





















RESEARCH ARTICLE OPEN ACCESS

The Interplay of Climate Change, Urbanisation, and Species Traits Shapes European Butterfly Population Trends

Pau Colom^{1,2}  | Ashley Tejada^{1,2}  | Simona Bonelli³  | Benoît Fontaine⁴  | Mikko Kuussaari⁵  | Dirk Maes^{6,7}  | Xavier Mestdagh⁸  | Miguel L. Munguira^{9,10}  | Martin Musche¹¹  | Lars B. Pettersson¹²  | David Roy^{13,14}  | Johannes Rüdiger¹⁵  | Martina Šašić¹⁶  | Reto Schmucki¹³  | Constanti Stefanescu^{17,18}  | Nicolas Titeux⁸  | Josef Settele^{11,19,20}  | Chris van Swaay²¹  | Javier Gordillo¹⁸  | Yolanda Melero^{1,2,18} 

¹Department of Evolutionary Biology, Ecology, and Environmental Sciences, University of Barcelona, Barcelona, Spain | ²Biodiversity Research Institute (IRBio), Barcelona, Spain | ³Department of Life Science and Systems Biology, University of Turin, Turin, Italy | ⁴Patrinat & CESCO UMR7204, MNHN-OFB-CNRS-SU, Paris, France | ⁵Finnish Environment Institute (Syke), Helsinki, Finland | ⁶Research Institute for Nature and Forest (INBO), Brussels, Belgium | ⁷Radboud Institute for Biological and Environmental Sciences (RIBES), Nijmegen, the Netherlands | ⁸Biodiversity Monitoring and Assessment Group, Environmental Sensing and Modelling Unit, Luxembourg Institute of Science and Technology, Belvaux, Luxembourg | ⁹Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Madrid, Spain | ¹⁰Departamento de Biología, Universidad Autónoma de Madrid, Madrid, Spain | ¹¹Helmholtz Centre for Environmental Research (UFZ), Department of Conservation Biology and Social-Ecological Systems, Halle, Germany | ¹²Biodiversity and Evolution, Department of Biology, Lund University, Lund, Sweden | ¹³UK Centre for Ecology & Hydrology, Wallingford, Oxfordshire, UK | ¹⁴Centre for Ecology and Conservation, University of Exeter, Penryn, UK | ¹⁵Department of Ecology, University of Innsbruck, Innsbruck, Austria | ¹⁶Croatian Natural History Museum, Zagreb, Croatia | ¹⁷Natural Sciences Museum of Granollers, Granollers, Catalonia, Spain | ¹⁸CREAF, E08193, Bellaterra, Cerdanyola del Vallès, Catalonia, Spain | ¹⁹German Society for the Conservation of Butterflies and Moths (GfS – Gesellschaft für Schmetterlingsschutz), Halle, Germany | ²⁰German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany | ²¹De Vlinderstichting – Dutch Butterfly Conservation, Wageningen, the Netherlands

Correspondence: Pau Colom (pcolom@ub.edu)

Received: 20 August 2025 | **Revised:** 20 January 2026 | **Accepted:** 23 January 2026

Handling Editor: Huijie Qiao

Keywords: aridification | climate warming | climatic niche | insect decline | population declines | precipitation trends | reproductive rate | trophic specialisation

ABSTRACT

Aim: To examine how butterfly population trends respond to climate change and urbanisation at a continental scale, and whether responses differ between urban and rural environments.

Location: 869 sites across 12 European countries, spanning six bioclimatic zones.

Time Period: 1976–2021.

Major Taxa Studied: Butterflies (Lepidoptera).

Methods: We analysed long-term monitoring data from > 8400 populations of 145 species representing a wide range of ecological and life-history traits. Population trends were modelled in relation to climate variables (temperature, precipitation and aridity), urbanisation (built-up surface), and their interactions with urban context (urban vs. rural) and species traits (trophic specialisation, body size, reproductive rate and thermal adaptation).

Results: Climate warming and aridification were consistently linked to population declines in both rural and urban contexts, while precipitation effects varied by location and species. Urbanisation alone did not predict trends, but the urban–rural context strongly modulated species' responses to warming, indicating potential synergies between climate change and urbanisation. The stronger impact of warming in urban populations likely reflects elevated baseline temperatures and reduced habitat suitability and connectivity in urban landscapes, limiting thermal buffering. Species with colder thermal niches and lower reproductive

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2026 The Author(s). *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

rates were most vulnerable to warming, as warming exceeds the thermal optima of cold-adapted species and lower reproductive rates limit their capacity to buffer climate-driven population declines. Under aridification, which can reduce host-plant availability, trophic specialists declined more in urban areas, whereas generalists unexpectedly declined more in rural sites, suggesting context-dependent constraints under increasing water limitation.

Main Conclusions: Our findings highlight the complex interplay between climate change, urban context, and species traits in driving population dynamics. Importantly, our results suggest that urbanisation generally amplifies the negative impact of climate change on insect population trends.

1 | Introduction

Urbanisation and climate change are accelerating biodiversity shifts in the Anthropocene (van Moorsel et al. 2022; Urban et al. 2024). In Europe, built-up surface area increased from 173.6 billion m² (ca. 4% of total land area) in 1975 to 464.6 billion m² (ca. 10.7%) in 2020 (EU Commission 2023); a tendency that has expanded worldwide and is projected to increase sixfold by 2050 (Gao and O'Neill 2020). In parallel, global temperatures have risen by 0.15°C–0.2°C per decade, and other climatic patterns (e.g., seasonality and precipitation patterns, including extreme events) have shifted in different directions across regions (Gulev et al. 2021).

Urbanisation generally results in small and isolated habitat patches, surrounded by a built matrix largely inhospitable to wildlife (Liu et al. 2016). The associated habitat loss and increased fragmentation can significantly restrict dispersal, establishment and persistence across suitable habitats, driving declines in diversity and abundance of many taxa, with specialist species being particularly affected and, consequently, communities becoming disproportionately dominated by generalist species (Fenoglio et al. 2020; Piano et al. 2020; Dri et al. 2021; Hou et al. 2023). Likewise, climate change also disrupts the environmental conditions species are adapted to, and hence population viability (Root et al. 2003; Parmesan 2006; Bellard et al. 2012; Cahill et al. 2013). Because the impact of climate change on local conditions is complex and depends on many factors affecting energy accumulations and diffusion, it is reasonable to expect that the impact of climate warming interacts with urbanisation, leading to contrasting population responses depending on the degree of urban development in the environments where species occur (Chapman et al. 2017; Urban et al. 2024). Climate-driven population declines may be intensified in urban environments due to the urban heat island effect and the limited availability of cold microclimates to buffer warming (Kaiser et al. 2016; Audusseau et al. 2024; Ganuza et al. 2025). Moreover, by increasing the areas of impervious surfaces, urbanisation has a direct impact on local water regimes, reducing groundwater recharge, limiting infiltration, and increasing the risk of drought (McGrane 2016; Pumo et al. 2017; Zhou et al. 2019). By altering the water cycle, urbanisation will influence the effect of precipitation and aridity on population responses.

Understanding how urbanisation and climate change interact and influence population changes over time is critical, as the processes that affect the intrinsic population growth rates precede colonizations, extinctions and changes in community composition (Collen et al. 2011). Extensive research has examined the effects of habitat loss, fragmentation and climate change on population trends, often supported by national monitoring programs and global repositories (e.g., Martay et al. 2017; Williams et al. 2022). However, among

the relatively few studies that have specifically examined the impacts of urbanisation and its interaction with climate change, most have focused on species occupancies based on presence/absence data or opportunistic counts (but see Dennis et al. 2017; Grünwald et al. 2024), limiting insights on long-term population responses.

While urbanisation and climate change represent broad-scale drivers of population decline, their impacts are rarely uniform across species. Some species may adapt and even thrive in urban environments by exploiting new resources or niches (i.e., urban exploiters; Korányi et al. 2021; Kurucz et al. 2021; Santana Marques et al. 2020). Similarly, climate change may allow some species to establish and expand populations in newly favourable conditions (Crossley et al. 2021; Jackson et al. 2022; Fürst et al. 2023). Ecological and life-history traits are key to understanding how species respond to pressures and changing environments. Thereby, variation in species traits can result in contrasting responses to urbanisation and climate change. For example, trophic generalist species may better cope with the reduced and shifting resources in novel and changing environments, while specialists that rely on specific resources are more vulnerable to these changes (Callaghan et al. 2020; Colom et al. 2022; Pla-Narbona et al. 2022). Dispersal capacity may also be critical: species with high mobility are predicted to move through fragmented habitats more easily, whereas less mobile species often confined to isolated patches are like to be more affected by habitat loss (Bommarco et al. 2010; Öckinger et al. 2010; Niebuhr et al. 2015). Thermal adaptation plays a crucial role in shaping species responses to climate change and urban warming (Audusseau et al. 2024). Species with narrow thermal niches centered in colder regions (i.e., cold-adapted species) are expected to be more negatively affected by climate warming and aridification (i.e., increasing aridity over the long-term), as conditions shift beyond their optimal range (Diamond et al. 2012; Engelhardt et al. 2022; Shirey et al. 2024). Lastly, species with longer active periods or multiple reproductive cycles per year experience a wider range of climatic conditions, which may provide them with a broader environmental niche (Franzén et al. 2020; Callaghan et al. 2021). Ultimately, species whose traits confer greater flexibility are more likely to thrive in changing environments and be more resilient to pressures exacerbated by urbanisation and climate change, providing them with a competitive advantage in an increasingly unpredictable world (Hahs et al. 2023; Sol et al. 2024).

