Temperature drives variation in flying insect biomass across a German malaise trap network

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ABSTRACT. 1. Among the many concerns for biodiversity in the Anthropocene, recent reports of flying insect loss are particularly alarming, given their importance as pollinators, pest control agents, and as a food source. Few insect monitoring programmes cover the large spatial scales required to provide more generalizable estimates of insect responses to global change drivers.

2. We ask how climate and surrounding habitat affect flying insect biomass using data from the first year of a new monitoring network at 84 locations across Germany comprising a spatial gradient of land cover types from protected to urban and crop areas.

3. Flying insect biomass increased linearly with temperature across Germany. However, the effect of temperature on flying insect biomass flipped to negative in the hot months of June and July when local temperatures most exceeded long-term averages.

4. Land cover explained little variation in insect biomass, but biomass was lowest in forests. Grasslands, pastures, and orchards harboured the highest insect biomass. The date of peak biomass was primarily driven by surrounding land cover, with grasslands especially having earlier insect biomass phenologies.

5. Standardised, large-scale monitoring provides key insights into the underlying processes of insect decline and is pivotal for the development of climate-adapted strategies to promote insect diversity. In a temperate climate region, we find that the positive effects of temperature on flying insect biomass diminish in a German summer at locations where temperatures most exceeded long-term averages. Our results highlight the importance of local adaptation in climate change-driven impacts on insect communities.

Key words. climate change, ecological gradients, insect monitoring, land cover, LTER, malaise trap, pollinator, thermal performance.

Introduction

Insects constitute a large proportion of terrestrial biodiversity and deliver essential ecosystem services such as pollination of the majority of wild plants and 75% of crop species (Losey & Vaughan, 2006; Vanbergen & Insect Pollinators Initiative, 2013). Insect biomass is a key constituent of energy flows in many food webs (Stepanian *et al.*, 2020), a measure of whole insect communities (Shortall *et al.*, 2009) and an indicator of ecosystem function (Dangles *et al.*, 2011; Barnes *et al.*, 2016). Climate change and anthropogenically altered land cover are likely drivers of insect declines, but their effects on insect biomass are still poorly characterised (Habel *et al.*, 2019). Amidst burgeoning evidence of widespread insect declines, standardised, and large-scale insect monitoring is needed to improve estimates of trends, and identify drivers (Didham *et al.*, 2020; Wagner, 2020).

Climate change is geographically pervasive (Wilson & Fox, 2020) and may explain insect decline in natural areas (e.g. Janzen & Hallwachs, 2019; Welti *et al.*, 2020b). Some insect taxa are benefiting from rising temperatures, which can increase local populations (Baker *et al.*, 2021) and range sizes (Termaat *et al.*, 2019). However, as temperatures continue to rise and increase more rapidly, negative impacts on insect productivity are expected (Warren *et al.*, 2018). This relationship is predicted by thermal performance theory, which hypothesises that insect fitness, as measured by biomass or other performance indicators, will have a unimodal response to temperature (Kingsolver & Huey, 2008; Sinclair *et al.*, 2016).

Responses of precipitation regimes to climate change vary with region, but forecasts generally suggest increased frequency of both heavy precipitation events and droughts (Myhre *et al.*, 2019). Drought can reduce nectar and pollen resources used by flower-visiting insects and change insect activity through reducing flower sizes and altering plant volatiles (Burkle & Runyon, 2016; Phillips *et al.*, 2018; Rering *et al.*, 2020). However, high precipitation increases insect mortality and shortens the period of time insects are flying (Totland, 1994). Indirect effects of precipitation on flying insects mediated by plants (e.g. altering plant phenology or nutrition) are context-dependent, but increasing rainfall in average to wet climates is often detrimental (Lawson & Rands, 2019).

Changing land cover due to human activities has been described as the largest threat to insect biodiversity (Wagner, 2020), with wide-ranging impacts from loss of resources and nesting locations at local scales, to fragmented habitats at larger scales (Newbold *et al.*, 2020). Agricultural areas currently cover around 11% of Earth's land, mostly constituted by intensively managed monocultures which support few insect species (Raven & Wagner, 2021). While well-managed urban green spaces can support insect communities (Theodorou *et al.*, 2020), both insect diversity (Fenoglio *et al.*, 2020; Piano *et al.*, 2020), and biomass (Macgregor *et al.*, 2019; Svenningsen *et al.*, 2020) have been shown to decline with urbanisation in many areas. Heavily human modified landscapes also come with associated pressures, including eutrophication, ploughing, and pesticide use with agricultural intensification (Goulson *et al.*, 2018; Carvalheiro *et al.*, 2020),

and light pollution from urban environments (Owens *et al.*, 2020).

Here, we ask how climate and land cover affect flying insect biomass across the growing season of 2019 in 84 locations ranging over seven degrees of latitude during the first year of monitoring of the German Malaise Trap Program. We hypothesise (H1) the effect of temperature on insect biomass will (i) be unimodal and (ii) decline at locations where temperatures exceed long-term averages. We hypothesise (H2) that flying insect biomass will decline with increasing precipitation due to reduced flying activity. Finally, we predict (H3) flying insect biomass will be lower in land cover types with larger anthropogenic impacts such as urban and agricultural areas. We additionally conducted an exploratory analysis to test whether the date of peak biomass varied with climate, land cover type, or elevation and to examine whether the identified significant environmental drivers of insect biomass were the result of co-variation with biomass phenology (e.g. if positive predictors resulted in capturing a phenological interval with higher biomass). The broad spatial coverage of our study allows us to examine drivers of flying insect biomass using a macroecological gradients approach (Pianka, 1966; Peters *et al.*, 2019).

