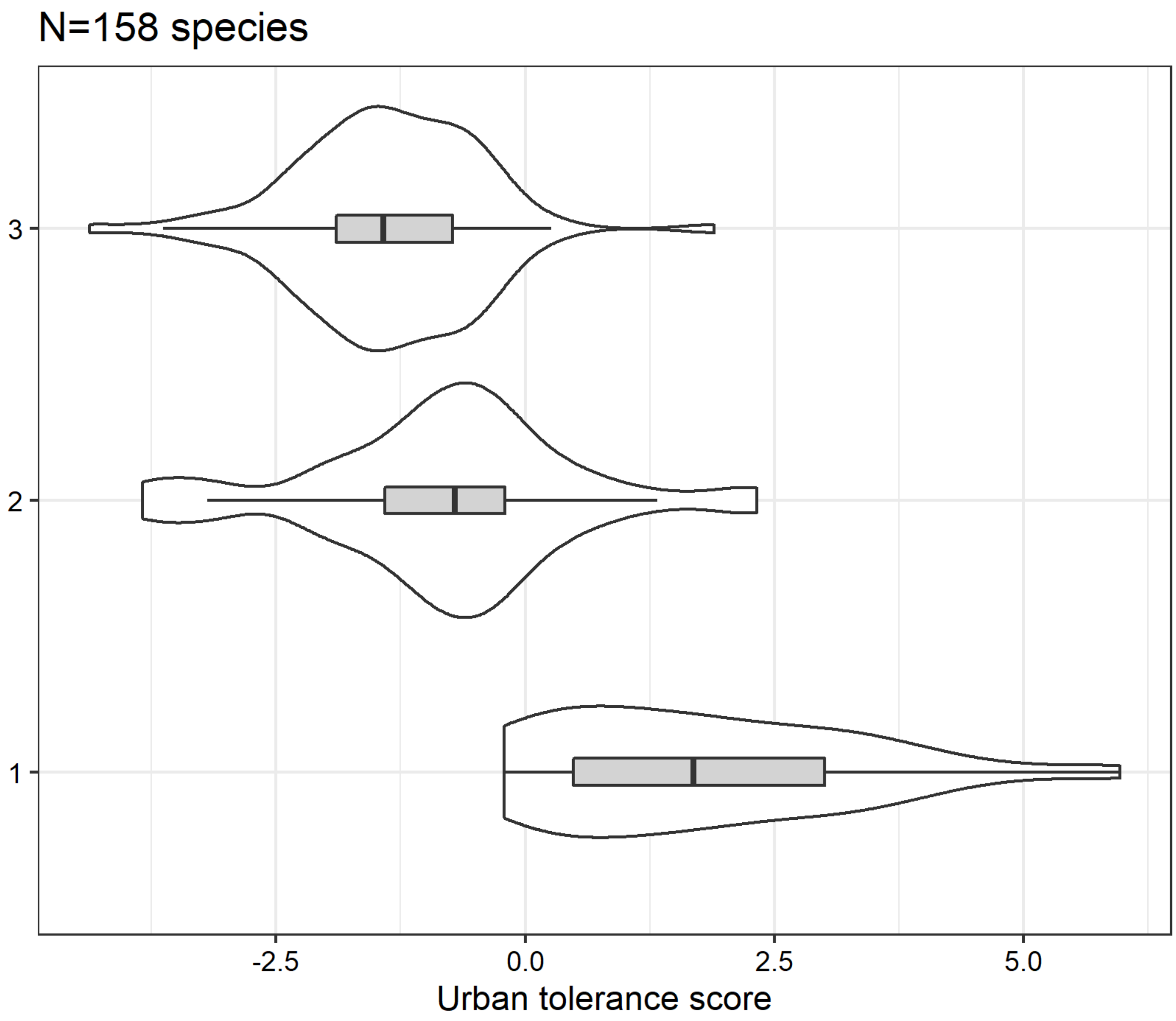

Figure S7. The results of our two different methods to quantify urban tolerance of butterflies throughout Europe.

SUPPLEMENTARY TABLES

Table S1. The countries included in analysis and the number of observations included for potential analyses in each country.

Country	ISO country code	Number of samples	Species richness
Sweden	SE	565214	126
Ireland	IE	144570	43
France	FR	83491	247
Germany	DE	51761	149
Spain	ES	36110	221
Portugal	PT	20614	116
Italy	IT	12791	220
Switzerland	CH	11128	162
Greece	GR	10762	173
Austria	AT	7113	149
Bulgaria	BG	5340	164
Slovenia	SI	4949	128
Norway	NO	4385	90
North Macedonia	MK	2919	140
Poland	PL	2919	91
United Kingdom	GB	2422	44
Hungary	HU	2411	108
Luxembourg	LU	1777	54
Croatia	HR	1492	107
Finland	FI	1205	69
Czechia	CZ	894	60
Denmark	DK	713	58
Slovakia	SK	626	72
Andorra	AD	562	115
Montenegro	ME	418	91
Albania	AL	253	76
Bosnia & Herzegovina	BA	139	56
Serbia	RS	135	57
Malta	MT	117	13
Liechtenstein	LI	63	26
Gibraltar	GI	50	17
Belgium	BE	17	7
Kosovo	XK	15	12
Monaco	MC	11	7
San Marino	SM	2	1

Table S2. Uploaded separately - table of raw data used for modelling in the analysis.