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RESEARCH ARTICLE

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Flying insect biomass is negatively associated with urban cover in surrounding landscapes

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Abstract

Aim: In this study, we assessed the importance of local- to landscape-scale effects of land cover and land use on flying insect biomass.

Location: Denmark and parts of Germany.

Methods: We used rooftop-mounted car nets in a citizen science project ("InsectMobile") to allow for large-scale geographic sampling of flying insects. Volunteers sampled insects along 278 five-km routes in urban, farmland, grassland, wetland and forest landscapes in the summer of 2018. The bulk insect samples were dried overnight to obtain the sample biomass. We extracted proportional land use variables in buffers between 50 and 1,000 m along the routes and compiled them into land cover categories to examine the effect of each land cover, and specific land use types, on insect biomass.

Aletta Bonn and Anders P. Tøttrup are joint senior authors.

Results: We found a negative association between urban cover and flying insect biomass (1% increase in urban cover = 1% [95% CI: −3.0 to 0.0] decrease in biomass in Denmark, and a 3% [95% CI: −3.0 to 0.0] decrease in Germany) at a landscape scale (1,000-m buffer). In Denmark, we also found positive effects of semi-natural land cover types, that is protected grassland (largest at the landscape scale, 1000 m) and forests (largest at intermediate scales, 250 m). Protected grassland cover had a stronger positive effect on insect biomass than forest cover did. For farmland cover, the positive association with insect biomass was not clearly modified by any variable associated with farmland use intensity. The negative association between insect biomass and urban land cover appeared to be reduced by increased urban green space.

Main conclusions: Our results show that land cover has an impact on flying insect biomass with the magnitude of this effect varying across spatial scales. However, the vast expanse of grey space in urbanized areas has a direct negative impact on flying insect biomass across all spatial scales examined.

KEYWORDS

biomass, citizen science, insects, land cover, land use intensity

1 | INTRODUCTION

The proportion of the Earth that is actively managed by humans continues to increase, with at least three-quarters of the global land area currently affected by human activities (IPBES, 2019). The IPBES Global Assessment draws a sobering picture of global biodiversity decline associated with human activities, although much of our understanding is based on vertebrates and plants. Most terrestrial animal species, however, are insects and other arthropods (Stork, 2018), and recent studies have found that many terrestrial arthropod groups are declining, particularly in Europe (e.g. Hallmann et al., 2017, 2020; van Klink et al., 2020; Thomas et al., 2004; Valtonen et al., 2017). At the same time, some insect groups, such as dragonflies, are expanding their distribution in Europe over recent decades (Bowler et al., 2021; Termaat et al., 2019). Changes in arthropod biomass, abundance and community composition are expected to have diverse and ramifying consequences, via alterations of food webs, nutrient recycling, pollination and pest control, but we still lack a comprehensive understanding of key drivers of biomass, composition, richness and diversity of insect communities (Seibold et al., 2019). Few studies have simultaneously compared insect biomass across multiple different habitat types and at different spatial scales (Hallmann et al., 2017; Uhler et al., 2021). Nonetheless, understanding relationships between insect biomass and land cover and land use is essential for conservation strategies aiming to mitigate insect loss.

Arguably, one of the most extreme land cover changes imposed by human activities is urbanization (Seto et al., 2012). However, urbanization is a complex process, and some cities offer more suitable habitats for insects than others do. At a landscape scale in Germany, insect biomass in urban habitats was low compared with agricultural landscapes, although richness was still higher than in, for example, farmland at a local scale (Uhler et al., 2021). Across several insect taxa, Piano et al. (2020) found that urbanization in Belgium was associated with a decline in insect diversity at multiple spatial scales. Similarly, a recent meta-analysis combining studies from across the world found a negative effect of urbanization on terrestrial arthropod diversity and abundance (Fenoglio et al., 2020). Cities with greater amounts of green space harbour higher insect pollinator abundance than cities with less green space (Turrini & Knop, 2015). Moreover, some insect species may even thrive in urban landscapes. A recent study found that Hymenoptera showed higher species richness and flower visitation rates in urban areas than in rural areas, with the opposite pattern exhibited by Lepidoptera and Diptera (Theodorou et al., 2020).

In the context of a European landscape, and especially for the countries examined in this study, the majority of land cover consist of highly human-modified landscapes (Denmark: 74%, Germany: 63.7%) with 61% agricultural areas, 13% settlements and infrastructure in Denmark (Statistics Denmark, 2019), and 50% of the land area used for farming and 13.7% human settlements and infrastructure in Germany (German Federal Statistics Office, 2015).

Similar to urbanization, land conversion for crop production also has substantial consequences for biodiversity. For example, declines in insect richness have been found to be steeper in semi-natural grassland areas embedded in a landscape with a high amount of arable fields compared with areas surrounded by forest (Seibold et al., 2019). Most studies on the impact of agricultural habitats have focused on comparisons among farming systems, for example conventional versus organic, rather than comparisons with semi-natural or natural habitats (e.g. Bengtsson et al., 2005; Bianchi et al., 2006; Boutin et al., 2009; Kleijn & Sutherland, 2003).

Insect species richness has been reported to be 30% higher, on average, in areas with organic farming, compared with the conventional alternative, although the positive effect varied over spatial scales, among taxa and functional groups (Bengtsson et al., 2005). In Germany, Red List Lepidoptera biomass and species richness were found to be twice as high in organic farmland compared with conventional farmland (Hausmann et al., 2020). In another study, Lepidopteran biomass was lower in arable areas than in woodland and grassland sites (Macgregor et al., 2019). Still, in general, it is less clear how much insect biomass in farmland (whether organic or conventional) differs from semi-natural areas, not to mention natural ecosystems.