Methods

German Malaise Trap Program

The German Malaise Trap Program currently comprises 31 German Long-Term Ecological Research (LTER-D) and National Natural Landscape sites (https://www.ufz.de/lter-d/index.php?de=46285). The programme was established in early 2019 to investigate long-term trends in flying insect biomass and species composition using DNA metabarcoding. One to six locations were selected at each site, each with one malaise trap installed. All traps measured 1.16 m² on each side (Supporting Information Fig. S1). We examine here the 2019 biomass data retrieved from 25 of the 31 sites; the remaining sites began sampling in 2020 and are not analysed in this study. To fill spatial gaps, we included eight sites in Bavaria from an additional project using the same malaise trap type and measurement methods. Overall, this study includes 1039 samples from 84 locations and 33 participating sites distributed across Germany (Fig. 1; Supporting Information Table S1) and a range of habitats (see *Land cover* below). Traps ran from early April to late October 2019 and were usually emptied every 2 weeks (14.03 days ± 0.06
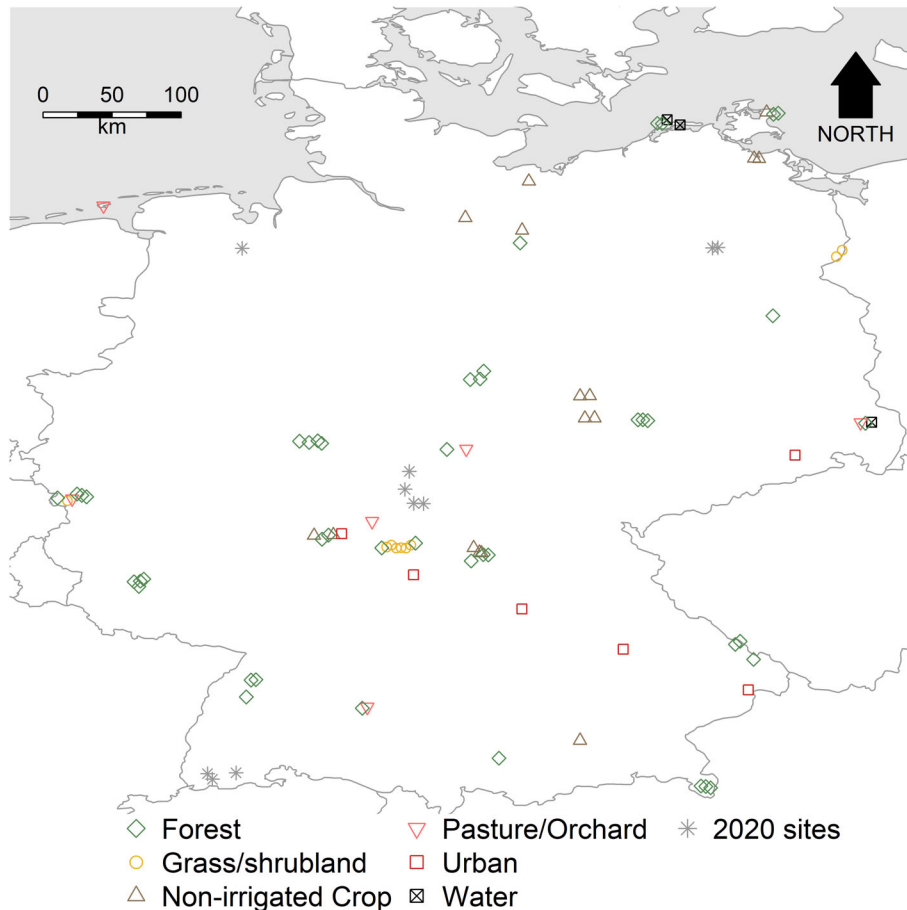

Fig 1. Malaise trap locations where samples were collected in 2019 are identified by the dominant land cover in the surrounding 1 km. Points coded as stars indicate trap locations at which sampling began in 2020 and are incorporated to show the full extent of the current programme but are not included in the analyses. Overlapping locations were jittered longitudinally to improve visualisation.
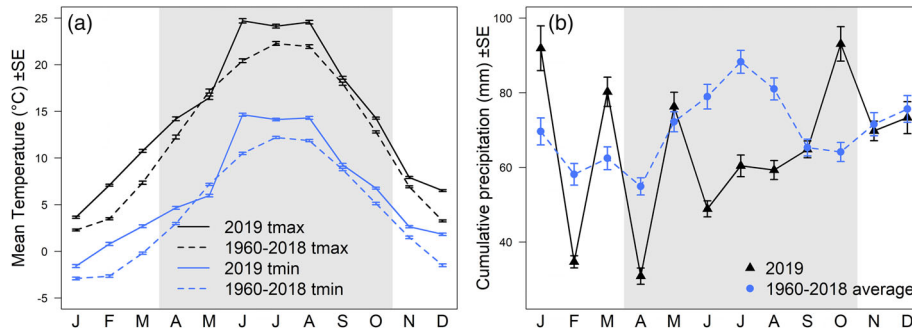
Fig 2. Comparison of climate at the 84 trap locations between 2019 and the long-term average (1960–2018) including average maximum monthly temperatures (tmax) and minimum monthly temperatures (tmin) in °C ± standard error (a) and cumulative monthly precipitation in mm ± standard error (b). Period of the year in which malaise trap sampling occurred is shaded in grey.