In this study, we investigate whether long-term population trends are associated with climate change (climate warming, reduced precipitation and aridification) and urban intensification (i.e., increasing built-up surface), and whether their effects depend on the spatial context and species traits. Specifically, we assess whether climatic responses differ between rural and

urban environments—anticipating that contrasts in landscape structure, microclimates, and hydrological conditions may modulate population responses. In addition, we evaluate whether species traits related to trophic specialisation, dispersal capacity, reproductive rate, and thermal adaptation explain heterogeneity in population responses to climate change and urban intensification (Table 1). Butterflies are particularly suitable for this purpose because they are extensively monitored, and have well-characterised life-history traits and climatic distributions (Schweiger et al. 2014; Middleton-Welling et al. 2020; Shirey et al. 2022). Therefore, to achieve these objectives, we analysed long-term time series of butterfly counts recorded by national and regional Butterfly Monitoring Schemes established across Europe (Sevilleja et al. 2020). Together, this framework allows us to assess population trends as the outcome of multiple environmental drivers, disentangling the independent effects of climate change and urban intensification from their modulation by urban context and species traits.

2 | Methods

2.1 | Butterfly Population Trend

We used the European Butterfly Monitoring Scheme (eBMS v5.0) dataset, which includes standardised butterfly count data from 19 countries, leveraging the collaborative work of 21 citizen science monitoring projects (Roy et al. 2020). This version of the eBMS dataset spans the period 1976 to 2021 (varying depending on the scheme, with a mean of 16 ± 11.3 years of data), covering 12,033 sites and 318 butterfly species across Europe (Figure S1a). Each monitoring scheme contributing to the eBMS database involves a network of sites where professional or skilled volunteers conduct regular (from weekly to monthly) butterfly counts along fixed transects, following the standardised ‘Pollard Walk’ protocol (Pollard and Yates 1993). Along these transects, all butterfly species are monitored during the butterfly flight season, which varies by climatic region from March to October.

To calculate annual abundance estimates for species populations, we used the regional GAM approach (Dennis et al. 2013; Schmucki et al. 2016). This two-stage method first fits a generalised additive model (GAM) with a Poisson distribution and log link function, capturing the seasonal variation in abundance counts of butterfly species over time within a specific region and year (i.e., the phenological flight curve). In the second stage, the standardised flight curve is used as an offset to account for species’ phenology in a log-linear model to predict the values of missing weekly counts for each site and year. This approach produces a complete time series of weekly counts—combining observed and imputed data—to calculate an annual abundance index for each species-site-year combination, thus minimising biases due to inter-annual variation in sampling effort.

Regions were defined accounting for climate and photoperiod, both recognised as ecological determinants of butterfly phenology (e.g., Hodgson et al. 2011). First, we classified all sites into ten bioclimatic zones according to Metzger et al. (2013). Second, we defined six latitudinal zones from 28.074N to 65.204N, ensuring a maximum day length variation of approximately 1.5 h within regions, using the summer solstice (June 21st) as the

reference day (Figure S1a). Each region was thus defined as a unique combination of bioclimatic and latitudinal zones.

To account for regional variation in species phenology, we fitted the two-stage method described above for each region (Schmucki et al. 2016), using the “flight_curve” function from the *rbms* package (Schmucki et al. 2022) for each species-region-year combination with five or more sites that met the following criteria: a minimum of ten weekly counts and the focal species observed in at least three different weeks. The maximum number of sites included to fit a regional GAM was 300 to balance computational demands and maintain a consistent and representative dataset. For cases with more than 300 available sites, we used an algorithm to select the “best informed” 300 sites based on the monitoring effort and each species occurrence, and to ensure a balanced spatial distribution of the selected sites across the region. For all species populations, we estimated and imputed the missing counts daily over the monitoring season using the corresponding regional flight curve with the function “impute_count” (Schmucki et al. 2022). We calculated annual abundance indices of species populations as the total of real and imputed counts per site and year. Finally, population trends for each species-site combination with ten or more years meeting the GAM inclusion criteria (i.e., ten weekly counts and the focal species observed in at least three different weeks) were calculated as the beta coefficient of year on the logarithm of annual abundance using generalised least squares models (GLS). An autoregressive correlation structure of order 1 was applied to the residuals to account for temporal autocorrelation. The resulting dataset included 8409 population trends for 145 species across 869 sites in 12 different countries, covering six European bioclimatic zones (Figure S1b).

2.2 | Ecological and Life-History Species Traits

We selected five traits known to predict butterfly population trends (Curtis et al. 2015; Eskildsen et al. 2015; Melero et al. 2016) and species urban affinity (Franzén et al. 2020; Callaghan et al. 2021; Pla-Narbona et al. 2022). One trait related to trophic specialisation: (i) the host-plant specialisation index (HSI), which quantifies the trophic specialisation of butterfly species in the larval stage based on the number of plant families, genera, and species they use. One trait related to body size (which in butterflies is often correlated with dispersal capacity, e.g., Sekar 2012): (ii) the wing index (WI), derived from forewing length and wingspan of both females and males. Two traits related to thermal niche: (iii) the species temperature index (STI), that is, the mean temperature within the species’ range, proxy of the thermal niche center; and (iv) the species temperature variation index (STVI), that is, the standard deviation of the temperature within the species range, proxy for the species thermal niche breadth. Both STI and STVI reflect species-level climatic associations based on their realised niche in Europe, that while not capturing population-level thermal limits, local adaptation, or microclimatic responses, allow the detection of general interspecific patterns across a continental scale (Schweiger et al. 2014). Finally, reproductive rate was assessed using: (v) the flight period length (FPL), measured as the average number of months of the year a species is observed in the adult stage. We selected this variable for its strong correlation with

TABLE 1 | Summary of hypothesized interactions between species traits (rows) and environmental stressors (columns) expected to influence butterfly population trends. Bolded row headers indicate the main trait variables; text in parentheses denotes the specific proxy used. Bolded column headers indicate environmental stressors; text in parentheses describes the associated trend variable. Thermal adaptation expectations are based on the combination of climate niche position (mean temperature across a species' European range) and breadth (temperature variability). See Methods for full definitions of traits and environmental trends.

	Urban intensification (Urbanisation trend in already urban sites)	Climate warming (Mean annual temperature trend)	Precipitation reduction (Mean annual precipitation trend)	Aridification (Mean annual aridity trend)
Trophic specialisation (host-plant specialisation)	Specialists are more affected due to higher vulnerability to urban-driven habitat loss		Specialists are more affected due to indirect negative impacts on their more limited resources	Specialists are more affected due to indirect negative impacts on their more limited resources
Body size –dispersal capacity (wing size)	Smaller species are more affected due to limited dispersal capacity in increasingly fragmented landscapes			
Reproductive rate (flight period length)	Species with higher reproductive rates can better cope with increasing urban warming	Species with higher reproductive rates can better cope with increasing temperatures		
Thermal adaptation (thermal niche position and breadth)	Cold-adapted species are more affected due to reduced availability of cool microclimates under increasing urban heat	Cold-adapted species are more negatively affected as warming pushes conditions beyond their climatic optimum		Cold-adapted species are more sensitive to aridification due to their reliance on cooler, moister environments

urban affinity and its advantage as a continuous proxy for reproductive output, avoiding discrete voltinism categories while remaining closely correlated with them (Callaghan et al. 2021; Pla-Narbona et al. 2022). Traits related to trophic specialisation, body size and reproductive rate were extracted from Middleton-Welling et al. (2020) and traits related to thermal tolerance from Schweiger et al. (2014). Out of the 145 species in our dataset, 19 lack data on thermal tolerance traits and two lack data on HSI (Table S1).

2.3 | Urbanisation Data

To assess urbanisation and its trends, we used the Global Human Settlement Layer (European Commission 2023). For each butterfly monitoring site, we extracted the built-up surface (m^2) from the GHS-BUILT-S R2023A raster dataset, derived from Sentinel-2 composite and Landsat data, using a 2×2 km grid centered on the centroid of the transect, with a resolution of 100×100 m. To calculate urbanisation trends, we first predicted the yearly built-up surface at each site by modelling the built data available in five-year intervals from 1975 to 2025, using four different models (linear, polynomial, exponential, and logarithmic). We then selected the model with the lowest AIC, with 99.3% of cases being exponential and 0.7% linear (cases where built-up surface remained zero over all the time series). Next, using the predicted data from the selected models, we calculated temporal trends for the specific subset of years corresponding to each species-site temporal series by determining the slope of the predicted values. This approach allows us to estimate the rate of change in urbanisation, accurately reflecting exponential growth patterns in the data.

Using the GHS-SMOD—R2023A dataset, sites were classified as urban if they belonged to urban clusters, defined as contiguous 1×1 km grid cells (connected by any edge or corner) with a density of at least 300 inhabitants per km^2 of permanent land and a total population of at least 5000 inhabitants in the cluster (European Commission 2023). Sites were classified as rural if they were present in grid cells that did not belong to urban clusters. Most rural sites have a population density below 300 inhabitants per km^2 ; however, some may have higher densities but do not form clusters with a sufficient total population to be considered urban. The categorization of sites as rural or urban (rural: $n = 745$ sites, 145 species; urban: $n = 115$ sites, 100 species; Figure S1c; Table S1) did not change during the study period. See Figure S2 for urbanisation trends for rural and urban sites.

2.4 | Climate Data

We used the ClimateDT tool (Marchi et al. 2024), which employs dynamic lapse-rate calculations for the spatial downscaling of climatic surfaces, to estimate climate trends at resolutions relevant to individual transects. This tool leverages CHELSA v2.1 (Karger et al. 2017), a global dataset of climatic measurements at 30 arcsec spatial resolution (1 km up to 500 m). Its algorithm accounts for variations in temperature with elevation and incorporates orographic effects on cloud cover and radiation, making it a highly reliable source for climate estimations in topographically diverse

areas. This ensures that our climate analyses are both more accurate and relevant to the specific conditions of our sites.

