

## SHORT COMMUNICATION

## The Ecology and Conservation of Urban Insects

# Insect biomass shows a stronger decrease than species richness along urban gradients

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## Abstract

1. Anthropogenic land cover change is a major driver of biodiversity loss, with urbanisation and farmland practices responsible for some of the most drastic modifications of natural habitats. The relative importance of different land covers for shaping insect communities, however, is unclear.
2. This study examines the effect of urban and farmland covers, along with land cover heterogeneity, at a landscape scale on species richness, evenness and biomass of flying insects using citizen science carnet sampling across Denmark.
3. Increasing urban cover had a negative effect on insect richness but an even stronger negative effect on biomass. Increased land cover heterogeneity did not mitigate the negative effect of urban cover. Insect assemblages also became more even with increased urban cover. Farmland cover had no significant effect on insect richness, evenness or biomass.
4. Based on our findings, the urban cover has a strong negative impact on insect communities, indicating that urbanisation could contribute to insect declines. Moreover, our findings indicate that insect loss occurs more through loss of biomass than loss of species, which may affect the ecosystem-level consequences of urbanisation.

## KEYWORDS

citizen science, Diptera, insect declines, insect monitoring, invertebrates, land use

## INTRODUCTION

Recent studies have documented declines in the abundance of individual insect species, total insect biomass, insect richness and community-level abundance (Forister et al., 2011; Hallmann et al., 2017; Thomas et al., 2004; Valtonen et al., 2017; van Klink et al., 2020). While such declines are not universal across taxa or regions (Baldock et al., 2015), they nonetheless appear to be common (van Klink et al., 2020). Anthropogenic land use changes are

one of the main threats to terrestrial biodiversity (Jaureguiberry et al., 2022; Newbold et al., 2015), especially to insects (Wagner et al., 2021).

Two key threats to insects are agricultural land use and urbanisation (Potts et al., 2010; Winfree et al., 2009). While the conversion of land to agriculture can have negative effects on insect biodiversity (Hallmann et al., 2017; Raven & Wagner, 2021), contingent on the form of agriculture (Beckmann et al., 2019), its relative importance in comparison to urbanisation is less clear. On one hand, urban

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areas have more impervious surfaces, additional potential stressors, such as light pollution, and overall proportionally less vegetation cover than agricultural areas (Grubisic et al., 2018). On the other hand, urban areas may have sufficient and diverse urban green spaces to compensate for the negative effects of nongreen urban areas (Turrini & Knop, 2015). Studies on different taxa report contrasting effects of urban cover on richness or abundance, with negative effects (Bates et al., 2011; Fenoglio et al., 2020; Fortel et al., 2014; Piano et al., 2020) or positive or neutral effects (Baldock et al., 2015; Theodorou et al., 2017).

These urban studies, however, tend to focus locally on green spaces within urban areas, which are just a small part of the urban ecosystem (Dunn et al., 2022). This is in contrast to studies of natural areas or farmland, which tend to consider those ecosystems more holistically (Batáry et al., 2020; Stein-Bachinger et al., 2021). As a result, most studies on insects in urban areas may underestimate the effects of nongreen areas. Because many urban areas are more grey than green, the biology of these green areas is likely to be poorly representative of the broader ecology of urban areas.

Insect communities can be measured in different ways, including biomass, abundance, diversity and richness. Studies of biodiversity change indicate that different patterns can emerge depending on the metric studied (Blowes et al., 2022). Previously, in Svenningsen et al. (2022), we found that flying insect biomass declined with increasing urban cover but tended to increase with farmland cover. However, it remains untested whether other metrics such as richness and evenness show the same patterns. A recent study suggests that biomass and richness responded differently to different land use gradients (Uhler et al., 2021).