SE; ranging 7–29 days). Insects were captured in 1 litre bottles filled with ca. 650 ml of an 80% alcohol solution. Some traps ran for shorter durations, e.g., due to snowfall, and several samples were lost due to animal or wind damage. By sampling across all times of day for the duration of the growing season, these data represent a wide variety of flying insect taxa across a large range of seasonal and diurnal flight periodicity.

Laboratory procedures

Insect biomass was wet weighed to preserve samples for future identification. Alcohol was filtered in a stainless steel sieve (0.8 mm mesh width) following the procedure in the study by Hallmann *et al.* (2017), with one modification: instead of waiting until alcohol drops occurred >10 s apart, samples were filtered for a standard 5 min prior to weighing to the nearest 0.01 g.

Climate

Monthly means of maximum and minimum temperatures, and monthly cumulative precipitation were extracted from each location from 2019 using the Terraclimate dataset (Abatzoglou *et al.*, 2018) and from 1960 to 2018 using the CRU-TS 4.03 dataset (Harris *et al.*, 2014) downscaled with WorldClim 2.1 (Fick & Hijmans, 2017). Data from both time periods (2019 and 1960–2018) were not available from either dataset alone. Both datasets have spatial resolutions of 2.5 arc minutes (~21 km^2) with our 84 trap locations occurring in 72 separate climate grid cells. While daily climate data are available from the German weather service (DWD), matching of trap locations to the nearest weather stations resulted in only 33 unique matches of the 84 locations to weather stations. We therefore opted to use monthly climate data from Terraclimate and WorldClim as these data optimised the spatial resolution of available datasets and as biomass data were not collected daily but in 2 week periods.

Monthly minimum and maximum temperatures in 2019 were highly correlated ($R^2 = 0.97$) and were higher than 1960–2018

averages, especially during summer months (Fig. 2a). Therefore, we used only maximum temperatures in our analyses (henceforth referred to as temperature). Annual precipitation was slightly lower in 2019 (784 mm ± 32 SE) relative to the 1960–2018 average (842 mm ± 32 SE), with summer months comprising the driest period, but high variation existed across months (Fig. 2b). No latitudinal temperature gradient existed across our sampling locations either in 2019 (Supporting Information Fig. S2a) nor across long-term averages (Supporting Information Fig. S2b), likely due to a negative correlation between elevation and latitude (Supporting Information Fig. S3). However, southern latitudes in 2019 experienced temperatures exceeding long-term averages to a greater degree than northern latitudes (Supporting Information Fig. S2c) and had higher precipitation (Supporting Information Fig. S2d).

Land cover

Land cover categories in a 1-km buffer around each location were extracted using the 2018 CORINE dataset (European Union, Copernicus Land Monitoring Service, 2018). Previous work suggests that at scales larger than 1-km, insects have weaker responses to land cover buffers (Seibold *et al.*, 2019). The 30 CORINE land cover types were pooled into eight categories: urban (7.5% of surrounding land cover), intensive agriculture (2.3%), non-irrigated agriculture (15.9%), pasture/orchard (12.7%), forest (44.7%), grassland/shrubland (12.1%), freshwater (3.9%), and saltwater (0.9%). Pasture is defined as areas heavily used for fodder production, while grasslands are defined as areas with little-to-moderate human influence (for more details on all land cover classifications, see: https://land.copernicus.eu/user-corner/technical-library/corine-land-cover-nomenclature-guidelines/html). To reduce variance inflation due to land cover categories being percentages, we removed land cover categories from our model testing the effects of land cover on insect biomass starting with the least common until the variance inflation factor (VIF) was <10 (Montgomery *et al.*, 2021); this removed the land cover types of freshwater, intensive agriculture, and saltwater, resulting in five categories of land cover

considered in analyses. VIF was calculated using the R package 'car' v. 3.0-11 (Fox & Weisberg, 2019).

Elevation

Elevation was extracted using the Digital Terrain Model with 200-m grid widths (DGM200) from the German Federal Agency for Cartography and Geodesy (GeoBasis-DE/BKG, 2013). Elevation varied from 0 m above sea level (asl) on a barrier island in northeast Germany to 1413 m asl in the German Alps.

All GIS data extraction was conducted in QGIS ver. 3.14 (QGIS.org, 2020).

Statistical analyses

To test the hypotheses that insect biomass would have a unimodal relationship with temperature (H1a), decline with increasing precipitation (H2), and decline with urban and agricultural areas (H3), we used an Akaike information criterion corrected for small sample sizes (AIC$_c$) framework (Burnham & Anderson, 2003); first building an *a priori* full model, comparing AIC$_c$ of models with and without spatial autocorrelation to test for spatial non-independence, and then comparing all possible reduced models of fixed effects using the *dredge* function in the R package 'MuMIn' v. 1.43.17 (Bartoń, 2020).