For each site and year, we extracted annual estimates of mean temperature, precipitation, and aridity. Aridity was calculated as the inverse of the De Martonne Index, which combines mean annual and seasonal precipitation with temperature to represent water availability and drought intensity (Jafarpour et al. 2023). These three climatic variables are important for butterfly populations as their shifts over the long term are closely associated with key ecological processes that influence butterfly population dynamics, such as changes in phenology, habitat suitability, and resource availability (Hill et al. 2021; Wilson and Fox 2021). Further, the strength of their effect can vary depending on the species and the population (Mills et al. 2017; Colom et al. 2021; Melero et al. 2022). We then used linear models to calculate climatic trends associated with each species-site temporal series (Figure S3).

2.5 | Statistical Analysis

Two different sets of linear mixed models were conducted to analyse the interaction effects on butterfly population trends. The first set of models analysed the interactions of urbanisation and climate trends (separately) with site type (rural or urban), including random slopes for species to account for inter-specific variation in population responses. However, urbanisation was only tested in already-urban sites (i.e., urban intensification) as the increase in built-up surface was minimal in rural sites (see Figure S2). Urbanisation trends showed very weak, nonsignificant correlations with climatic trends ($r = 0.04$ – 0.1 , $p > 0.05$), whereas some climatic trends themselves were correlated (e.g., temperature–aridification: $r = 0.6$; precipitation–aridification: $r = -0.87$). We therefore modelled the impact of each environmental driver on population trends separately to avoid multicollinearity and confounding effects.

The second set of models analysed the interaction between environmental trends (urbanisation and climate) and species traits, in the sense of the established hypothesis (Table 1). In all models, population trend (beta coefficient of the annual abundance models) was the response variable, and species, site and climate region were included as random factors. Additionally, we incorporated the inverse of the variance of the population trends as weights in the models to account for the uncertainty associated to the population trend estimates. First, we fitted four models in which we tested the effects of urbanisation and climate trends (temperature, precipitation and aridity), with site type (rural vs. urban) included as an interacting factor for climate variables. For the climate models, we restricted the analyses to the 100 most common species in both rural and urban sites to ensure comparability by avoiding biases due to different species composition in urban and rural sites (but see Figure S4a–d for plot effects including all the species). Second, we developed models for the interactions between environmental trends and species, based on prior hypotheses (Table 1). We conducted the models separately for rural and urban sites, using all species with available data for all five traits (rural = 126; urban = 90) to ensure comparable results between different site types and trait models. In the trait models, all continuous variables were standardised (mean = 0, SD = 1) to compare interaction effect

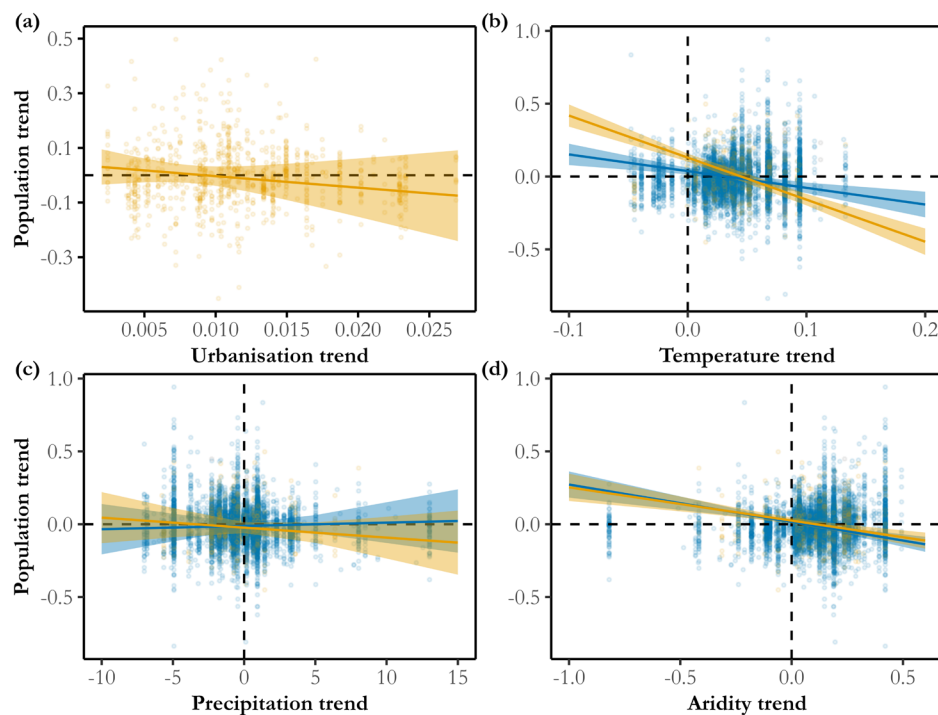


FIGURE 1 | Relationships between butterfly population trends and urbanisation and climate trends across rural (blue) and urban (orange) sites. Points represent raw data, while lines indicate model predictions with 95% confidence intervals. The models tested the interactions between each predictor: (a) urbanisation trend; (b) temperature trend; (c) precipitation trend; (d) aridity trend; and environmental type (rural vs urban). Analyses were restricted to the 100 common species found in both environmental types across six climate regions. $N = 7796$ population trends.

sizes across traits and identify which one best explains variation in species responses. Quadratic terms were not included in the models, as exploratory analyses did not reveal significant nonlinear patterns between population trends and urbanisation or climate shifts for most species. All models were fitted using the `glmmTMB` package (Brooks et al. 2017) in R version 4.3.3 (R Core Team 2020).

We tested whether species responses to environmental trends showed significant phylogenetic signal, which would indicate the need to account for shared evolutionary history. Using both Blomberg's K and Pagel's λ , we found no evidence of phylogenetic structure in species-level population trends ($K = 0.075$, $p = 0.819$; $\lambda \approx 0$, $p > 0.99$) or in species-level random intercepts from GLMMs (all $K < 0.06$ and $p > 0.8$). This indicates that phylogenetic relatedness does not explain similarity in species responses to environmental change in our study system, and thus phylogenetic correction was not necessary in our models.

To focus on ecologically meaningful patterns, we report results from models where fixed effects explained at least 1% of the variance in population trends (marginal $R^2 \geq 0.01$). Full results, including models with lower explanatory power, are provided in (Table S3).

3 | Results

3.1 | Urbanisation and Climate Effects on Rural and Urban Populations

Contrary to our expectations, the overall effect of urban intensification (i.e., urbanisation in already urban sites) on

population trends was not significant (Figure 1a; Table 2; Table S2). Regarding climate change, population declines were associated with climate warming in both urban and rural sites, with stronger negative impacts in urban populations (Figure 1b; Table 2; Table S2). According to our model, a temperature increase of 0.02°C per year was associated with an average decrease in butterfly abundance of 2.3% per year for rural populations and of 5.7% per year in urban populations, meaning that, over one decade of climate warming, urban populations would decline by 23.4% more than rural populations. On the other hand, precipitation had contrasting effects on population trends in rural and urban contexts (Figure 1c; Table 2; Table S2); for example, an increase of 10 mm/year in precipitation was associated with an average annual abundance increase of 2.3% in rural populations, and a decrease of 6.6% per year in urban ones. While this effect was significant, precipitation explained less than 1% of the variance in population trends (marginal $R^2 < 0.01$). Both rural and urban populations declined with aridification, with rural populations showing significantly steeper declines (Table 2; Table S2). However, the magnitude of the difference was relatively low (Figure 1d), for example, an increase of $0.1^\circ\text{C}/\text{mm}$ was associated with an annual decline of 2.5% in rural populations and 2.2% in urban ones.

3.2 | The Role of Traits in Species' Response to Urbanisation and Climate Change

3.2.1 | Inter-Specific Responses to Urbanisation Trends

None of the interactions between urban intensification and species traits (Table 1) substantially improved explanatory power

TABLE 2 | Results of interactions between (a) environmental trends (urbanisation, temperature, precipitation and aridity) and environment type (rural vs. urban); and between environmental trends and species traits (HSI – host plant specialisation index; WI – wing index; FPL – flight period length; STI – species temperature index; STVI – species temperature variation index) in (b) rural sites and (c) urban sites. Test statistics for each model term are shown: Difference in Akaike's information criterion AIC (ΔAIC), marginal R^2 , coefficient estimate (effect size), standard error (SE), z -value (Z), p -value (p).