As part of the InsectMobile project in Denmark, as described in Svenningsen et al. (2021), we worked with citizen scientists to collect samples of flying insects from a wide variety of habitats, ranging from seminatural to urban to completely rural settings. While we focus on spatial patterns, the results have also relevance for understanding drivers of declines through time (Blüthgen et al., 2022). Here, we extend our previous work (Svenningsen et al., 2022) to compare the impacts of urban and farmland covers on insect richness, biomass and evenness. Additionally, our new analysis included an additional sampling year. Following our previous analysis, we expected a stronger impact of urban cover compared with farmland cover on biomass. In addition, we expected that species richness would decrease with increasing urban cover, but that it would be less affected than biomass, since urban areas can support relatively diverse communities for some taxa (Buchholz & Egerer, 2020; Theodorou et al., 2020; Wenzel et al., 2020). We expected that communities in both urban areas and farmland areas might be less even as increasing land use intensity creates few winners but many losers. We further tested whether land cover heterogeneity modified the impact of increasing urban cover (Estrada-Carmona et al., 2022). We hypothesised that land cover heterogeneity would positively influence insect biodiversity and reduce the negative impacts of increasing urban cover.

## MATERIALS AND METHODS

### Data collection

In June 2018 and 2019, volunteers recruited by the Natural History Museum of Denmark collected flying insects with rooftop-mounted insect nets on their cars. The citizen scientists received a simple sampling protocol and video tutorials and FAQ sheets along with the sampling equipment (see extended methods in Appendix S1). The cars were driven along 5 km routes back and forth (total route 10 km), for landscape-level sampling, through urban, farmland, grassland, wetland and forest landscapes across the extent of Denmark. In total, 168 volunteers participated in 2018 and 178 in 2019, with 120 volunteers being involved in both years. In 2018 and 2019, 323 and 335 routes were sampled, respectively, with 191 sampled in both years and 276 sampled in 1 year. Each route was sampled twice on the same day: midday sampling (12:00–15:30) and evening sampling (17:00–20:30). Proportional land cover for each route was extracted using ArcGIS within a buffer of 1000 m on either side of each route, from the Danish land cover dataset, and the number of stops along the routes was calculated using traffic light and other stop data (see the Appendix S1 for further details). The routes varied in urban cover between 0% and 85.3% (median = 6.7%, interquartile range = 4.3, 12.7) and farmland cover between 0% and 88.7% (median = 57.1%, interquartile range = 38.6, 72.2).

Upon receipt of the samples from the citizen scientists, we checked whether the samples were in suitable condition for further analysis (Appendix S1). DNA metabarcoding and quantitative polymerase chain reaction (qPCR) were conducted on the dried bulk insect samples using a non-destructive DNA buffer to extract DNA while preserving the external structure. CO1, a commonly used mitochondrial DNA (mtDNA) gene in arthropod studies, was targeted for DNA metabarcoding using a universal insect primer. Sequencing libraries underwent demultiplexing and processing with cutadapt and the DADA2 pipeline. We ran the LULU algorithm (Frøslev et al., 2017) on all DADA2 processed samples, which combines sequence similarity and co-occurrence patterns to detect potentially erroneous sequences. DNA metabarcoding and bioinformatics protocols are further explained in the Appendix S1.

For each sample, we calculated richness, biomass and evenness. For richness, we compared observed, rarefied and estimated richness. Observed richness was the total number of identified species. Rarefied richness standardised comparisons by equalising sampling effort. For this, we subsampled the amplicon sequence variant (ASV) table to equalise the number of reads in each sample to the minimum read abundance observed, before generating rarefied richness and Shannon diversity values using the `rrarefy` function from the R package `vegan` (Oksanen et al., 2019). Since these metrics tend to underestimate the true alpha diversity (Lande et al., 2000), estimated richness was calculated for the samples using the `breakaway` package (Willis, 2022), which allows the use of all reads in the ASV table while incorporating unobserved ASVs (bias correction) and a measurement error model (variance adjustment; Willis, 2019). All richness variables