The full model contained the response variable of sample biomass in mg day^{-1} from all 84 locations and was log10 (x + 1) transformed to correct for a log-skewed distribution. Fixed predictors of temperature (H1a), precipitation (H2), % cover of the five most dominant land cover categories (H3), elevation, the second degree polynomial of sampling period (covariates), and a random effect of trap location to account for repeated observations. We tested five models fitting spatial autocorrelation (exponential, Gaussian, linear, rational quadratic, and spherical correlation) and compared their AIC$_c$ values with a model without a spatial correlation argument (Zuur *et al.*, 2009). The model with the lowest AIC$_c$ was the model without a spatial autocorrelation term; thus we proceeded with this model when selecting for fixed effects. Models with a ΔAIC$_c$ < 2 are considered parsimonious (Burnham & Anderson, 2003) and reported.

Mixed models were fitted using the R package 'nlme' v. 3.1-153 (Pinheiro *et al.*, 2021). All analyses were conducted in R ver. 4.1.1 (R Core Team, 2021). We included the second degree polynomial of the sampling period to capture the season pattern of biomass. Sampling period refers to the half-month period most overlapping trap sampling days and is numerical (e.g. first half of April = sampling period 1). Temperature and precipitation predictors correspond to the month in which the majority of sampling days occurred. Temperature was first included as a second-order polynomial; however, while all top models included the fixed effect of this term, the second-order polynomial term of temperature was never significant; thus, we replaced this parameter with a linear temperature term. We initially intended to include the 2019 deviation in monthly maximum temperatures from long-term averages (Δ temperature) as

a driver, in addition to a temperature and precipitation interaction to test drought effects, but these terms caused variance inflation with sampling period and thus were excluded. In order to adjust variances to be within the same orders of magnitude, precipitation and elevation were scaled by dividing by 100. The full model was specified as:

```
log10(biomass) ~ temperature + I
(precipitation/100) + I(elevation/100) +
forest + grassland/shrubland + non-irrigated
crop + pasture/orchard + urban + poly
(period,2), random=~1|location
```

We additionally examined our hypothesis that flying insect biomass will decline when local temperatures exceed long-term averages (H1b) and examine how responses varied across sampling months. We were prohibited from including Δ temperature in the mixed model due to high variance inflation with sampling period. With the aim of reducing complexity due to variation in timing of sample collection across locations and eliminating repeated sampling within a location per month, we calculated an average value of biomass (mg day^{-1}) per location and month by computing a monthly weighted average of insect biomass. Our calculation assumes traps caught the same amount of biomass each day within a sample and allocates sample biomass to each month weighed by the number of sampling days (e.g. for a trap run with 1 day in month A and 13 days in month B we assumed 1/14th of the biomass was collected in month A and 13/14ths was in month B). With these assumptions, the average biomass Bij (mg day^{-1}) of location i in month j is a weighted average of the n samples occurring in the month according to the following formula:

$$B_{i,j} = \frac{\sum\limits_{k=1}^{n} \left(b_{ijk} \times D_{k,j} \div D_k \right)}{\sum\limits_{k=1}^{n} D_{k,j}} \quad (1)$$

where b_{ijk} is the total biomass (mg) at location i occurring at least partially in month j for a sample k, n is the total number of samples occurring at least partially in month j for location i, $D_{k,j}$ is the number of sampling days occurring in month j for a given sample k, and D_k is the total number of sampling days for a given sample k.

For each month (April–October), we then tested for an interaction between monthly temperature and Δ temperature (2019 temperature minus the long-term average temperature) for the corresponding location/month on log10 transformed $B_{i,j}$. We visualised the results using the R package 'effects' v. 4.2-0 (Fox & Weisberg, 2019).

To visualise changes in flying insect biomass with land cover, we plotted biomass day^{-1} over median day of sampling for locations corresponding to each dominant land cover. Dominant land cover refers to the land cover type with the highest percentage in the 1 km buffer surrounding each location. The AIC$_c$ analysis is our primary test of differences in biomass between land cover types and uses land cover percentages rather than dominant land

covers. However, we additionally used Welch's t-tests to identify significant differences between $log10(x + 1)$ transformed $B_{i,j}$ for all locations, and locations corresponding to each dominant land cover within each month. No locations had surroundings dominated by intensive agriculture. Locations dominated by saltwater ($n = 1$) and freshwater ($n = 2$) were excluded due to low replication.

Peak biomass

To calculate the day of the year of peak biomass, we fit splines on the relationship between biomass (mg day^{-1}) of each sample and the median day of the year of each sample for each location using the 'smooth.spline' base function in programme R. We then extracted the day of the year when the maximum value of the fitted spline occurred (see Supporting Information Fig. S4 for an example). We excluded locations where the maximum extracted value occurred at either end of the sampling interval, assuming these sampling locations may not have captured the peak biomass date; in total, we were able to calculate peak biomass date for 73 locations. We then followed the same AIC$_c$ model selection procedure as was used for determining drivers of insect biomass to conduct model selection on drivers of peak biomass. The full *a priori* model was a linear regression which included the response variable of peak biomass date, and the explanatory variables of the average monthly 2019 temperature from the beginning of the year (January) to the last main sampling month (October), the average Δ temperature from January to October, the cumulative precipitation from January to October, elevation, and the % cover of the five most dominant land cover categories. Precipitation and elevation were scaled by dividing by 100.