Independent variable	Interacting covariable	(a) Species in both rural and urban environments (100 species)				(b) Species in rural environments (126 species)				(c) Species in urban environments (90 species)			
		ΔAIC	R^2_m	Effect size (SE)	$Z(p)$	ΔAIC	R^2_m	Effect size (SE)	$Z(p)$	ΔAIC	R^2_m	Effect size (SE)	$Z(p)$
Urbanisation			0.004	−4.21 (5.31)	−0.79 (0.43)								
Temperature	Site type	0	0.06	−1.73 (0.06)	−27.5 (<0.01)								
Precipitation	Site type	5983	0.001	−0.01 (<0.01)	−15.5 (<0.01)								
Aridity	Site type	21,059	0.052	0.03 (0.01)	2.5 (0.011)								
Urbanisation	HSI									2813	0.006	−0.003 (<0.01)	34.3 (<0.01)
	WI									0	0.002	−0.0051 (<0.01)	−63.3 (<0.01)
	FPL									1678	0.003	0.0045 (<0.01)	48.1 (<0.01)
	STI									3973	0.003	−0.0003 (<0.01)	−3.65 (<0.01)
	STVI									3304	0.004	0.0024 (<0.01)	26.1 (>0.01)
Temperature	FPL					1142	0.06	0.0014 (<0.0001)	33 (>0.01)	1353	0.15	0.0017 (<0.0001)	14.2 (>0.01)
	STI					0	0.054	0.0023 (0.0001)	47.4 (<0.01)	0	0.142	0.0051 (<0.0001)	39.5 (>0.01)
	STVI					895	0.051	0.0015 (<0.0001)	36.8 (<0.01)	1265	0.165	−0.0023 (<0.0001)	−17.1 (<0.01)
Precipitation	HSI					854	0.043	−0.0035 (<0.0001)	−82.7 (>0.01)	0	0.015	0.0090 (<0.0001)	86.2 (>0.01)
Aridity	HSI					7866	0.076	0.0022 (<0.0000)	49.8 (>0.01)	0	0.066	−0.0075 (<0.0001)	−67.1 (>0.01)
	STI					0	0.083	0.0049 (0.0001)	101.8 (>0.01)	4184	0.074	0.0019 (<0.0001)	17.3 (>0.01)
	STVI					8280	0.082	−0.00 (<0.0000)	−45.4 (<0.01)	3407	0.085	−0.0039 (<0.0001)	−32.8 (<0.01)

(marginal $R^2 < 0.01$) of urban intensification, indicating that urbanisation was a poor predictor of population trends, even when accounting for interspecific differences (Table 2; Table S3).

3.2.2 | Inter-Specific Responses to Temperature Trends

Warming trends had a stronger negative impact on cold-adapted species—those with cold and narrow thermal niches (Table 1)—although the interaction with thermal niche breadth varied by urban context (Table 2, Table S3). In rural populations, the impact of warming intensified as both the STI (thermal niche position) and STVI (thermal niche breadth) decreased (Figure 2a). For instance, a temperature increase of 0.01°C per year led to an average population decline of 0.72% annually for the warmest-centered species and up to 1.56% for the coldest-centered, with effects also stronger for species with narrower niches (1.19% vs. 0.9% in broader-niche species). In urban sites, the warmest-centered species declined by 1.3% annually and the coldest-centered by 3.3%; however, in contrast to rural sites, species with broader thermal niches declined more than those with narrower niches (2.8% vs. 2.2% annually; Figure 2b).

In line with our hypothesis on the role of reproductive rate (Table 1), we found a consistent pattern across both rural and urban environments: species with longer flight periods—used here as a proxy of reproductive rate—were less negatively affected by warming than those with shorter flight periods (Table 2, Table S3, Figure 2a,b). A temperature increase of 0.01°C per year led to annual declines of 1.04% for species with the shortest flight periods versus 0.86% for those with the longest in rural sites, and 2.7% versus 2.4% in urban sites.

3.2.3 | Inter-Specific Responses to Precipitation Trends

The expected relationship between population responses and precipitation trends (Table 1) was observed in urban environments but, unexpectedly, the opposite pattern was found in rural populations (Table 2; Table S3). In rural sites, reduced precipitation was associated with stronger declines in host plant generalists than in specialist species (Figure 2c); with annual declines of 13%–4.5%, respectively, with a precipitation decrease of 10mm/year. In urban environments, however, we found the opposite pattern with relatively large decline for host-plant specialists (Figure 2d), with declines up to 26.9% per year for specialists and increase of 2.3% per year for generalists when precipitation decline by 10mm per year.

3.2.4 | Inter-Specific Responses to Aridity Trends

We found support for the predicted relationship between trophic specialisation and aridity trends (Table 1) only in urban populations (Table 2; Table S3). In urban sites, increasing aridity was associated with stronger declines in host-plant specialists than in generalists (Figure 2f); for instance, a $0.1^\circ\text{C}/\text{mm}$ per year increase in aridity led to annual population declines ranging from 1.9% in generalists to 5.1% in specialists. In contrast, rural populations showed the opposite trend (Figure 2e), with generalists declining more than specialists (2.4% vs. 1.6%). Regarding thermal adaptation, we expected cold-adapted species—those with narrower and colder-centered thermal niches—to be more sensitive to aridity (Table 1). Species with colder thermal niche centers consistently declined more than warm-adapted species in both rural

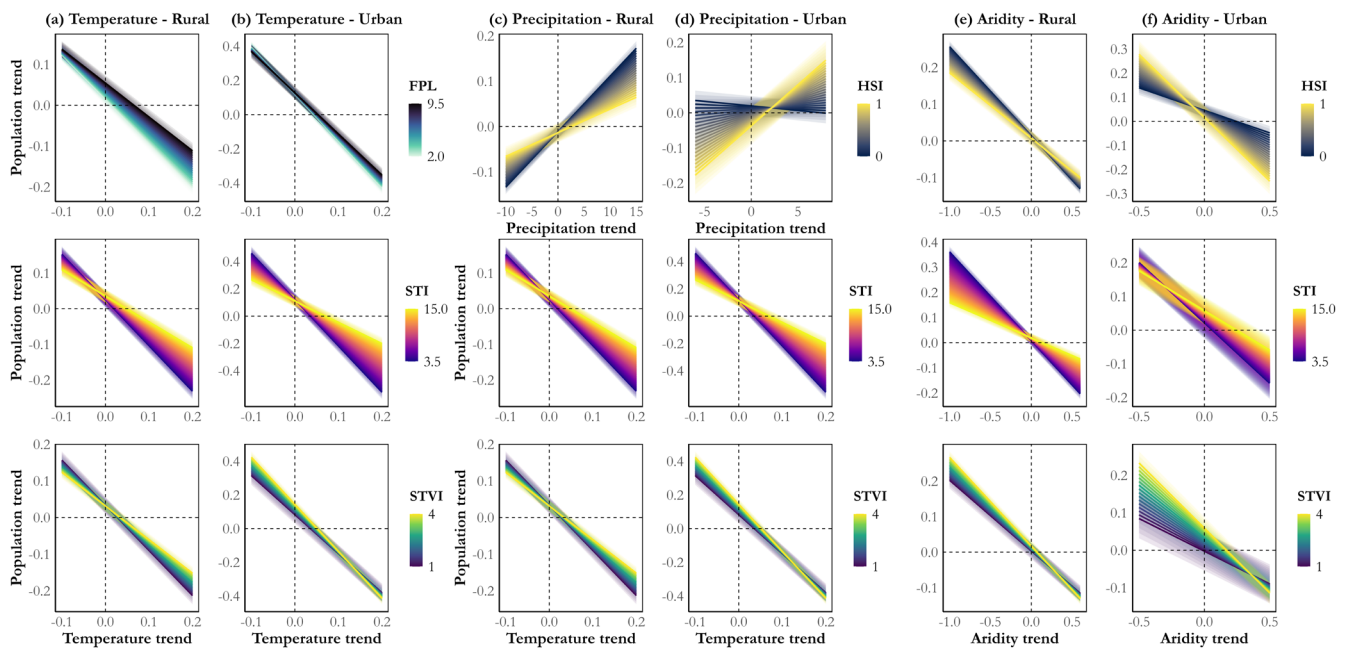


FIGURE 2 | Relationships between butterfly population trends (Y-axis) and environmental trends (X-axis) interacting with species traits. Each row corresponds to a specific species trait: HSI (host-plant specialisation index), FPL (flight month average), STI (species temperature index), and STVI (species temperature variation index). Each column pair represents a unique predictor (temperature) (a, b), precipitation (c, d), aridity (e, f), for rural and urban sites separated in different models. Lines represent model predictions for 20 intervals of the species trait range, with shaded areas representing 95% confidence intervals. Dashed lines indicate a trend value of 0, separating positive from negative trends (e.g., warming vs. cooling for temperature trends in X-axis). Models included only species with available data for all five species traits (rural = 126; urban = 90).

and urban environments (Figure 2e,f). For example, an aridity increase of 0.1°C/mm per year led to declines ranging from 1.4% to 3.4% in rural sites and from 2.4% to 3.6% in urban sites, for the warmest- to coldest-centered species, respectively. However, contrary to expectations, species with broader thermal niches experienced greater declines than those with narrower ones in both contexts (e.g., 2.5% vs. 1.8% in rural sites, and 3.4% vs. 1.8% in urban sites; Figure 2e,f).

4 | Discussion

Climate warming and aridification were the main drivers of butterfly population declines across Europe, while precipitation trends alone showed little explanatory power. Urban intensification did not have a direct effect on population trends. However, the urban–rural context played a critical role in shaping species responses to climate warming, suggesting a potential synergy between warming and urbanisation. Trait-based analyses further revealed that species' thermal affinities and ecological traits modulate their sensitivity to climate change, helping to explain the variability in population responses across species and environments.

4.1 | General Effects of Urbanisation and Climate on Urban and Rural Populations

The stronger impact of warming on urban populations supports the hypothesis that urban areas generally exacerbate thermal constraints on insects. While some species may possess pre-adaptations or evolved traits in urban environments (e.g., heat tolerance in a common European moth; Merckx et al. 2024) that may help to cope with thermal stress, most insects rely on adjusting their behaviour and finding cold microclimates to optimise thermoregulation and buffer the impact of warming (Suggitt et al. 2018; Bladon et al. 2020; Vives-Inglá et al. 2023). Yet in urban environments, the effectiveness of these strategies may be limited due to elevated baseline temperatures from the urban heat island effect and high habitat fragmentation (Urban et al. 2024), which can intensify population collapses during climate extremes and hinder recovery by limiting dispersal and connectivity (Oliver et al. 2015). Overall, our results suggest that the impact of warming will escalate as urban expansion continues, imposing greater thermal stress on insect populations.