In this study, we investigated the spatial patterns in insect biomass across two European countries, Denmark (northern Europe) and Germany (central Europe). We sampled insects over a range of land covers, from semi-natural to highly managed, and from entirely urban to completely rural. For our study, we motivated community scientists or citizen scientists to sample flying insects with car nets as part of the InsectMobile project. Car nets have been employed for biting flies, mosquito and beetle sampling by professionals and amateurs for more than half a century (e.g. Bidlingmayer, 1966; Dyce et al., 1972; Roberts & Irving-Bell, 1985), but have not been used as a standardized insect sampling method before. Our approach has the advantage of allowing multiple land covers to be sampled nearly simultaneously across large scales in a uniform and standardized way.

We examined insect biomass among major land cover types: urban, farmland, grassland, wetland and forest across Denmark and parts of Germany. Grasslands, wetlands and forests are often considered semi-natural in western and northern Europe because they are, to some extent, human-modified compared with natural ecosystems. Forests are mostly managed in both countries. We focused on insect biomass for several reasons: it aligns with reported declines of insect biomass (Hallmann et al., 2017); it is a relevant measure for ecosystem functioning (Barnes et al., 2016); and it is a measure of resource availability for higher trophic levels. Overall, we expected that insect biomass would be negatively affected by increasing human-modified land cover and more intense land use. Specifically, we predicted that urban habitats would have a negative effect on insect biomass, as would, perhaps to a lesser extent, agricultural lands. In addition, we expected that insect biomass would be positively associated with semi-natural habitats.

2 | METHODS

2.1 | Citizen science sampling with car nets

We recruited 180 citizen scientists to drive with car nets in close proximity to their home address in June and July 2018. The car net was funnel-shaped with a detachable sampling bag at the far end for sample collection. Metal guy-line adjusters enabled adjustment to car length and allowed the net to be used on most car types (Figure 1). The measurements of the net were as follows: front height: 75 cm; front width: 100 cm; length: 140 cm; width of sampling bag: 29 cm; mesh size at the bottom (grey fabric): 2 × 1 mm; and mesh size for the rest of the net (white fabric): ~0.3 mm. Custom tent poles (L: 209 cm, D: 8 mm) supported the opening of the net (see also Supplementary Information in Svenningsen et al. (2021)).

FIGURE 1 Two volunteers sampling insects on a farmland route in Jutland (Denmark) during June 2018. Photos by Jan Skriver

Citizen scientists were recruited by the Natural History Museum of Denmark (NHMD) and the German Centre for Integrative Biodiversity Research (iDiv) during spring 2018. The citizen scientists received a simple sampling protocol, and video tutorials and FAQ sheets along with the sampling equipment (Data S1(VI)).

Sampling was carried out along 211 routes from 1 to 30 June 2018 in Denmark, and along 67 routes between 25 June and 8 July 2018 in Germany (Figure 2). Sampling of each route was carried out once during two time intervals on the same day: between 12 and 15 h (midday) and again between 17 and 20 h (evening) with a maximum speed of 50 km/h and weather conditions of at least 15°C, an average wind speed of maximum 6 m/s and no rain. Insects were collected in individual sampling bags that were placed in 96% pure ethanol and stored in double-sealed plastic bags before the citizen scientists sent the samples back to the research institutions.

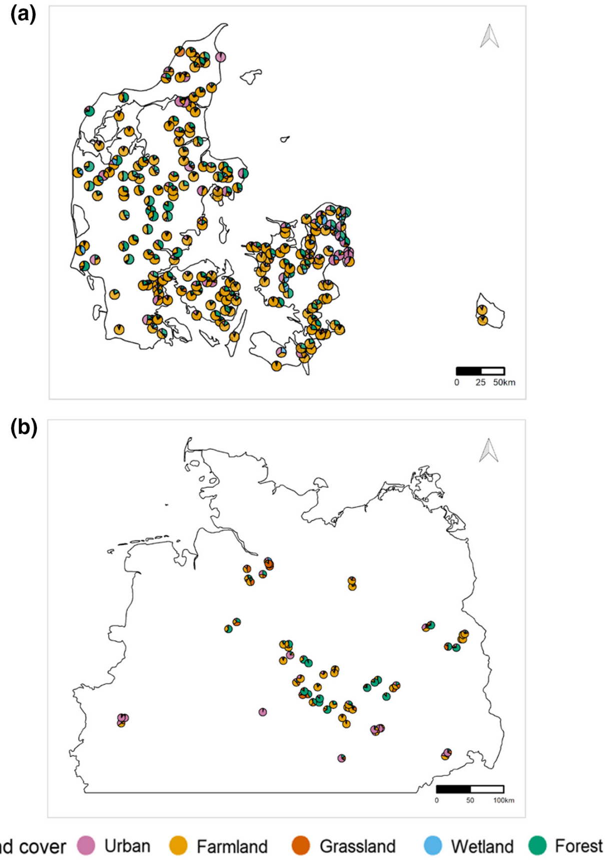


FIGURE 2 Location of car net sampling routes in two European countries, (a) Denmark (211 routes) and (b) Germany (67 routes). Pie chart points illustrate the proportional land cover at the 1,000-m buffer for each sampling location

2.2 | Route design

Across both countries, routes were created across five land cover types: farmland, grassland, wetland, forest and urban areas. No route could be designed to fit 100% to one land cover type, but each route was designed to target a specific land cover type. Each sampling event was either driven in one direction for 10 km or 5 km driven back and forth, to cover as much of the targeted land cover type as possible. The routes were constructed in ArcGIS and QGIS using information from Google Earth, Google Maps and OpenStreetMap (OSM), including data from Danish authorities on land cover types in Denmark, and also using the German ATKIS data (Amtliches Topographisch-Kartographisches Informationssystem) in Germany. Based on the target land cover, in Denmark, 64 urban, 59 farmland, 63 grassland, 62 wetland and 66 forest routes were designed. In Germany, 12 urban, 15 farmland, 12 grassland, 17 wetland and 14 forest routes were created.