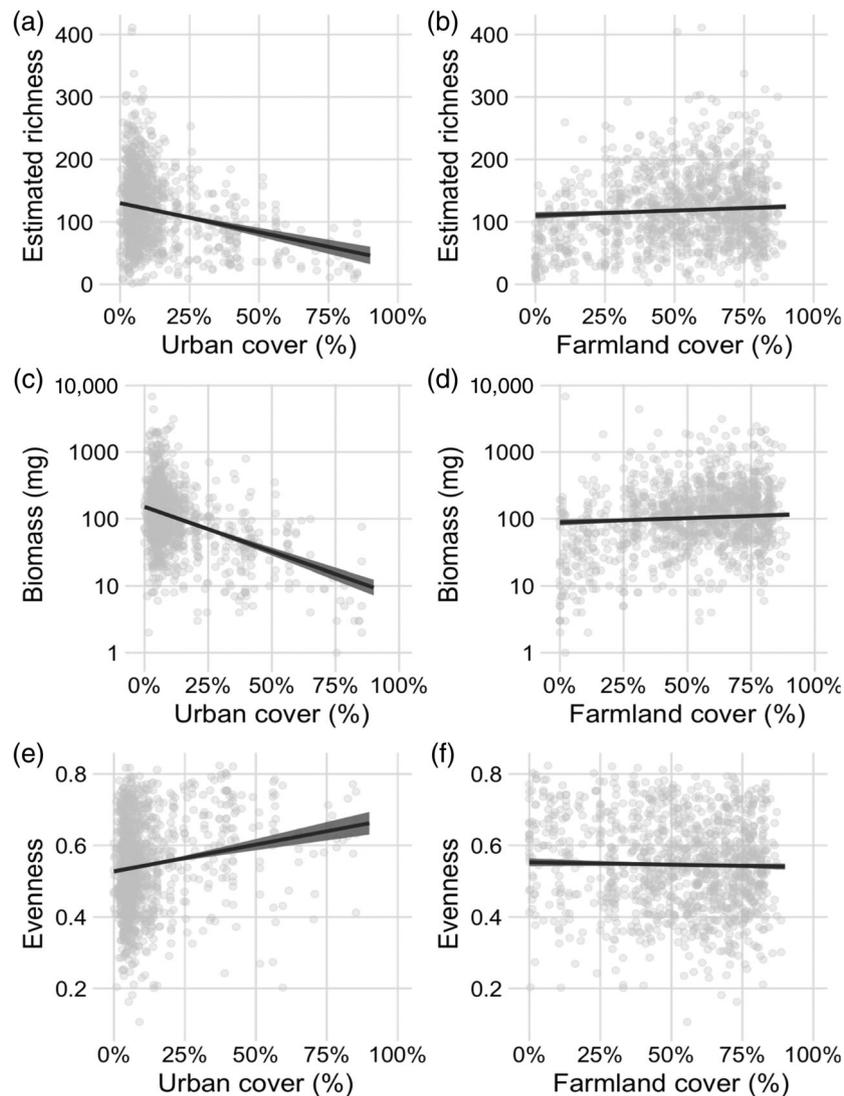
were highly correlated, so we picked estimated richness for our response variable for the main analysis (Figure S1). Biomass was based on the total sample dry weight (in mg) after the insects had been removed from the 96% EtOH and dried overnight at 50°C in a heat cabinet. Evenness was calculated by dividing rarefied Shannon diversity with the natural logarithm of observed richness.

## Analysis

To test our first main question, we built mixed-effect models to test the relative importance of urban cover and farmland cover. These models had an insect response variable (richness, log biomass or evenness), land use predictors (urban and farmland covers), controlling variables (time of day, day of year, number of traffic stops along the route, year) and a route random effect. We included the number of

traffic stops along each route in the analysis to account for the effect that stopping might have on individuals escaping the carnets. We retained all variables in the model regardless of significance to test our hypothesis since we expected all played some role, even if small. We checked correlations between the land cover predictor variables prior to including them in the model (Figure S2, all <0.7). To test our second main question, we ran an additional set of models that tested the interaction between each land cover and land cover heterogeneity, where the latter was calculated as the Shannon diversity index of all coarse land covers.

To assess differences in how much each response variable (richness, evenness and biomass) changed along an urban cover gradient, we calculated their % change over the full gradient that was sampled. To do this, we used the fitted models to predict the response variable values at zero and maximum urban cover, holding all other covariates at their mode or median values. We then estimated the percentage



**FIGURE 1** Effects of farmland and urban covers on richness, biomass and evenness of sampled flying insect assemblages. The lines are the predicted regression lines and 95% confidence intervals. Increased urban cover decreases flying insect richness and biomass, but communities become more even (Tables S1–S3).

change in each variable as the difference in the predicted values divided by the value at a baseline of zero urban cover. All analyses were conducted within the R statistical software (R Core Team, 2022). See the Appendix S1 for details on all packages used.