While climate warming, precipitation change, and aridification are interrelated components of climate change, they impose distinct climatic pressures for butterflies (Roy et al. 2001; WallisDeVries et al. 2011; Ubach et al. 2022), showing distinct relationships with butterfly population trends and their interactions with urban context. Aridification, reflecting the combined effects of increased temperature and reduced precipitation, was associated with population declines in both rural and urban environments, though with slightly stronger effects in rural sites. Over the long term, an increase in aridity leads to a reduction of water availability, impacting the quality and availability of their nectar and host plants (Carnicer et al. 2019; van Bergen et al. 2020; Brunet et al. 2025), as well as shifts in the timing of plant growth and flowering—key processes that support

butterfly development and adult foraging (Dalton et al. 2023; Donoso et al. 2016; Gil-Tapetado et al. 2023). Although the negative effects of aridity may be partially buffered in urban environments through active management of green spaces—such as irrigation in parks and gardens that help sustain floral resources and reduce water stress (Baldock et al. 2019)—our results show that aridity still had a similarly negative impact on butterfly populations across both environments, with only slightly weaker effects in urban environments.

Precipitation changes alone, independent of temperature, explained little of the variation in butterfly population trends on the European scale. This likely reflects the high spatiotemporal variability of precipitation patterns across the continent, as well as the context-dependent nature of its ecological impacts. Precipitation can influence butterflies in multiple, sometimes opposing ways depending on species phenology, seasonality, and local conditions (Roy et al. 2001; Ubach et al. 2022), making its effects less consistent and generalizable than those of temperature and aridity, which show clearer and more directional trends over time in Europe (Gulev et al. 2021).

While climate shifts had clear, generalised impacts on butterfly populations, urbanisation itself did not significantly influence the overall population trends in our continental-scale study system. This result contrasts with several studies showing that urbanisation is a major factor shaping insect species composition and population abundance across spatial gradients (Knop 2016; Merckx and Van Dyck 2019; Tzortzakaki et al. 2019; Kuussaari et al. 2021; Maes et al. 2022; Pla-Narbona et al. 2022). However, there has been no prior evidence of the impact of urban intensification on decadal population trends. In our system, the absence of an urbanisation effect may be explained by the fact that urban communities represent a pre-filtered subset of the regional species pool (Gathof et al. 2022; Pla-Narbona et al. 2022; Roper-Edwards and Hurlbert 2024), where the most sensitive taxa have already been lost due to earlier habitat loss and fragmentation. Because systematic butterfly monitoring expanded across Europe mainly from the 1990s onwards, our analyses capture population trends during a period when substantial declines and community shifts driven by land-use change had likely already occurred, meaning that the trends reported in our study operate on already strongly altered assemblages (Habel et al. 2016, 2024). Moreover, the lack of data of rural sites experiencing significant long-term urbanisation over our study period (Figure S2), limited the possibility to test the impact of rural-urbanisation on butterfly population trends. This highlights the importance of maintaining long-term monitoring in areas potentially sensitive to urban development.

4.2 | The Role of Species Traits to Shape Population Responses to Climate Shifts

Our results demonstrate that thermal niche characteristics of species are key predictors of population responses to climate shifts at a continental scale. We found that in rural environments, climate warming had the strongest negative impact on cold-adapted species—those with narrow thermal niches centered in colder regions. These findings align with growing

evidence that cold-adapted species are particularly vulnerable to climate warming, as rising temperatures push them beyond their thermal limits (Trisos et al. 2020), contributing to steeper declines and range contractions compared to warm-adapted species (Bowler et al. 2015; Hällfors et al. 2024; Shirey et al. 2024). In urban environments, we found a consistent interaction with thermal niche position—indicating stronger declines in cold-centered species. However, our hypothesis was not fully supported, as species with broader rather than narrower thermal niches were more negatively affected by warming. A similar pattern emerged in response to aridification across both rural and urban populations. These results suggest a complex interaction between niche position and breadth but may partly result from a confounding effect. In our European multi-species dataset, butterfly species with broader niches tend to be centered in colder regions. This moderate correlation ($r = -0.29$, $p = 0.001$, $n = 126$; Figure S5) likely arises because thermal niche traits were calculated based only on the European distributions of these species (Schweiger et al. 2014). Cold-centered species—such as *Coenonympha tullia*, *Lasiommata petropolitana*, or *Lycaena hippothoe* (Table S1)—mainly occupy northern latitudes that are well represented within Europe, while warm-centered species—such as *Pyronia cecilia*, *Zerynthia rumina*, or *Glaucopsyche melanops* (Table S1)—extend further south into Africa, beyond the European boundaries. Consequently, niche breadths for species centered in warmer regions may be underestimated relative to those centered in cooler regions (Barbet-Massin et al. 2010; Titeux et al. 2017). Further, species adaptations (at the population level) to local climatic conditions occur in many butterfly species (Roy et al. 2015; Melero et al. 2022), making them especially vulnerable to climate independently of their climatic niche center and breadth (which are defined at the species level), and of their location (Melero et al. 2025).

We found strong evidence that species with lower reproductive rates were more negatively affected by climate warming, consistently across both rural and urban environments. While butterflies generally have high reproductive rates, those with even higher potential—such as species capable of producing multiple generations per year—have often more positive population trends compared to species producing single generations per year (Macgregor et al. 2019; Wepprich et al. 2019; Michielini et al. 2021; Colom et al. 2022). Species producing multiple reproductive outputs during the season have the potential of falling into evolutionary traps under warming by initiating additional late-season generations that fail to complete development before winter (Van Dyck et al. 2015). However, populations that increase their reproductive outputs later in the season often experience population growth in the following year (Kerr et al. 2020; Wepprich et al. 2025), suggesting that increasing the number of generations under warming represents an adaptive response to climate change.

We expected trophic specialists (i.e., butterflies whose larvae feed on a few plant species) to be especially impacted by a progressive reduction in precipitation and increasing aridity, as their limited diet makes them more sensitive to host plant declines under water stress. In contrast, generalist species, which exploit a broader array of host plants, may better buffer these changes by shifting to more drought-tolerant or persistent plant species within their diet. This pattern was only found in

urban populations, suggesting that the reduction of native host plant richness with increasing urbanisation (Clark et al. 2007; Miles et al. 2019; Hou et al. 2023) may amplify the impact of precipitation reduction and aridity on specialist species, leaving them particularly exposed to resource decline in these environments. Surprisingly, we found the opposite pattern in rural environments, with generalists being more negatively affected by increasing drought conditions. One possible explanation is that under environmental stress, generalists may face ecological trade-offs that limit their performance compared to specialists. Theoretical and empirical studies have shown that niche breadth is often constrained by trade-offs, such that generalists perform less efficiently than specialists on any given resource (Futuyma and Moreno 1988; Ravigné et al. 2009). Under increasing water limitation, generalists may struggle to maintain performance when multiple resource options decline simultaneously in availability or quality (Carvajal Acosta et al. 2023), whereas specialists may possess finer-tuned physiological or behavioural adaptations to cope with host plant decline or chemical changes (Gely et al. 2020; Gutbrodt et al. 2011). Further research is needed to evaluate whether generalists are systematically more vulnerable to increasing drought in rural environments due to ecological trade-offs. Future studies could refine our predictions by incorporating additional traits, such as habitat specialisation or species' biogeographic distributions, although these trait dimensions are likely partly captured by the traits considered here.

4.3 | The Role of Species Traits in Modulating Population Responses to Urbanisation

We explored several traits previously shown to influence species' sensitivity to urbanisation (Franzén et al. 2020; Callaghan et al. 2021). For example, body size has been positively linked to urban tolerance in butterflies and moths, presumably due to the higher dispersal capacity it confers in fragmented landscapes (Merckx et al. 2018; Kuussaari et al. 2021; Pla-Narbona et al. 2022). However, despite the ecological plausibility of these traits, their inclusion did not substantially improve the explanatory power of urban intensification on population trends.

This lack of strong, trait-based patterns suggests that species responses to urbanisation are difficult to capture through broad species-level traits alone. Urban environments are inherently heterogeneous, shaped by local management, land-use history, and spatial context (McDonnell and Hahs 2015; Aronson et al. 2016), which likely interact in complex and region-specific ways with species ecology and life-history (Diamond et al. 2015). In this light, the lack of clear trait-based predictors does not undermine the ecological importance of the traits themselves but highlights the context-dependence and multi-dimensionality of urban pressures (Piano et al. 2020). Trait-based approaches may yield clearer insights when applied at finer spatial scales or when combined with more detailed descriptors of urban landscape structure, management, and connectivity. Nevertheless, our findings reinforce that the urban context remains critical, as it strongly modulates species responses to climate change, a key driver of population declines across a continental scale.

Acknowledgements

This work has been made possible by the participation of more than one hundred thousand citizen scientists involved in coordinated monitoring projects across Europe over the past four decades. The UK BMS is organised and funded by Butterfly Conservation, the UK Centre for Ecology and Hydrology, British Trust for Ornithology, and the Joint Nature Conservation Committee. The Irish BMS is funded by the Heritage Council and the Department of Culture, Heritage and the Gaeltacht. The Dutch BMS is a co-operation between Dutch Butterfly Conservation and Statistics Netherlands (CBS), part of the Network Ecological Monitoring (NEM) and financed by the Ministry of Agriculture, Nature and Food Quality (LNV). The German BMS is a cooperation between the Helmholtz Centre for Environmental Research—UFZ, German Butterfly Conservation (GfS) and science4you. The Catalan BMS is funded by the Department of Climate Action, Food, and Rural Agenda of the Government of Catalonia and the Barcelona Provincial Council. The Finnish BMS is coordinated by the Finnish Environment Institute and funded by the Finnish Ministry of Environment. The Swedish BMS is coordinated by Lund University and is funded by the Swedish Environmental Protection Agency. The BMS Spain is coordinated by the association SOCEME, with the collaboration of Autonomous University of Madrid (UAM), Spanish Ministry of Environment (MITECO), Spanish National Parks Agency (OAPN), Sierra Nevada Global Change Observatory, and ICTS-Doñana (Doñana Biological Station, CSIC). The ZERYNTHIA BMS is supported by the Basque Country Government, Cantabria Government and Valle de Aranguren Council (Navarre). The Luxembourg BMS is coordinated by the Luxembourg Institute of Science and Technology and financially supported by the Ministry of the Environment, Climate and Biodiversity. We thank Thomas Merckx for his valuable and constructive feedback.