2.3 | Sample processing

Upon receipt of the samples from the citizen scientists, we checked whether the samples were in suitable condition for further analysis, for example no ethanol leakage from the sampling bags. To ensure data quality, we only included samples in the analysis where all metadata was registered on the sampling sheet provided for the volunteers. We allowed for a 10% (=500 m) deviation from the route, if the citizen scientist was able to clearly show how the route was altered. The majority of the returned samples were suitable for further processing: 80% in Denmark and 97% in Germany. Insects were removed from the sampling bag with a squeeze bottle containing 96% EtOH and forceps. Empty 15- or 50-ml centrifuge tubes were weighed, and the insects were transferred to the tubes. The insects were dried overnight at 50°C in an oven (>18 h), and the tubes containing the dry insects were weighed (Mettler Toledo ME303 in Denmark, Quintix® Precision Balance 310 g × 1 mg in Germany) to obtain sample biomass (in total mg).

2.4 | Environmental data

According to Seibold et al. (2019), the effect of land covers on insect communities levels off at a 1,000-m buffer for grassland and forest sites. Therefore, we extracted land use predictors for insect biomass from four buffer zones for each route: 50 m, 250 m, 500 m and 1,000 m in five categories (urban, farmland, grassland, wetland and forest). The buffers were calculated as linear buffers around each route. A comprehensive overview of land cover categories and their definitions are listed in Data S1(I). Land use intensity data for Denmark were extracted for farmland and urban routes (Data S1; Table S1.2).

We extracted potential car stop variables to account for sampling heterogeneity. We obtained the number of traffic lights or stops of any type (e.g. roundabouts, pedestrian crossings, stop signs, railroad crossings) within a 25- to 30-m buffer using OSM. For Danish routes, we obtained the number of roundabouts using data from the Danish Map Supply provided by SDFE (Agency for Data Supply and Efficiency) (GeoDenmark data), since data on roundabouts in Denmark were limited to three records in OSM. Mean hourly temperature and wind were extracted for each route including date and time band from the nearest weather station using the rdwd R package for German routes. For Danish routes, temperature (within increments from 15 to 20, 20 to 25 and 25 to 30°C), average wind speed (within increments from light breeze, 1.6–3.3; gentle breeze, 3.4–5.5; and moderate breeze, 5.5–7.9 m/s) and sampling time (hh:mm) were registered by the citizen scientists.

2.5 | Statistical analyses

The German and the Danish datasets were analysed separately while applying the same modelling approaches and methods to enable comparison.

2.6 | General model

To test the impact of land cover on insect biomass, we analysed log biomass as the response in mixed-effects models assuming a normal distribution, with land cover or land use variables as our main explanatory variables. We used biomass +1, since there were a few zeros in the German samples ($n = 5$, corresponding to 4% of the samples). In Germany, when biomass was >0, the median and range was 143 mg (1–2,295 mg). In Denmark, the sample biomass median and range was 104 mg (3–4,356 mg). To control for other factors causing variation in insect biomass, we included the day of the year, time band (midday versus evening), time of day (centred around each time band and then nested within time band as a predictor), weather variables (temperature and wind) and other measures of possible sampling variation (log-transformed number of traffic lights, or other stops, sampling duration and average speed) (hereafter called controlling variables). Additionally, to account for potential non-independence of data points, we included random effects for route and citizen scientist (i.e. driver and car). The mixed-effects models were fitted using "lmer" in the lme4 R package (Bates et al., 2015).

Hence, the general form of the mixed-effects model was as follows:

$$\log(\text{Biomass}+1) \sim \text{Urban land cover} + \text{Farmland cover} + \text{Grassland cover} + \text{Wetland cover} + \text{Forest cover} + \text{Time.band} + \text{Time.band:Time} + \text{Day} + \log(\text{StopNumber}+1) + (1|\text{DriverID}) + (1|\text{RouteID}) \quad (1)$$

We consistently found no effect of weather variables (probably because of little variation, as the samples were taken under similar weather conditions), as well as sampling duration or average speed of the car, and therefore, they were not included in the final models. To examine spatial autocorrelation, we plotted correlograms and calculated Moran's I using the DHARMa R package (Hartig, 2020), but did not find evidence for spatial autocorrelation in the residuals of the fitted model of Equation 1 ($p = .3$) (Data S1(III)).

2.7 | Land cover as ecological predictors

2.7.1 | Simple regression models

We first tested the effect of each land cover and buffer combination (5 land covers × 4 buffer widths) on insect biomass in simple regression models (i.e. one land cover variable per model, but including controlling variables of time, day and stops as well). We used these simple models to identify the best buffer width (i.e. one with the largest effect size) for each land cover (Data S1; Figure S2.1). For the Danish data, we found a grassland outlier route containing around 40% grassland cover, where all other routes with grassland contained less than half of that cover (<20%). We excluded this route from the analysis as non-representative (Data S1; Table S2.2 & Figure S2.2).

2.7.2 | Multiple regression models

We built a linear mixed-effects model that included all five of the land cover variables (at the best buffer width for each one) and the controlling variables, day of the year, time band, time of day, and log-transformed number of traffic lights or stops. We examined variation inflation factors to check for collinearity issues (see also Data S1(III)).

2.8 | Comparison between land covers

We included multiple comparisons with a general linear hypothesis test from the package "multcomp" (Hothorn et al., 2008) to compare the effect sizes of each land cover type on insect biomass (i.e. regression slopes) while still accounting for correlations between land cover proportions in the multiple regression model.

The patterns from the above models suggested that the proportion of urban cover relative to other land covers had the strongest effect on insect biomass. To check whether we could identify differences among the other land cover variables, we ran another analysis in which we subset the dataset to routes with only low levels of urban cover (<5%). After this step, the routes mostly varied in the amount of the other land covers, minimizing the effect of urban cover. We ran similar models as above with this data subset except with only tested the effect of the four other land covers on insect biomass (Data S1(IV)).