## RESULTS AND DISCUSSION

In total, 1144 samples were collected, with an average insect biomass of 109 mg (interquartile range = 53.9, 204 mg). Insect richness within each sample strongly decreased with increasing urban cover (Figure 1a, Table S1), with a predicted loss of 61% over the full urban gradient. Evening samples had higher species richness than midday samples, as did samples from 2019 compared to 2018 (Table S1). The effect of urban cover on biomass was even stronger than the effect on richness (Figure 1c), with a predicted loss of biomass of 93% over the full urban gradient. Biomass also tended to be higher in the evening and in 2019 (Table S2). Evenness of the sampled insect assemblage increased with increasing urban cover (Figure 1e, Table S3).

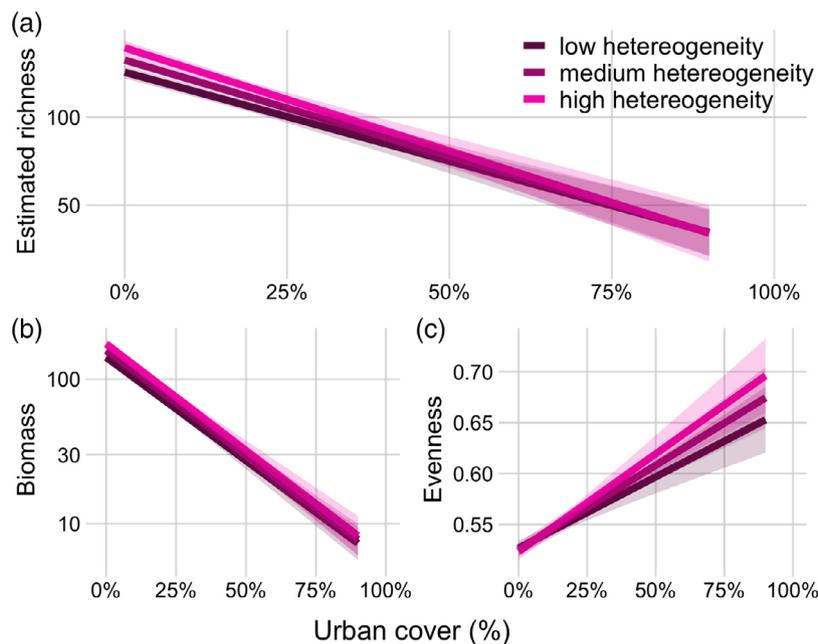
We found no effect of farmland cover on richness (Figure 1b, Table S1), biomass (Figure 1d, Table S2) or evenness (Figure 1f, Table S3).

Our results are similar to recent studies that report associations between biomass and richness loss (Hallmann et al., 2021) and the largest decreases in urban areas (Uhler et al., 2021). Biomass and richness loss along urban gradients may be explained by the combined effects of reduced total area of habitat (as more green habitat becomes grey), chemical and light pollution (Owens et al., 2020) and other factors, such as frequent mowing, that reduce the habitat diversity needed to support a diverse community (Proske et al., 2022).

Interestingly, while insect richness and biomass both decreased with increasing urban cover, biomass was only moderately correlated with richness ( $r = 0.44$ ; Figure S2). This low correlation may indicate that common species, forming the bulk of insect biomass, show greater decreases than rare species (Hallmann et al., 2021), which is consistent with the predicted increase in the evenness of the community along the urban gradient.

Land cover heterogeneity did not significantly modify the effects of land cover on any of the biodiversity response metrics (Figure 2, Tables S4–S6). However, there was a tendency for higher species richness with greater land cover heterogeneity (main effect shown in Table S4). While one might imagine that heterogeneity in urban environments might buffer the effects of urbanisation, we suspect that the effects of urbanisation on insect biomass are sufficiently large in magnitude that they swamp any modest influence of heterogeneity.