Results

Mean flying insect biomass averaged 2329 ± 79 SE mg day^{-1} and ranged from near zero to 17 543 mg day^{-1}. Biomass increased from 734 ± 98 SE mg day^{-1} in early April, to a peak of 5356 ± 401 SE mg day^{-1} in late June, declining to 568 ± 111 SE mg day^{-1} in late October. AIC$_c$ model comparison selected two competing top models (Supporting Information Table S2) with both containing temperature, percent forest cover, and sampling period, and the second model additionally containing elevation as predictors of flying insect biomass (Table 1). The two top models explained 43–45% of the variance in flying insect biomass without location information (marginal R^2) and 73% of flying insect biomass was accounted for when including location identity as a random effect (conditional R^2; Supporting Information Table S2).

Climate

Flying insect biomass increased with 2019 temperature (Table 1 (a); Supporting Information Fig. S5a) and declined with increasing elevation (Table 1(b); Supporting Information Fig. S5b). There was a significant interaction between temperature and Δ temperature in the mid-season sampling months of June and July. In these

Table 1. Top AIC$_c$ models. AIC$_c$ model selection for predictors of flying insect biomass resulted in two top models (a and b).

	Est	SE	df	t-value	P
(a) Model 1					
Intercept	2.278	0.122	952	18.73	<0.001
%forest	−0.319	0.109	82	−2.93	0.004
poly(period,1)	−4.124	0.329	952	−12.52	<0.001
poly(period,2)	−4.402	0.707	952	−6.23	<0.001
tmax	0.047	0.005	952	9.53	<0.001
(b) Model 2					
Intercept	2.211	0.123	952	18.04	<0.001
elevation	0.036	0.013	81	2.72	0.008
%forest	−0.487	0.122	81	−4	<0.001
poly(period,1)	−4.129	0.329	952	−12.54	<0.001
poly(period,2)	−4.288	0.707	952	−6.07	<0.001
tmax	0.048	0.005	952	9.69	<0.001

See Supporting Information Table S2 for AIC$_c$ parameters. Both models include the random variable of trap location. T-tests use Satterthwaite's method. Poly(period,1) and poly(period,2) indicate the first- and second-order terms of the second degree polynomial for sampling period, respectively. Other predictor variables include the percent forest in a surrounding 1 km buffer (%forest) and monthly maximum temperature (tmax). Model characteristics include estimate (Est), standard error (SE), degrees of freedom (df), t-value, and P-value (P).

2 months, temperature had a positive effect on flying insect biomass at locations with low Δ temperatures, shifting to a negative effect of temperature on flying insect biomass at locations with high Δ temperatures (Fig. 3; Supporting Information Table S3). Significant interactions between temperature and Δ temperatures were not found in other sampling months (Fig. 3; Supporting Information Table S3). The slope of the effect of temperature on flying insect biomass was steeper with lower Δ temperatures in April, August, and September, though not significantly. This pattern flipped in May and October where the slope of the effect of temperature on flying insect biomass was steeper with higher Δ temperatures, likely due to colder temperatures in these months, though again the interaction was not significant (Fig. 3; Supporting Information Table S3).

Land cover

Flying insect biomass declined with % forest in the 1 km buffer surrounding each trap location (Table 1). No other land cover categories appeared as drivers of flying insect biomass. Categorising locations by dominant land cover suggested grassland/shrublands had the highest biomass in the mid growing season (June/July; Fig. 4c), while non-irrigated cropland supported above-average biomass at either end of the growing season (May and September; Fig. 4e). Higher biomass in urban-dominated locations (April and July–September; Fig. 4f) may be due to urban-dominated locations being in southern Germany (Fig. 1) which tended to be slightly warmer (Supporting Information Fig. S2).
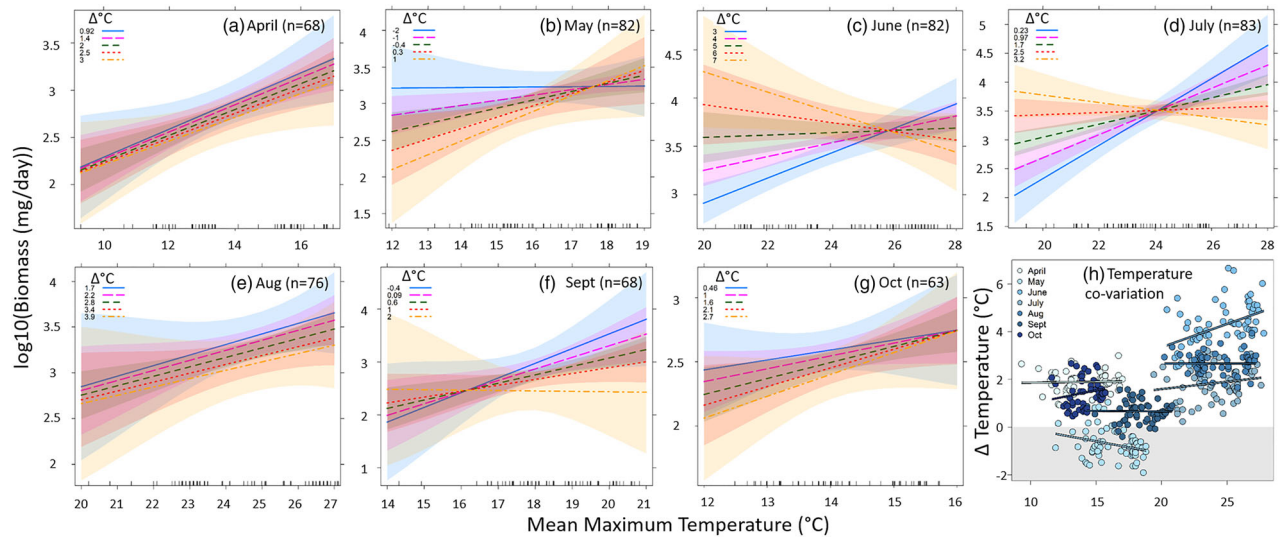
Fig 3. The effect of temperature on flying insect biomass was positive at the beginning of the growing season in (a) April, and (b) May regardless of Δ temperature (2019 temperature minus the long-term average temperature), shifted from positive to negative with increasing Δ temperature in (c) June and (d) July, and again became more positive with temperature independent of Δ temperature in (e) August, (f) September, and (g) October. Number of locations with sampling (*n*) within each month are provided within panels a–g. While hotter months tended to have higher Δ temperatures, there was no consistent relationship between temperature and Δ temperatures within months (h). Significant interactions between temperature and Δ temperature occurred in June and July; all model coefficients are provided in the Supporting Information Table S3.