2.9 | Covariate transformations

To simplify interpretation of the model coefficients and enable comparison across the countries, we kept the land cover predictors on their original scale (i.e. % of land cover within the buffer) in our main models described above. In these models, coefficients could be interpreted as log change in insect biomass per 1% change in land cover of a specific type. However, we also ran additional analyses with transformed land cover variables to more explicitly account for the fact that the land cover predictors were compositional data (i.e. they sum close to 100% across most routes). First, we used a varimax-rotated PCA to reduce the five land cover variables into two axes that captured most of the variation in land cover compositions among the routes, using the "psych" R package (Revelle, 2020) (Data S1(III)). Second, we applied the isometric log-ratio transformation (Egozcue et al., 2003), creating land cover predictors that reflect the relative ratios of each type, using the "complmrob" R package (Kepplinger, 2019). These transformations reduced the correlations among the land cover predictors and hence any problems associated with collinearity. In both cases, we ran our original model structure (Equation 1), except with these transformed covariates as predictors instead of the original land cover variables (Data S1(III,IV)).

2.10 | Land use intensity as ecological predictors

We further investigated whether variables associated with the intensity of farmland and urban land use within the 1,000-m buffer explained variation in insect biomass. We restricted this analysis to the Danish routes because of the larger sample size and to samples with the target land cover above the 50% quantile along the routes to ensure the route was dominated, as far as possible, by that land cover. For urban routes, 164 samples were retained for analysis. For farmland routes, 163 samples were retained. To account for the association between general land cover and the land use intensity, we calculated the proportional cover of the land use intensity variable within the land cover variable (i.e. the proportion of green space within the urban land cover). For the urban analysis, we investigated whether urban green space had an effect on insect biomass. For the farmland analysis, we investigated whether farming practice, that is organic versus conventional farming types, had an effect on insect biomass. We constructed models similar to Equation 1 to test whether the effect of urban cover depended on the land use intensity properties of the urban cover, and similarly whether the effect of farmland cover depended on the land use intensity properties of the farmland cover. Varimax-rotated PCA axes were used to define land use intensity gradients, which were used as explanatory variables in mixed-effects models (Data S1(III)).

All analyses were carried out in R (version 3.6.3).

3 | RESULTS

3.1 | Land cover

3.1.1 | Denmark

In Denmark, the land cover along the routes was dominated by farmland (mean coverage 54%), urban (mean coverage 12%) and forest cover (mean coverage 16%). The largest effect sizes for urban, farmland and grassland were associated with buffers of 1,000 m, 250 m for forest and 50 m for wetland (Data S1; Figure S2.1A). We found positive effects of grassland, farmland and forest cover on insect biomass (Table 1, Figure 4A). When we compared effects between land covers, the effect of urban cover was significantly more negative than the effects of grassland, farmland and forest cover (Table 1). The fixed effects explained 37% of the variation in the multiple regression model. In addition, we found a positive effect of sampling day with an increase in biomass throughout June, higher biomass in the evening compared with midday and an increase in biomass with time within the three-hour midday sampling (Data S1; Table S2.1). Urban cover had a high correlation with potential stops along the routes, but stops were included as a confounder in all models (Data S1; Figure S3.2). From the model output, generalized variance inflation factors (GVIFs) were high for urban and farmland cover (4.8 and 5.4, respectively).

To check for the effect of correlations among the variables, we used a PCA to define independent land cover axes. The PCA defined an axis of change between farmland and urban land cover (urbanization gradient) and an axis of change between farmland and forest cover (forest gradient) (Data S1; Figure S3.1A). We found the urbanization gradient to have a negative effect on insect biomass (Data S1; Table S3.1). Routes with low biomass samples (within the bottom 20% of biomass samples, <48.8 mg) were dominated by urban and farmland cover, whereas routes with high sample biomass (within top 20% of biomass samples, >262 mg) were dominated by farmland cover (see Figure 3C). In contrast, there was no effect of the forest gradient on biomass. Isometric log transformation of land covers similarly supported a negative effect of urban cover and had lower GVIFs (Data S1; Table S4.3). In a model that excluded routes based on a relatively high urban cover (>5%, 105 samples retained), the proportions of the other land covers explained no variation in insect biomass (Data S1; Table S4.1).

Since we found an effect of time band (more insects in the evening (Data S1(II), Figure 5A)), we explored whether the effect of land cover differed with sampling time, but we did not find any evidence of an interaction between land cover and time band.

3.1.2 | Germany

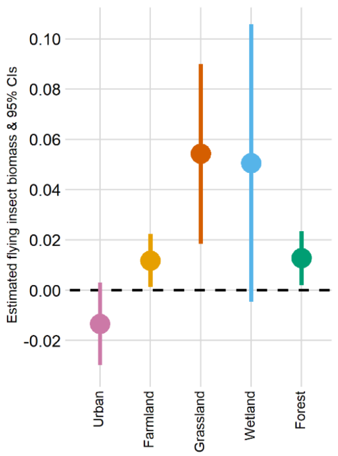
In Germany, the land cover along the routes was dominated by farmland (mean coverage 37%), urban (mean coverage 21%) and forest cover (mean coverage 26%). All land covers except forest had the largest effect sizes associated with 1,000-m buffers; forest cover had similar effect sizes with buffers of 250, 500 and 1,000 m (Data S1; Figure S2.1B). Although the main effect of the urban cover on insect biomass was not significant, the effect of urban cover was significantly more negative than the effects of forest, grassland and farmland (Table 1, Figure 4B). We did not find any difference between the effect of farmland cover and the other open semi-natural habitats, nor between grassland and wetland or forest. Insect biomass was generally higher in the evening and with a later sampling time during the evening routes. The fixed effects of the multiple regression model explained 36% of the variation in insect biomass (Data S1; Table S2.2). Generalized variance inflation factors (GVIFs) of the model were high for urban and farmland cover (9.7 and 10.8, respectively).