Many studies have now shown that, locally, urban green spaces can be both biodiverse and high in biomass (Theodorou et al., 2020; Turrini & Knop, 2015). This pattern has been observed even in highly packed cities, such as in Manhattan in New York City (Guénard et al., 2015), which clearly demonstrates opportunities for insect conservation in urban areas. But many urban studies have focussed on sampling only greenspaces (Goddard et al., 2010; Matthies et al., 2017; Williams & Winfree, 2013). However, most urban areas are not green; hence, previous research has focused on the subset of habitats where biodiversity and biomass are likely to be highest. With our carnet sampling approach, we sampled insects at a landscape-scale across both green and grey spaces. In doing so, we studied not the highest biodiversity and biomass patches but rather the average condition across urban areas.



**FIGURE 2** Interaction between land cover heterogeneity and urban cover on flying insect assemblages. Land cover heterogeneity did not significantly modify the effect of urban cover for any of the response variables, although land cover heterogeneity overall has a positive effect on richness and biomass (Tables S4 and S5).

By combining our approach with DNA metabarcoding, we were also able to consider multiple metrics of insect communities. Specifically, we considered biomass, which is likely to correlate with some functional aspects of insect communities (decomposition, predation) as well as taxonomic richness. Uniquely, barcoding approaches allow the inclusion of small and hard to identify species. Our flying insect assemblages were dominated by Diptera (flies—6951 ASVs), a group for which relatively little is known about their biology and ecology, followed by Hymenoptera (ants, bees and wasps—2145 ASVs), Coleoptera (beetles—1672 ASVs) and Hemiptera (true bugs—923 ASVs). In total, sequences were assigned to 327 families of which the three most frequent families were gall midges (1092 ASVs), followed by nonbiting midges (991 ASVs), a parasitoid wasp family (767 ASVs) and Darwin wasp (642 ASVs). Our results are similar to other studies where Diptera was also reported to be less diverse in urban areas (Mulieri et al., 2011; Theodorou et al., 2020), with similar changes also in Coleoptera and Lepidoptera (Bergerot et al., 2010; Fenoglio et al., 2020).

Urban areas cover a much smaller area of the land than farmland, both in our study region and in many other countries. Urbanisation as a process of sprawling cities with effects on land cover change, fragmentation, temperature and soil sealing, however, continues across the globe and is therefore an increasingly important threat (Grimm et al., 2008; Pickett et al., 2011). In contrast to our previous study, we found no evidence for an effect of farmland cover on biomass with an additional sampling year; however, the effect found in our previous study was weaker and more sensitive to analytical decisions than the effect of urban cover (Svenningsen et al., 2022).

By expanding the InsectMobile study with an extra sampling year and new biodiversity metrics, we have stronger evidence that increasing urban cover has a pronounced negative effect on not only flying insect biomass but also on insect richness. Changes in arthropod biomass, abundance and community composition may result in substantial effects on complex food networks (Faeth et al., 2005) and ecosystem functions and services (Losey & Vaughan, 2006; Shochat et al., 2006; Turrini et al., 2016). For instance, this could result in an impoverished pollination service (Grimm et al., 2008; Harrison & Winfree, 2015; Miles et al., 2019) and loss of food for insectivorous birds (Bowler et al., 2019; Grames et al., 2023). A thorough knowledge of the consequences of urbanisation on different taxonomic arthropod groups is essential to assist and motivate city planners, green space managers and citizens in protecting and improving urban biodiversity (Dearborn & Kark, 2010; Standish et al., 2013). We hope our findings contribute to a call for action for conservation and restoration of insect diversity, not only in natural and agricultural areas but also in urban areas, to fulfil the 2030 goals of the Global Biodiversity Framework.

#### AUTHOR CONTRIBUTIONS

**Cecilie S. Svenningsen:** Conceptualization; writing – original draft; data curation; formal analysis; visualization; project administration. **Birte Peters:** Formal analysis; writing – original draft; conceptualization. **Diana E. Bowler:** Formal analysis; visualization; writing – original

draft; supervision; conceptualization. **Robert R. Dunn:** Writing – review and editing; conceptualization. **Aletta Bonn:** Writing – review and editing; conceptualization; supervision. **Anders P. Tøttrup:** Conceptualization; writing – review and editing; project administration; funding acquisition; supervision.

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#### CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

#### DATA AVAILABILITY STATEMENT

The code and data that support the findings of this study are available in the Zenodo database at <https://zenodo.org/record/8420450>.

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## SUPPORTING INFORMATION

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

**Appendix S1.** Supporting Information.

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