Funding

This research and PC were funded by the research projects MEDYCI Grant PID2020-113133RB-I00 funded by MCIN/AEI/10.13039/501100011033, and SATURNO Grant CNS2022-135489 funded by MICIU/AEI/10.13039/501100011033 and by the European Union NextGenerationEU/PRTR.

Ethics Statement

The authors have nothing to report.

Consent

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Butterfly count datasets used for this study are available from the European Butterfly Monitoring Scheme via a signed licence agreement (<https://butterfly-monitoring.net/>). Data of species traits was obtained from the European & Maghreb butterfly trait database (<https://butterflytraits.github.io/European-Butterfly-Traits/index.html>). Climate data was extracted from the CHELSA 1.2 dataset using the ClimateDT Downscaling Tool (<https://www.ibbr.cnr.it/climate-dt/>). Urbanisation data was extracted from the Global Human Settlement Layer (<https://human-settlement.emergency.copernicus.eu/>). R codes and datasets to replicate all the analyses are available in Zenodo (<https://zenodo.org/records/18479385>).

References

- Aronson, M. F. J., C. H. Nilon, C. A. Lepczyk, et al. 2016. "Hierarchical Filters Determine Community Assembly of Urban Species Pools." *Ecology* 97: 2952–2963.
- Audusseau, H., R. Schmucki, S. Croci, and V. Dubreuil. 2024. "Sustainable Urban Planning Needs Stronger Interdisciplinarity and Better Co-Designing: How Ecologists and Climatologists Can Fully Leverage Climate Monitoring Data." *Wiley Interdisciplinary Reviews: Climate Change* 15: e912. <https://doi.org/10.1002/wcc.912>.
- Baldock, K. C. R., M. A. Goddard, D. M. Hicks, et al. 2019. "A Systems Approach Reveals Urban Pollinator Hotspots and Conservation Opportunities." *Nature Ecology & Evolution* 3: 363–373.
- Barbet-Massin, M., W. Thuiller, and F. Jiguet. 2010. "How Much Do We Overestimate Future Local Extinction Rates When Restricting the Range of Occurrence Data in Climate Suitability Models?" *Ecography* 33: 878–886.
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. "Impacts of Climate Change on the Future of Biodiversity." *Ecology Letters* 15: 365–377.
- Bladon, A. J., M. Lewis, E. K. Bladon, et al. 2020. "How Butterflies Keep Their Cool: Physical and Ecological Traits Influence Thermoregulatory Ability and Population Trends." *Journal of Animal Ecology* 89: 2440–2450.
- Bommarco, R., J. C. Biesmeijer, B. Meyer, et al. 2010. "Dispersal Capacity and Diet Breadth Modify the Response of Wild Bees to Habitat Loss." *Proceedings of the Royal Society B: Biological Sciences* 277: 2075–2082.
- Bowler, D. E., P. Haase, I. Kröncke, et al. 2015. "A Cross-Taxon Analysis of the Impact of Climate Change on Abundance Trends in Central Europe." *Biological Conservation* 187: 41–50.
- Brooks, M., K. Kristensen, K. J. van Benthem, et al. 2017. "Package 'glm-mTMB' R Topics Documented."
- Brunet, J., D. W. Inouye, E. E. Wilson Rankin, and T. C. Giannini. 2025. "Global Change Aggravates Drought, With Consequences for Plant Reproduction." *Annals of Botany* 135: 89–104.
- Cahill, A. E., M. E. Aiello-Lammens, M. Caitlin Fisher-Reid, et al. 2013. "How Does Climate Change Cause Extinction?" *Proceedings of the Royal Society B: Biological Sciences* 280: 20121890.
- Callaghan, C. T., Y. Benedetti, J. H. Wilshire, and F. Morelli. 2020. "Avian Trait Specialization Is Negatively Associated With Urban Tolerance." *Oikos* 129: 1541–1551.
- Callaghan, C. T., D. E. Bowler, and H. M. Pereira. 2021. "Thermal Flexibility and a Generalist Life History Promote Urban Affinity in Butterflies." *Global Change Biology* 27: 3532–3546.
- Carnicer, J., C. Stefanescu, M. Vives-Inglá, et al. 2019. "Phenotypic Biomarkers of Climatic Impacts on Declining Insect Populations: A Key Role for Decadal Drought, Thermal Buffering and Amplification Effects and Host Plant Dynamics." *Journal of Animal Ecology* 88: 376–391.
- Carvajal Acosta, A. N., A. A. Agrawal, and K. Mooney. 2023. "Plant Water-Use Strategies as Mediators of Herbivore Drought Response: Ecophysiology, Host Plant Quality and Functional Traits." *Journal of Ecology* 111: 687–700.
- Chapman, S., J. E. M. Watson, A. Salazar, M. Thatcher, and C. A. McAlpine. 2017. "The Impact of Urbanization and Climate Change on Urban Temperatures: A Systematic Review." *Landscape Ecology* 32: 1921–1935.
- Clark, P. J., J. M. Reed, and F. S. Chew. 2007. "Effects of Urbanization on Butterfly Species Richness, Guild Structure, and Rarity." *Urban Ecosystems* 10: 321–337.