The PCA suggested two dominant axes of land cover variation: an axis of change between farmland to urban cover and an axis of change between grassland and forest. Testing these PCA axes instead of the five land cover variables as predictors of insect biomass supported the urbanization gradient as being the most important for decreasing insect biomass. Consistent with these patterns, routes with low biomass samples (within the bottom 20%, <46 mg of insects sampled) were dominated by the urban cover. By contrast, in the routes with high biomass yields (within the top 20%, >502 mg), the mean landscape composition was dominated by farmland cover (see Figure 3a–c).

Similar results were found when land cover variables were isometric log-ratio-transformed, and this reduced multicollinearity

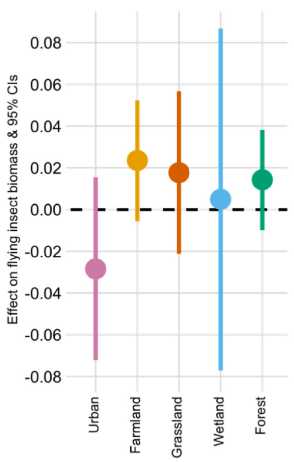
TABLE 1 Output of the linear mixed-effects model on insect log(biomass+1) for (A) Denmark and (B) Germany. The model includes all land cover and controlling variables; however, this table only shows the effect of the land covers. For the full model output with controlling predictors, see Data S1; Table S2.1 for Denmark and Data S1; Table S2.2 for Germany. All land cover variables were kept in their original units to facilitate interpretation. Shown is the estimated effect change in biomass of each explanatory variable and 95% confidence intervals (land cover predictor in the left figure); that is, with increasing farmland cover, there is an increase in insect biomass. A pairwise comparison between land covers (Compared to) shows whether the effect is significantly larger or smaller in the land cover (Difference) compared with the other land covers (comparison of slopes). Significant variables are in bold ($p < .05$), and trends ($p < .1$) are in italic. The marginal R^2 considers only the variance of the fixed effects, while the conditional R^2 considers both the fixed and random effects

(a) Denmark



	log(Biomass + 1)	
Land cover predictor	*Compared to*	*Difference (95% CIs)*
Urban$_{(1000\ m)}$	Farmland$_{(1000\ m)}$	**-0.03 (-0.04 – -0.01)**
	Grassland$_{(1000\ m)}$	**-0.07 (-0.11 – -0.02)**
	Wetland$_{(50\ m)}$	*-0.06 (-0.13 – 0.00)*
	Forest$_{(250\ m)}$	**-0.03 (-0.04 – -0.01)**
Farmland$_{(1000\ m)}$	Grassland$_{(1000\ m)}$	**-0.04 (-0.08 – -0.00)**
	Wetland$_{(50\ m)}$	-0.06 (-0.14 – 0.01)
	Forest$_{(250\ m)}$	-0.00 (-0.01 – 0.01)
Grassland$_{(1000\ m)}$	Wetland$_{(50\ m)}$	0.00 (-0.07 – 0.07)
	Forest$_{(250\ m)}$	**0.04 (0.00 – 0.08)**
Wetland$_{(50\ m)}$	Forest$_{(250\ m)}$	0.04 (-0.02 – 0.09)
Marginal R^2 / Conditional R^2		0.373 / 0.658

(b) Germany



	log(Biomass + 1)	
Land cover predictor	*Compared to*	*Difference (95% CIs)*
Urban$_{(1000\ m)}$	Farmland$_{(1000\ m)}$	**-0.05 (-0.09 – -0.01)**
	Grassland$_{(1000\ m)}$	**-0.05 (-0.09 – -0.00)**
	Wetland$_{(1000\ m)}$	-0.03 (-0.14 – 0.07)
	Forest$_{(250\ m)}$	**-0.04 (-0.08 – -0.00)**
Farmland$_{(1000\ m)}$	Grassland$_{(1000\ m)}$	0.01 (-0.02 – 0.03)
	Wetland$_{(1000\ m)}$	0.02 (-0.08 – 0.11)
	Forest$_{(250\ m)}$	0.01 (-0.004 – 0.02)
Grassland$_{(1000\ m)}$	Wetland$_{(1000\ m)}$	0.01 (-0.07 – 0.10)
	Forest$_{(250\ m)}$	0.00 (-0.02 – 0.02)
Wetland$_{(1000\ m)}$	Forest$_{(250\ m)}$	-0.01 (-0.09 – 0.07)
Marginal R^2 / Conditional R^2		0.359 / 0.831

Generalized variance inflation factors for the Danish model: farmland = 4.8, urban = 5.4, grassland = 1.2, wetland = 1.3, forest = 2.9 and potential stops = 2.9. Similar patterns are obtained when the land cover variables are square-root-transformed, after which the GVIFs are all <4.4. *Generalized variance inflation factors for the German model*: farmland = 10.82, urban = 9.66, grassland = 4.91, wetland = 1.26, forest = 10.24 and potential stops = 4.63. Similar patterns are obtained when the land cover variables are square-root-transformed, after which the GVIFs are all <4.7.

among the variables (Data S1; Table S4.4). After excluding all sites with relatively high urban cover (>5%), we still did not find any role of the other land uses in explaining variation in insect biomass among the routes, but this subset only contained 26 samples. Just as for Denmark, there was no evidence of interactions between land cover and time of day, suggesting the differences between urban cover and the other land uses were similar for insects sampled at midday and in the evening (Figure 5a,b).