Peak biomass

The day of the year of peak biomass varied from 148.5 (28 and 29 May) to 219 (7 August) across the 73 trap locations from which it was estimable [averaging 175.1 (24 June) ± 1.6 days SE]. Model selection resulted in 12 models with ΔAIC$_c$ < 2 (Supporting Information Table S4). The most consistent result was earlier peak biomass dates in locations with more
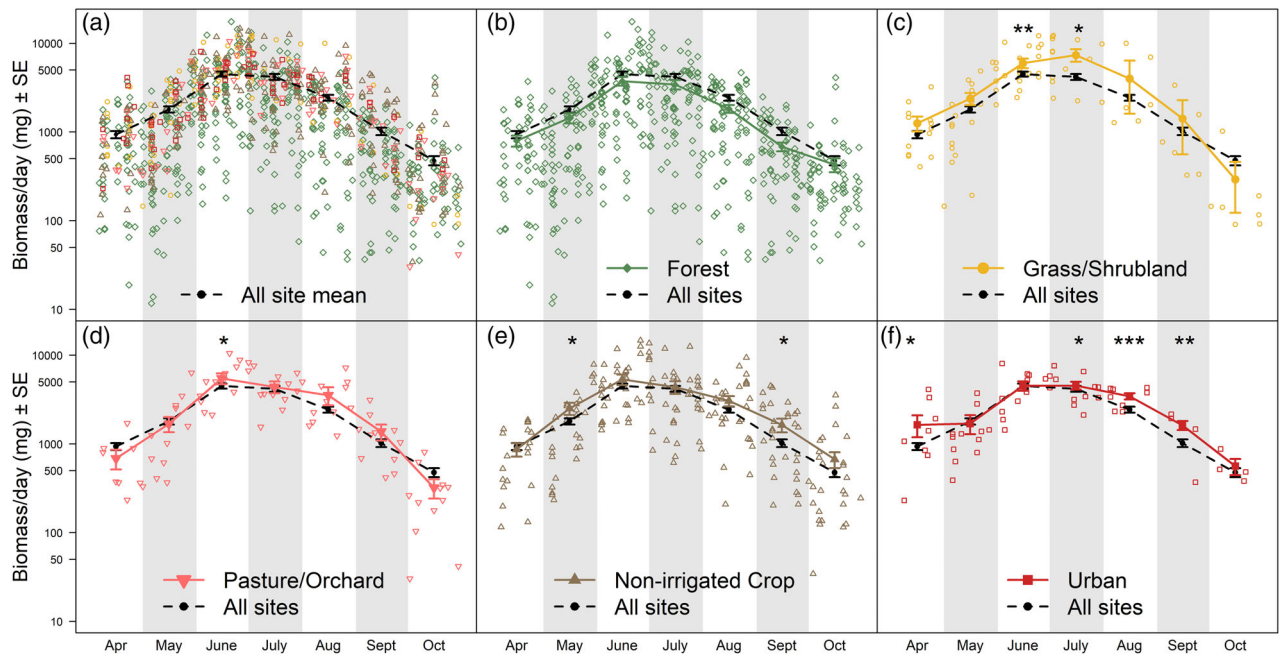

Fig 4. Biomass over the median sampling day across all 84 trap locations (a), and comparisons between all locations and locations with surroundings dominated by forests (b; *n* = 44), grassland/shrubland (c; *n* = 9), pasture/orchard (d; *n* = 6), non-irrigated cropland (e; *n* = 16), and urban environments (f; *n* = 6). Point shapes and colours in panel (*d*) match the dominant land category following shapes and colours in panels b–f. Mean and standard error are provided for biomass within each land cover category and month. Stars indicate significant differences within each month between dominant land cover categories and all-location averages (* = 0.05 > *P* > 0.01, ** = 0.01 > *P* > 0.001, *** = *P* < 0.001).

surrounding grassland/shrubland. Other drivers of peak biomass date included earlier peak biomass date with increasing elevation, Δ temperature, and percent forest, and later peak biomass date with increasing precipitation, percent pasture/orchard, and percent urban surroundings. However, the predictive power of the best models of peak insect biomass date was low (R^2 s ranging from 0.07 to 0.14; Supporting Information Table S4).