- Collen, B., L. Mcrae, S. Deinet, et al. 2011. "Predicting How Populations Decline to Extinction." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 366: 2577–2586.
- Colom, P., M. Ninyerola, X. Pons, A. Traveset, and C. Stefanescu. 2022. "Phenological Sensitivity and Seasonal Variability Explain Climate-Driven Trends in Mediterranean Butterflies." *Proceedings of the Royal Society B: Biological Sciences* 289: 20220251.
- Colom, P., A. Traveset, D. Carreras, and C. Stefanescu. 2021. "Spatio-Temporal Responses of Butterflies to Global Warming on a Mediterranean Island Over Two Decades." *Ecological Entomology* 46: 262–272.
- Crossley, M. S., O. M. Smith, L. L. Berry, et al. 2021. "Recent Climate Change Is Creating Hotspots of Butterfly Increase and Decline Across North America." *Global Change Biology* 27: 2702–2714.
- Curtis, R. J., T. M. Brereton, R. L. H. Dennis, C. Carbone, and N. J. B. Isaac. 2015. "Butterfly Abundance Is Determined by Food Availability and Is Mediated by Species Traits." *Journal of Applied Ecology* 52: 1676–1684.
- Dalton, R. M., N. C. Underwood, D. W. Inouye, M. E. Soulé, and B. D. Inouye. 2023. "Long-Term Declines in Insect Abundance and Biomass in a Subalpine Habitat." *Ecosphere* 14: 9.
- Dennis, E. B., S. N. Freeman, T. Brereton, and D. B. Roy. 2013. "Indexing Butterfly Abundance Whilst Accounting for Missing Counts and Variability in Seasonal Pattern." *Methods in Ecology and Evolution* 4: 637–645.
- Dennis, E. B., B. J. T. Morgan, D. B. Roy, and T. M. Brereton. 2017. "Urban Indicators for UK Butterflies." *Ecological Indicators* 76: 184–193.
- Diamond, S. E., R. R. Dunn, S. D. Frank, N. M. Haddad, and R. A. Martin. 2015. "Shared and Unique Responses of Insects to the Interaction of Urbanization and Background Climate." *Current Opinion in Insect Science* 11: 71–77.
- Diamond, S. E., L. M. Nichols, N. McCoy, et al. 2012. "A Physiological Trait-Based Approach to Predicting the Responses of Species to Experimental Climate Warming." *Ecology* 93: 2305–2312.
- Donoso, I., C. Stefanescu, A. Martínez-Abraín, and A. Traveset. 2016. "Phenological Asynchrony in Plant–Butterfly Interactions Associated With Climate: A Community-Wide Perspective." *Oikos* 125: 1434–1444.
- Dri, G. F., C. S. Fontana, and C. d. S. Dambros. 2021. "Estimating the Impacts of Habitat Loss Induced by Urbanization on Bird Local Extinctions." *Biological Conservation* 256: 109064.
- Engelhardt, E. K., M. F. Biber, M. Dolek, et al. 2022. "Consistent Signals of a Warming Climate in Occupancy Changes of Three Insect Taxa Over 40 Years in Central Europe." *Global Change Biology* 28: 3998–4012.
- Eskildsen, A., L. G. Carvalheiro, W. D. Kissling, J. C. Biesmeijer, O. Schweiger, and T. T. Høye. 2015. "Ecological Specialization Matters: Long-Term Trends in Butterfly Species Richness and Assemblage Composition Depend on Multiple Functional Traits." *Diversity and Distributions* 21: 792–802.
- European Commission. Joint Research Centre. 2023. *GHSL Data Package 2023*. Publications Office of the European Union.
- Fenoglio, M. S., M. R. Rossetti, and M. Videla. 2020. "Negative Effects of Urbanization on Terrestrial Arthropod Communities: A Meta-Analysis." *Global Ecology and Biogeography* 29: 1412–1429.
- Franzén, M., P. E. Betzholtz, L. B. Pettersson, and A. Forsman. 2020. "Urban Moth Communities Suggest That Life in the City Favours Thermophilic Multi-Dimensional Generalists." *Proceedings of the Royal Society B: Biological Sciences* 287: 20193014.
- Fürst, J., K. Bollmann, M. M. Gossner, P. Duelli, and M. K. Obrist. 2023. "Increased Arthropod Biomass, Abundance and Species Richness in an Agricultural Landscape After 32 Years." *Journal of Insect Conservation* 27: 219–232.
- Futuyma, D. J., and G. Moreno. 1988. "The Evolution of Ecological Specialization." *Annual Review of Ecology and Systematics* 19: 207–233.
- Ganuza, C., S. Redlich, S. Rojas-Botero, et al. 2025. "Warmer Temperatures Reinforce Negative Land-Use Impacts on Bees, but Not on Higher Insect Trophic Levels." *Proceedings of the Royal Society B: Biological Sciences* 292: 20243053.
- Gao, J., and B. C. O'Neill. 2020. "Mapping Global Urban Land for the 21st Century With Data-Driven Simulations and Shared Socioeconomic Pathways." *Nature Communications* 11: 2302.
- Gathof, A. K., A. J. Grossmann, J. Herrmann, and S. Buchholz. 2022. "Who Can Pass the Urban Filter? A Multi-Taxon Approach to Disentangle Pollinator Trait–Environmental Relationships." *Oecologia* 199: 165–179.
- Gely, C., S. G. W. Laurance, and N. E. Stork. 2020. "How Do Herbivorous Insects Respond to Drought Stress in Trees?" *Biological Reviews* 95: 434–448.
- Gil-Tapetado, D., C. D. Soria, J. F. Gómez, J. M. Sesma, and F. J. Cabrero-Sañudo. 2023. "Aridity Could Have Driven the Local Extinction of a Common and Multivoltine Butterfly." *Ecological Entomology* 48: 40–54.
- Grünwald, J., A. Aunipš, M. Brambilla, et al. 2024. "Ecological Traits Predict Population Trends of Urban Birds in Europe." *Ecological Indicators* 160: 111926.
- Gulev, S. K., P. W. Thorne, J. Ahn, et al. 2021. "Changing State of the Climate System." In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, 287–422. Cambridge University Press.
- Gutbrodt, B., K. Mody, and S. Dorn. 2011. "Drought Changes Plant Chemistry and Causes Contrasting Responses in Lepidopteran Herbivores." *Oikos* 120: 1732–1740.
- Habel, J. C., A. Segerer, W. Ulrich, O. Torchyk, W. W. Weisser, and T. Schmitt. 2016. "Butterfly Community Shifts Over Two Centuries." *Conservation Biology* 30: 754–762.
- Habel, J. C., W. Ulrich, P. Gros, and M. Teucher. 2024. "Butterfly Loss in Urban Landscapes and Nature Reserves." *Journal for Nature Conservation* 78: 126562.
- Hahs, A. K., B. Fournier, M. F. J. Aronson, et al. 2023. "Urbanisation Generates Multiple Trait Syndromes for Terrestrial Animal Taxa Worldwide." *Nature Communications* 14: 4751.
- Hällfors, M. H., R. K. Heikkinen, M. Kuussaari, et al. 2024. "Recent Range Shifts of Moths, Butterflies, and Birds Are Driven by the Breadth of Their Climatic Niche." *Evolution Letters* 8: 89–100.
- Hill, G. M., A. Y. Kawahara, J. C. Daniels, C. C. Bateman, and B. R. Scheffers. 2021. "Climate Change Effects on Animal Ecology: Butterflies and Moths as a Case Study." *Biological Reviews* 96: 2113–2126.
- Hodgson, J. A., C. D. Thomas, T. H. Oliver, B. J. Anderson, T. M. Brereton, and E. E. Crone. 2011. "Predicting Insect Phenology Across Space and Time." *Global Change Biology* 17: 1289–1300.
- Hou, Y., J. Li, G. Li, and W. Qi. 2023. "Negative Effects of Urbanization on Plants: A Global Meta-Analysis." *Ecology and Evolution* 13: e9894.
- Jackson, H. M., S. A. Johnson, L. A. Morandin, L. L. Richardson, L. M. Guzman, and L. K. McGonigle. 2022. "Climate Change Winners and Losers Among North American Bumblebees." *Biology Letters* 18: 20210551.
- Jafarpour, M., A. Adib, M. Lotfifard, and Ö. Kisi. 2023. "Spatial Evaluation of Climate Change-Induced Drought Characteristics in Different Climates Based on De Martonne Aridity Index in Iran." *Applied Water Science* 13: 133.

- Kaiser, A., T. Merckx, and H. Van Dyck. 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.
- Karger, D. N., O. Conrad, J. Böhner, et al. 2017. "Climatologies at High Resolution for the Earth's Land Surface Areas." *Scientific Data* 4: 170122.
- Kerr, N. Z., T. Wepprich, F. S. Grevstad, E. B. Dopman, F. S. Chew, and E. E. Crone. 2020. "Developmental Trap or Demographic Bonanza? Opposing Consequences of Earlier Phenology in a Changing Climate for a Multivoltine Butterfly." *Global Change Biology* 26: 2014–2027.
- Knop, E. 2016. "Biotic Homogenization of Three Insect Groups due to Urbanization." *Global Change Biology* 22: 228–236.
- Korányi, D., V. Szigeti, L. Mezőfi, E. Kondorosy, and V. Markó. 2021. "Urbanization Alters the Abundance and Composition of Predator Communities and Leads to Aphid Outbreaks on Urban Trees." *Urban Ecosystems* 24: 571–586.
- Kurucz, K., J. J. Purger, and P. Batáry. 2021. "Urbanization Shapes Bird Communities and Nest Survival, but Not Their Food Quantity." *Global Ecology and Conservation* 26: e01475.
- Kuussaari, M., M. Toivonen, J. Heliölä, et al. 2021. "Butterfly Species' Responses to Urbanization: Differing Effects of Human Population Density and Built-Up Area." *Urban Ecosystems* 24: 515–527.
- Liu, Z., C. He, and J. Wu. 2016. "The Relationship Between Habitat Loss and Fragmentation During Urbanization: An Empirical Evaluation From 16 World Cities." *PLoS One* 11: e0154613.
- Macgregor, C. J., C. D. Thomas, D. B. Roy, et al. 2019. "Climate-Induced Phenology Shifts Linked to Range Expansions in Species With Multiple Reproductive Cycles Per Year." *Nature Communications* 10: 4455.
- Maes, D., H. Van Calster, M. Herremans, and H. Van Dyck. 2022. "Challenges and Bottlenecks for Butterfly Conservation in a Highly Anthropogenic Region: Europe's Worst Case Scenario Revisited." *Biological Conservation* 274: 109732.
- Marchi, M., G. Bucci, P. Iovieno, and D. Ray. 2024. "ClimateDT: A Global Scale-Free Dynamic Downscaling Portal for Historic and Future Climate Data." *Environments* 11: 82.
- Martay, B., M. J. Brewer, D. A. Elston, et al. 2017. "Impacts of Climate Change on National Biodiversity Population Trends." *Ecography* 40: 1139–1151.
- McDonnell, M. J., and A. K. Hahs. 2015. "Adaptation and Adaptedness of Organisms to Urban Environments." *Annual Review of Ecology, Evolution, and Systematics* 46: 261–280.
- McGrane, S. J. 2016. "Impacts of Urbanisation on Hydrological and Water Quality Dynamics, and Urban Water Management: A Review." *Hydrological Sciences Journal* 61: 2295–2311.
- Melero, Y., L. C. Evans, M. Kuussaari, et al. 2022. "Local Adaptation to Climate Anomalies Relates to Species Phylogeny." *Communications Biology* 5: 1–9.
- Melero, Y., L. C. Evans, M. Kuussaari, et al. 2025. "Species Responses to Weather Anomalies Depend on Local Adaptation and Range Position." *Communications Biology* 8: 660.
- Melero, Y., C. Stefanescu, and J. Pino. 2016. "General Declines in Mediterranean Butterflies Over the Last Two Decades Are Modulated by Species Traits." *Biological Conservation* 201: 336–342.
- Merckx, T., A. Kaiser, and H. Van Dyck. 2018. "Increased Body Size Along Urbanization Gradients at Both Community and Intraspecific Level in Macro-Moths." *Global Change Biology* 24: 3837–3848.
- Merckx, T., M. E. Nielsen, T. Kankaanpää, T. Kadlec, M. Yazdani, and S. M. Kivelä. 2024. "Continent-Wide Parallel Urban Evolution of Increased Heat Tolerance in a Common Moth." *Evolutionary Applications* 17: e13636.
- Merckx, T., and H. Van Dyck. 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.
- Metzger, M. J., R. G. H. Bunce, R. H. G. Jongman, R. Sayre, A. Trabucco, and R. Zomer. 2013. "A High-Resolution Bioclimate Map of the World: A Unifying Framework for Global Biodiversity Research and Monitoring." *Global Ecology and Biogeography* 22: 630–638.
- Michielini, J. P., E. B. Dopman, and E. E. Crone. 2021. "Changes in Flight Period Predict Trends in Abundance of Massachusetts Butterflies." *Ecology Letters* 24: 249–257.
- Middleton-Welling, J., L. Dapporto, E. García-Barros, et al. 2020. "A New Comprehensive Trait Database of European and Maghreb Butterflies, Papilionoidea." *Scientific Data* 7: 1–10.
- Miles, L. S., S. T. Breitbart, H. H. Wagner, and M. T. J. Johnson. 2019. "Urbanization Shapes the Ecology and Evolution of Plant-Arthropod Herbivore Interactions." *Frontiers in Ecology and Evolution* 7: 310.
- Mills, S. C., T. H. Oliver, R. B. Bradbury, et al. 2017. "European Butterfly Populations Vary in Sensitivity to Weather Across Their Geographical Ranges." *Global Ecology and Biogeography* 26: 1374–1385.
- Niebuhr, B. B. S., M. E. Wosniack, M. C. Santos, et al. 2015. "Survival in Patchy Landscapes: The Interplay Between Dispersal, Habitat Loss and Fragmentation." *Scientific Reports* 5: 11898.
- Öckinger, E., O. Schweiger, T. O. Crist, et al. 2010. "Life-History Traits Predict Species Responses to Habitat Area and Isolation: A Cross-Continental Synthesis." *Ecology Letters* 13: 969–979.
- Oliver, T. H., H. H. Marshall, M. D. Morecroft, T. Brereton, C. Prudhomme, and C. Huntingford. 2015. "Interacting Effects of Climate Change and Habitat Fragmentation on Drought-Sensitive Butterflies." *Nature Climate Change* 5: 941–946.
- Parmesan, C. 2006. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669.
- Piano, E., C. Souffreau, T. Merckx, et al. 2020. "Urbanization Drives Cross-Taxon Declines in Abundance and Diversity at Multiple Spatial Scales." *Global Change Biology* 26: 1196–1211.
- Pla-Narbona, C., C. Stefanescu, J. Pino, et al. 2022. "Butterfly Biodiversity in the City Is Driven by the Interaction of the Urban Landscape and Species Traits: A Call for Contextualised Management." *Landscape Ecology* 37: 81–92.
- Pollard, E., and T. J. Yates. 1993. *Monitoring Butterflies for Ecology and Conservation: The British Butterfly Monitoring Scheme*. Springer Science & Business Media.
- Pumo, D., E. Arnone, A. Francipane, D. Caracciolo, and L. V. Noto. 2017. "Potential Implications of Climate Change and Urbanization on Watershed Hydrology." *Journal of Hydrology* 554: 80–99.
- R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Ravigné, V., U. Dieckmann, and I. Olivieri. 2009. "Live Where You Thrive: Joint Evolution of Habitat Choice and Local Adaptation Facilitates Specialization and Promotes Diversity." *American Naturalist* 174: E141–E169.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. "Fingerprints of Global Warming on Wild Animals and Plants." *Nature* 421: 57–60.
- Roper-Edwards, I. R., and A. H. Hurlbert. 2024. "Arthropod Community Composition in Urban Landscapes Is Shaped by Both Environmental Filtering and Dispersal Limitation." *PLoS One* 19: e0297507.
- Roy, D. B., N. Bourn, S. Collins, et al. 2020. *Assessing Butterflies in Europe. Executive Summary*. Butterfly Conservation Europe.