3.2 | Land use intensity in Denmark

3.2.1 | Urbanization and green space gradients

The varimax-rotated PCA axes (Data S1; Figure S5.2, Table S5.1) were extracted as gradients for analysis, where the first axis defined the urbanization gradient and the second axis defined the urban green space gradient. We found a negative effect of urbanized areas on

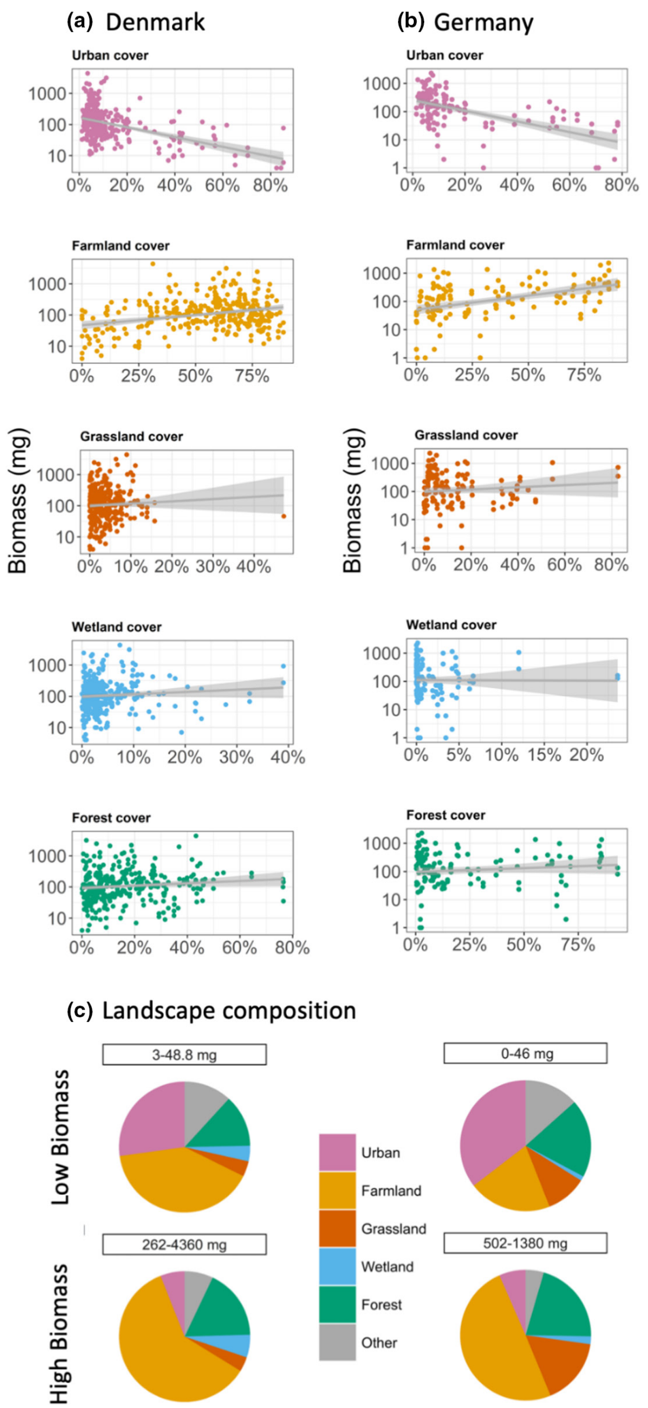


FIGURE 3 Scatterplots show the simple relationships between per cent of each land cover and insect biomass. (a) Denmark and (b) Germany. (c) Pie charts show the mean land cover composition of routes with the lowest 20% quantile and upper 20% quantile of biomass samples

insect biomass (Data S1; Table S5.3) and a tendency towards higher insect biomass with an increase in urban green cover compared with an increase in intense urban cover (95% CI [−0.00 to 0.18], $p = .05$), that is large cities with multistorey buildings, inner city areas and commercial districts (Data S1(V)).

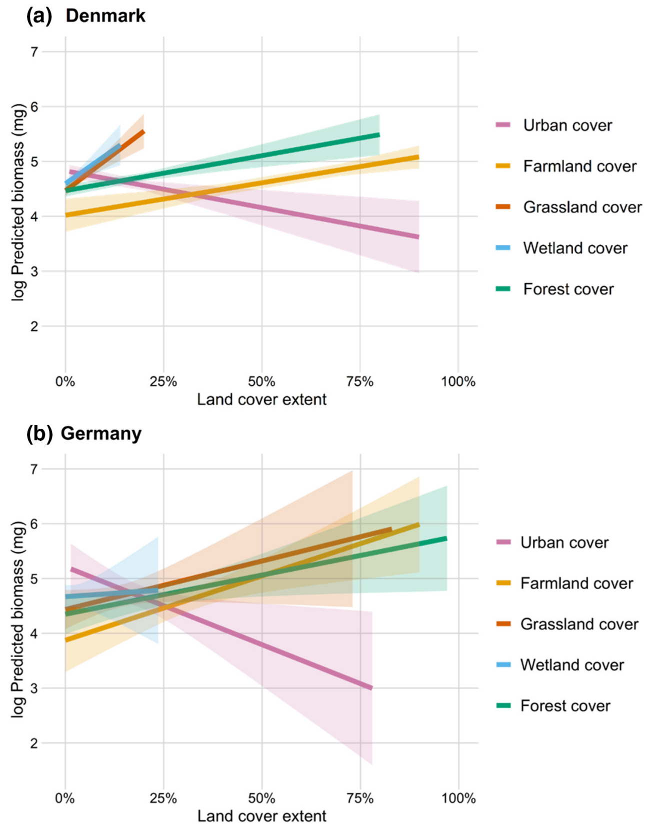


FIGURE 4 Partial effects of each land cover when all other predictors are held fixed at their means for (a) Denmark and (b) Germany. Predicted log(biomass+1) (mg) on the y-axis and proportional land cover on x-axis. Based on the full model for each country to illustrate the relative effect of each land cover, land cover buffer sizes for Denmark were modelled on urban, farmland and grassland cover = 1,000 m, 50 m for wetland cover and 250 m for forest cover. For the German data, land cover buffer sizes used for modelling were 1,000 m for urban, farmland, grassland and wetland cover, and 250 m for forest cover. Shaded areas around each line are the standard error of the fit

3.2.2 | Farmland gradients

The rotated PCA axes were extracted as gradients where the first axis described the organic farmland gradient and the second axis defined the conventional semi-extensive/extensive gradient (Data S1; Table S5.4). The gradients did not significantly explain variation in insect biomass (Data S1; Table S5.6).