Discussion

In a study of 84 locations widely distributed across Germany, we found strong effects of temperature on flying insect biomass. Biomass increased linearly with temperature in contrast to the unimodal relationship predicted by our first hypothesis (H1a). However, when large positive deviations from long-term average temperatures were combined with the hotter summer months of June and July, temperature no longer had a positive effect on flying insect biomass, in support of our second hypothesis (H1b). Temperatures in June 2019 were especially hotter than long-term averages across trap locations (averaging 4.3 °C ± 0.1 SE). In contrast, insect biomass only increased with temperature in May 2019, which was cold relative to the long-term averages (averaging −0.7 °C ± 0.1 SE). The negative effect of large deviations from long-term temperature averages in the hotter summer months suggests insects are adapted to local temperature conditions. Rapid rises in temperature may exceed locally established tolerance limits or greatly alter the quality and quantity of resources used by insects, having negative effects on flying insect communities even in colder climate regions.

A decelerating benefit of temperature in locations with greater increases in temperature is consistent with previous long-term studies of insects. In a study of ant communities across North America conducted 20 years apart, sites with the largest increases in temperature had the largest declines in colony density (Kaspari *et al*., 2019). Similarly, Hallmann et al. (2017) found biomass loss over time was greatest in mid-summer, when temperatures were highest, even as temperature had an overall positive effect on flying insect biomass. Moreover, flying insects may be more affected by rising temperatures than non-flying insects as they cannot buffer high temperatures by burrowing in soil or plant tissue (Baudier *et al*., 2015; Wagner, 2020). We predict future monitoring will detect increasingly negative effects of temperature due to ongoing climate warming, as temperature begins to exceed species' optimum temperature ranges.

Climate change predictions for Germany suggest slight increases in cumulative annual precipitation, with shifts in the timing of rainfall towards wetter summers and drier summers (Bender *et al*., 2017). The 2019 growing season matched this prediction with June, July and August being much drier than the long-term average and with the wettest month of the study period being October. As insects can detect changes in barometric pressure and will stop flying if they sense storms approaching (Pellegrino *et al*., 2013), we predicted increased rainfall would result in reduced flight activity, thus reducing insect biomass. However, precipitation was not a significant predictor of flying insect biomass as predicted by H2, potentially due to low variation in precipitation across locations.

With ~75% of global land significantly altered by human activities (IPBES, 2019), land cover change and land use intensification are major contributors to insect declines (Potts *et al*., 2010; Winfree *et al*., 2011; Díaz *et al*., 2019). In contrast to H3, we did not detect negative effects of urban and agricultural land cover on flying insect biomass. The strongest effect of surrounding land cover was reduced insect biomass in forests. Forests may provide fewer floral resources than open fields (Jachuła *et al*., 2017). Alternatively, forest vegetation structure may limit insect movement through the landscape, reducing trap catch in comparison to open systems like grasslands (Cranmer *et al*., 2012). The absence of an effect of heavily human-impacted habitats on flying insect biomass may be due to a minority of our locations surrounded by high proportions of these land cover types, especially intensive agriculture. Higher temperatures in urban areas may explain the above average biomass in spring and late summer/autumn but also increase insects' vulnerability in urban areas to future warming in mid-summer. Additionally, large variability exists in insect habitat quality of urban areas and agricultural land, ranging from paved expanses and areas with intensive pesticide use to urban gardens and low-intensity organic farms (Bengtsson *et al*., 2005; Hausmann *et al*., 2020). While moderately impacted by human activity, non-irrigated agricultural areas, pasture land, and orchards in this study tended to support higher biomass, suggesting these land use types may provide suitable habitats for Germany's flying insects. Alternatively, fertilisation and the prevalence of monoculture on conventional farms may increase insect biomass through alleviating nutrient limitation and providing high concentrations of host plants, while not benefiting insect biodiversity (Root, 1973; Haddad *et al*., 2000).

While the date of peak biomass ranged from late May to early August across trap locations and varied with land cover types, the percent variance explained by environmental drivers was low (7–14% of variance explained). The average temperature at trap locations was not a predictor of the date of peak biomass, suggesting the overall positive response of flying insect biomass was not driven by shifts in biomass phenology. However, top models included a weak effect of locations with higher Δ temperatures having earlier peak biomass dates. Land cover types and temperature may also interact in their effects on flying insect biomass, though our number of trap location prohibited the examination of interaction terms. Earlier peak biomass dates in grasslands and forests compared to urban areas and pasture/orchard is indicative of differences between more natural and more human-modified areas and supported by previous work finding later phenologies of butterflies (Diamond *et al*., 2014) and flower bloom times (Li *et al*., 2021) in urban areas.