- Roy, D. B., T. H. Oliver, M. S. Botham, et al. 2015. "Similarities in Butterfly Emergence Dates Among Populations Suggest Local Adaptation to Climate." *Global Change Biology* 21: 3313–3322.
- Roy, D. B., P. Rothery, D. Moss, E. Pollard, and J. A. Thomas. 2001. "Butterfly Numbers and Weather: Predicting Historical Trends in Abundance and the Future Effects of Climate Change." *Journal of Animal Ecology* 70: 201–217.
- Santana Marques, P., L. Resende Manna, T. Clara Frauendorf, E. Zandonà, R. Mazzoni, and R. El-Sabaawi. 2020. "Urbanization Can Increase the Invasive Potential of Alien Species." *Journal of Animal Ecology* 89: 2345–2355.
- Schmucki, R., C. A. Harrower, and E. B. Dennis. 2022. "rbms: Computing Generalised Abundance Indices for Butterfly Monitoring Count Data. R Package Version 1.1.3."
- Schmucki, R., G. Pe'er, D. B. Roy, et al. 2016. "A Regionally Informed Abundance Index for Supporting Integrative Analyses Across Butterfly Monitoring Schemes." *Journal of Applied Ecology* 53: 501–510.
- Schweiger, O., A. Harpke, M. Wiemers, and J. Settele. 2014. "Climber: Climatic Niche Characteristics of the Butterflies in Europe." *ZooKeys* 367: 65–84.
- 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.
- Sevilleja, C. G., S. Collins, M. S. Warren, et al. 2020. "Assessing Butterflies in Europe – European Butterfly Monitoring Schemes – Network Development: Technical Report."
- Shirey, V., E. Larsen, A. Doherty, et al. 2022. "LepTraits 1.0 A Globally Comprehensive Dataset of Butterfly Traits." *Scientific Data* 9: 382.
- Shirey, V., N. Neupane, R. Guralnick, and L. Ries. 2024. "Rising Minimum Temperatures Contribute to 50 Years of Occupancy Decline Among Cold-Adapted Arctic and Boreal Butterflies in North America." *Global Change Biology* 30: e17205.
- Sol, D., Y. Melero, L. Fuzessy, and C. González-Lagos. 2024. *Urbanization. Behavioural Responses in a Changing World: Changes and Applications*. Oxford University Press.
- Suggitt, A. J., R. J. Wilson, N. J. B. Isaac, et al. 2018. "Extinction Risk From Climate Change Is Reduced by Microclimatic Buffering." *Nature Climate Change* 8: 713–717.
- Titeux, N., D. Maes, T. Van Daele, et al. 2017. "The Need for Large-Scale Distribution Data to Estimate Regional Changes in Species Richness Under Future Climate Change." *Diversity and Distributions* 23: 1393–1407.
- Trisos, C. H., C. Merow, and A. L. Pigot. 2020. "The Projected Timing of Abrupt Ecological Disruption From Climate Change." *Nature* 580: 496–501.
- Tzortzakaki, O., V. Kati, M. Panitsa, E. Tzanatos, and S. Giokas. 2019. "Butterfly Diversity Along the Urbanization Gradient in a Densely-Built Mediterranean City: Land Cover Is More Decisive Than Resources in Structuring Communities." *Landscape and Urban Planning* 183: 79–87.
- Ubach, A., F. Páramo, M. Prohom, and C. Stefanescu. 2022. "Weather and Butterfly Responses: A Framework for Understanding Population Dynamics in Terms of Species' Life-Cycles and Extreme Climatic Events." *Oecologia* 199: 427–439.
- Urban, M. C., M. Alberti, L. De Meester, et al. 2024. "Interactions Between Climate Change and Urbanization Will Shape the Future of Biodiversity." *Nature Climate Change* 14: 436–447.
- van Bergen, E., T. Dallas, M. F. DiLeo, et al. 2020. "The Effect of Summer Drought on the Predictability of Local Extinctions in a Butterfly Metapopulation." *Conservation Biology* 34: 1503–1511.
- Van Dyck, H., D. Bonte, R. Puls, K. Gotthard, and D. Maes. 2015. "The Lost Generation Hypothesis: Could Climate Change Drive Ectotherms Into a Developmental Trap?" *Oikos* 124: 54–61.
- van Moorsel, S., E. Thébault, V. Radchuk, et al. 2022. "Predicting Effects of Multiple Interacting Global Change Drivers Across Trophic Levels." *Global Change Biology* 29, no. 5: 1223–1238.
- Vives-Inglá, M., J. Sala-García, C. Stefanescu, et al. 2023. "Interspecific Differences in Microhabitat Use Expose Insects to Contrasting Thermal Mortality." *Ecological Monographs* 93: e1561.
- WallisDeVries, M. F., W. Baxter, and A. J. H. van Vliet. 2011. "Beyond Climate Envelopes: Effects of Weather on Regional Population Trends in Butterflies." *Oecologia* 167: 559–571.
- Wepprich, T., J. R. Adrion, L. Ries, J. Wiedmann, and N. M. Haddad. 2019. "Butterfly Abundance Declines Over 20 Years of Systematic Monitoring in Ohio, USA." *PLoS One* 14: 1–21.
- Wepprich, T., E. Henry, and N. M. Haddad. 2025. "Voltinism Shifts in Response to Climate Warming Generally Benefit Populations of Multivoltine Butterflies." *Ecology Letters* 28: e70018.
- Williams, J. J., R. Freeman, F. Spooner, and T. Newbold. 2022. "Vertebrate Population Trends Are Influenced by Interactions Between Land Use, Climatic Position, Habitat Loss and Climate Change." *Global Change Biology* 28: 797–815.
- Wilson, R. J., and R. Fox. 2021. "Insect Responses to Global Change Offer Signposts for Biodiversity and Conservation." *Ecological Entomology* 46: 699–717.
- Zhou, Q., G. Leng, J. Su, and Y. Ren. 2019. "Comparison of Urbanization and Climate Change Impacts on Urban Flood Volumes: Importance of Urban Planning and Drainage Adaptation." *Science of the Total Environment* 658: 24–33.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Spatial distribution of study sites across Europe categorised by climatic regions and site types. **Figure S2:** Temporal trends in the proportion of urbanised area for rural (green colour) and urban sites (red colour) from 1975 to 2025. **Figure S3:** Boxplots showing the variation in (a) temperature trend, (b) precipitation trend, and (c) aridity trend across rural and urban sites. **Figure S4:** Relationships between butterfly population trends and urbanisation and climate trends across rural (orange) and urban (blue) sites using all species available (i.e., not only common species in rural and urban sites: 145 species in rural sites and 100 species in urban sites). **Figure S5:** Correlation heatmap among species traits based on Pearson correlation coefficients. **Table S1:** Summary of the 145 butterfly species and their traits used in the analyses. **Table S2:** Complete results of the GLMMs testing interaction effects of environmental trends and site type (rural vs. urban) on butterfly population trends. **Table S3:** Complete results of the GLMMs testing interaction effects of environmental trends and species traits on butterfly population trends. Each interaction was tested separately for rural and urban sites.