4 | DISCUSSION

Using an innovative combination of citizen science and car net sampling, we were able to simultaneously sample a large geographic area with 278 transects in a highly anthropogenic landscape. In doing so, we sampled the flying insects adjacent to both public and private lands, including highly populated cities, relatively remote forests and wetlands, and intensive agricultural fields. This sampling approach

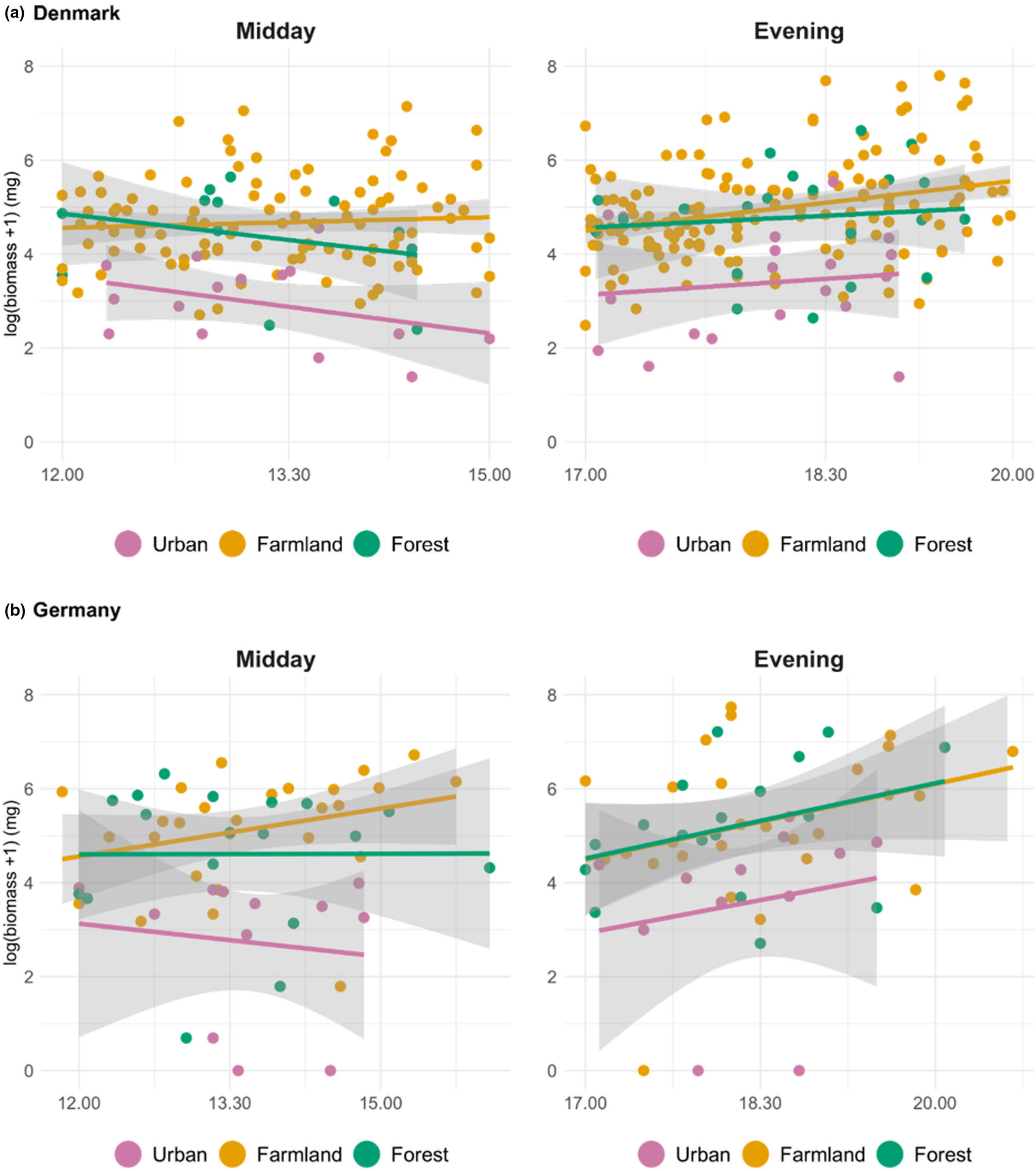


FIGURE 5 Sampling time effects on insect biomass. (a) Denmark and (b) Germany: overall effect of sampling time on insect biomass on land covers where the maximum proportional cover could be assigned to a specific land cover category at the 1,000-m buffer. Coloured land covers and shaded areas correspond to the standard error of the fit. We do not show wetland and grassland since these were rarely the dominant land cover along a route

revealed a consistent spatial pattern in insect biomass across the two countries, namely lower biomass associated with urbanization.