Comparison with Hallmann et al. (2017)

A recent study (Hallmann *et al*., 2017) reported large declines in flying insect biomass from 63 German locations over 27 years. However, sampling locations greatly varied with years and the majority of locations (58/63) were clustered in central-west Germany (covering just 2° of latitude). Average insect biomass reported by Hallmann *et al*. (2017) varied from

9192 mg day^{-1} in 1989 to 2531 mg day^{-1} in 2016 (May–September average; no April 1989 sampling was conducted). In comparison, our traps collected a monthly average of 2404 mg day^{-1} in May–September. However, Hallmann *et al.* (2017) used traps that were ~46% larger (~1.75 m^2 per side) than ours (~1.2 m^2), suggesting higher trap catch in our study relative to the last sampling year (2016) in the study by Hallmann *et al.* (2017), if trap size has an appreciable positive effect on catch. This discrepancy is most likely due to differences in sampling locations as our study covers a wider range of locations and habitats than those examined in the study by Hallmann *et al.* (2017). However, we cannot rule out an increase in biomass of flying insects in Germany in 2019 compared to the previous years assessed in the study by Hallmann *et al.* (2017).

Caveats

Insect biomass is a common currency ecosystem-level measure of insect productivity and is an index of energy availability for higher trophic levels. Nonetheless, from biomass alone, we cannot differentiate variation in abundance, body size, species diversity, or dominance. High temperatures may reduce insect body sizes within species (Atkinson, 1994; Klockmann *et al.*, 2017; Polidori *et al.*, 2020) or favour smaller species (Bergmann, 1848; Daufresne *et al.*, 2009; Merckx *et al.*, 2018). Larger-bodied species are more likely to have become rare earlier in the last century than smaller species (Koh *et al.*, 2004; Mattila *et al.*, 2006; Seibold *et al.*, 2015; Coulthard *et al.*, 2019; Rocha-Ortega *et al.*, 2020; though see Hallmann *et al.*, 2020). Climate and land cover change may otherwise alter insect communities by favouring particular trophic levels (Welti *et al.*, 2020a), invasive (Ju *et al.*, 2017), or pest species (Bernal & Medina, 2018).

Besides examining only biomass, our study comes with several other caveats of note. While spatially broad and with high intensity of seasonal sampling, the study examines only samples collected within a single year. Such space-for-time, or ecological gradients approaches have a long and fruitful history in ecology and are a useful method for providing predictions of temporal trends in the absence of time series (Pianka, 1966; Peters *et al.*, 2019), but differences in climatic variation across space versus time can sometimes lead to different predictions (Blois *et al.*, 2013). Our study year (2019) was an exceptionally hot year in the region, which, along with other annual conditions, may affect our results. Further, while we detected no effects of precipitation on flying insect biomass. This may be due to the interacting effects of temperature and precipitation on flying insects which we were not able to access due to variance inflation of climatic variables. For example, the combination of high temperatures and humidity has long been known to increase the probability of flight in several insect groups (Rudolfs, 1925; Contreras *et al.*, 2013). The lack of an overall unimodal relationship with temperature may be a result of the coarse taxonomic (flying insects) and temporal (~2 weeks) sample resolution in comparison to other studies (e.g. Kühsel & Blüthgen, 2015). Finally, malaise traps do not collect all flying insects with larger insects like butterflies often being underrepresented.

Future directions: importance of large-scale insect monitoring programmes

In this first study of flying insect biomass from the German Malaise Trap Program, we find that even in a temperate climate, the positive effect of temperature on flying insect biomass diminished when combined with high positive deviations in temperature from the long-term average, and hotter mid-summer months. These interactions could not have been elucidated without growing season-long monitoring across a large number of locations including a thermal gradient. Large-scale, long-term standardised monitoring is a critical tool to disentangle potential drivers of insect decline and understand how this varies with region and taxa. Empirical studies of insect communities often lack the spatial coverage to be broadly representative across habitats (but see Jeliazkov *et al.*, 2016; Wepprich *et al.*, 2019; Forister *et al.*, 2021). Meta-analyses have large spatial coverage, but must reckon with variable research goals and methodologies (Gurevitch & Mengersen, 2010). Spatially distributed monitoring efforts of ecological communities primarily target plants and vertebrates but not insects (Eggleton, 2020). Notable exceptions include mosquito and ground beetle monitoring by the US National Ecological Observation Network (Thorpe *et al.*, 2016), and several regional-scale Lepidoptera monitoring programmes (Kühn *et al.*, 2008; e.g. Dennis *et al.*, 2019; van Swaay *et al.*, 2019). The Global Malaise Trap Program, operating since 2012 (http://biodiversitygenomics.net/projects/gmp/), and the Swedish Malaise Trap Program (operational from 2003 to 2006; Karlsson *et al.*, 2020) are taxonomic treasure troves, though neither measure biomass. The German Malaise Trap Program helps to fill the gap of a distributed, standardised, and continuous monitoring programme of flying insects for Germany. Malaise traps are currently being considered as a standard component of European insect biodiversity surveys at eLTER sites (https://elter-projects.org/), and this programme provides a blueprint for a coordinated large-scale malaise trap sampling network (Haase *et al.*, 2018). As highlighted by the recent insect decline debate (Wagner *et al.*, 2021), comprehensive and standardised monitoring is critical to meet the challenge of unravelling insect trends and drivers in the Anthropocene.

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Data Availability Statement

Insect biomass data are available on figshare: https://doi.org/10.6084/m9.figshare.17075486.v1

[Correction added on 07 Dec 2021, after the first online publication: data availability statement has been updated]

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting Information

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