Urban cover was only a moderate fraction of the total land cover, but its effects extended to landscape scales. Hence, urban cover has a larger effect than would be expected given its area alone. Although an increase in urban green space tended to lessen the negative effect of urbanization, it did not fully counterbalance the negative effect. Our results are consistent with a recent meta-analysis that found an overall negative effect of urbanization on arthropod diversity and abundance (Fenoglio et al., 2020), 42% less biomass in urban compared with semi-natural environments (Uhler et al., 2021), as well as a study showing declines of insect diversity with urbanization at multiple spatial scales (Piano et al., 2020). In large part, this may be due to the reduced vegetation biomass and productivity per unit area in urban habitats where much of the landscape is impervious surface, such as cement or rooftops (Uhler et al., 2021). While studies that focus on local, green habitats in cities often find those habitats to be biological-diverse (Brunbjerg et al., 2018; Guénard et al., 2015; Mody et al., 2020; Theodorou et al., 2020; Turrini & Knop, 2015), such studies may risk missing the broader picture that the unsampled grey spaces of cities are likely to have low biomass, a reality reflected in our results from both Denmark and Germany. Our approach of sampling across a transect of several km, while having limitations, integrates the effects of green and grey urban spaces on biomass and may provide a more complete picture of the mean biomass of insects in a volume of air space over the city.

Farmland is by far the dominant land cover in both of our study countries, and hence, farming practices could have potentially the most widespread impacts on insect biomass. We found a positive effect of farmland cover on insect biomass in Denmark and a similar tendency in Germany. However, when we excluded the most urban routes (>5% urban cover), the effect of farmland cover on insect biomass was weaker, suggesting part of the farmland effect may have been driven by its negative correlation with urban cover. In addition, farmland cover tended to be less strongly associated with insect biomass than semi-natural land cover, including grassland. Although studies have found a negative effect of agriculture on insects (Benton et al., 2002; Seibold et al., 2019), our assumption of lower biomass with an increase in agricultural cover was not supported by our results. Instead, we found comparable biomass of insects in farmland and semi-natural areas. This might be explained by higher availability of food sources than expected within farmland. Indeed, the density of herbivorous insects has been positively correlated with nitrogen loading in the landscape (Haddad et al., 2000; Ritchie, 2000), and nitrogen loading is expected to be highest in areas with high farmland cover. Hence, higher plant biomass and productivity, and more nutrient input and higher leaf N content may explain the positive correlation of insect biomass with farmland cover. Moreover, since we focused on biomass, greater biomass might be primarily caused by a few common and highly abundant species, that is agricultural pests and their predators. An alternative contributing explanation may be the low habitat quality of semi-natural and forest habitats in the study regions. For instance, the Danish forest is among the most well-managed production forests in Europe, leaving very low amounts of deadwood and other important insect habitats compared with a more natural baseline situation (FOREST EUROPE, 2020).

In Denmark, we found a more positive effect of semi-natural grassland on insect biomass compared with forest cover, but not compared with wetland cover. This effect was not found in Germany, which could be due to the smaller sample size or because the semi-natural grassland cover could not be distinguished from agricultural grassland, for example grass leys, whereas the grassland cover category in our Danish analysis consisted of meadows, salt meadows and grassland under the Danish Protection of Nature Act Section 3. In Denmark, similar to the German study by Uhler et al. (2021), we found the largest difference in biomass between urban and semi-natural land covers, although the urban biomass on average was only 6.4% lower than in semi-natural covers compared with 42% lower urban biomass found by Uhler et al. (2021). The pronounced difference in effect of land covers may be explained by the sampling method; that is, malaise traps sample insects in the local habitat (Steinke et al., 2021), whereas car nets sample insect activity on a landscape scale. Uhler et al. (2021) also sampled insects for a longer period of time and accounted for other abiotic factors associated with a longer sampling period, which further reduces the comparability between the two studies.

Since we found similar effects of land cover for insects flying during midday and evening, there is some evidence that taxa, which are active during different parts of the day, are similarly impacted by variation in land cover. However, biomass is only one measure of an insect community and other measures, such as richness, diversity and composition, may show contrasting patterns. For instance, biomass may increase, but species richness may decrease if the increase in biomass is driven by common large-bodied or multiple small generalist species (Uhler et al., 2021). Nevertheless, temporal abundance, biomass and observed species richness declines for hoverflies have been shown to be interlinked (Hallmann et al., 2021), but this pattern may well vary between arthropod groups and requires further investigations.

Like any study, our approach has some limitations. Car net sampling shares some of the same sampling bias as other sampling methods; that is, they sample insect activity, especially taxa that disperse well, rather than the entire insect fauna of the habitat. Also, the land cover of both our European study countries is already highly modified by human activities, even beyond farmland and urban regions. The effect of natural land cover on insect biomass is likely very different for areas and countries with large extents of undisturbed nature. It was not part of the scope of our study to examine how flying insect biomass may respond to patterns of habitat connectivity or configuration. However, integration and connectivity of suitable insect habitat within human-disturbed landscapes may have a positive effect on some insect taxa in an otherwise hostile landscape (Boetzl et al., 2021; Sirami et al., 2019; Turrini & Knop, 2015). Furthermore, the summer of our surveys, 2018, was exceptionally hot and dry in both countries; for example in Denmark, it was the driest year in almost 100 years (Damberg, 2018). As such, the differences in biomass across the land cover types might have been affected by the drought.

Overall, we found that urbanization is consistently associated with decreases in insect biomass and appeared to be the dominant driver of spatial variation of insect biomass across our two study countries in Europe. Given the rapid growth of cities around the world, this decrease has the potential for widespread consequences and cascading effects on other species. By sampling across long transects of both grey and green urban areas, we show clear effects of reduced biomass that were not evidenced before across a large scale. In addition, we show the relative importance of other land covers, particularly in Denmark, where we found that semi-natural areas, especially grassland and wetland, tended to have higher insect biomass per relative percentage cover than both urban and farmland areas, signalling their importance for insect conservation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Supplementary data to this article can be found online at Svenningsen, Svenningsen et al. (2022), Flying insect biomass is negatively associated with urban cover in surrounding landscapes, Dryad, Dataset, https://doi.org/10.5061/dryad.547d7wm9f. Scripts used for the statistical analysis can be accessed on GitHub: https://github.com/CecSve/InsectMobile_Biomass.

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BIOSKETCH

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