Urbanisation-driven homogenisation is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects

Running title Homogenisation of urban butterflies and moths

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Abstract

Aim We test whether urbanisation drives biotic homogenisation. We hypothesise that declines in abundance and species diversity of aerial insects are exacerbated by the urbanisation-driven loss of species with low habitat generalism, mobility and warm-adaptedness. We predict this homogenisation to be more pronounced for nocturnal taxa, and at wider scales for mobile taxa.

Location Belgium

Time period Summers 2014-2015

Major taxa studied Lepidoptera

Methods We compare communities along urbanisation gradients using a shared, replicated and nested sampling design, in which butterflies were counted within 81 grassland and macro-moths light-trapped in 12 woodland sites. We quantify taxonomic and functional community composition, the latter via community-weighted means and variation of species-specific traits related to specialisation, mobility and thermophily. Using linear regression models, variables are analysed in relation to site-specific urbanisation values quantified at seven scales (50-3200 m radii). At best-fitting scales, we test for taxonomic homogenisation.

Results With increasing urbanisation, abundance, species richness and Shannon diversity severely declined, with butterfly and macro-moth declines due to local- versus landscape-scale urbanisation (200 vs. 800-3200 m radii, respectively). While taxonomic homogenisation was absent for butterflies, urban macro-moth communities displayed higher nestedness than non-urban communities. Overall, communities showed mean shifts towards generalist, mobile and thermophilous species, displaying trait convergence too. These functional trait models consistently fit best with urbanisation quantified at local scales (100-200 m radii) for butterfly communities, and at local to wider landscape scales (200-800 m radii) for macro-moth communities.

Main conclusions Urban communities display functional homogenisation which follows urbanisation at scales linked to taxon-specific mobility. Light pollution may explain why homogenisation was more pronounced for the nocturnal taxon. We discuss that urbanisation is likely to impact flying insect communities across the globe, but also that impacts on their ecosystem functions and services could be mitigated via multi-scale implementation of urban green infrastructure.

Keywords: artificial light at night (ALAN), biotic homogenisation, butterflies, community filtering, dispersal ability, habitat specialisation, macro-moths, thermophily, urban ecology, urban green infrastructure

Introduction

Urbanisation is a prominent case of human-induced rapid environmental change, with our planet currently urbanizing rapidly (Seto, Güneralp, & Hutyra, 2012). Not only are towns and cities typified by extensive loss and fragmentation of (semi)natural habitats, they are also characterised by higher ambient temperatures (i.e. the urban-heat-island (UHI) effect) and higher levels of artificial light at night (ALAN) than surrounding rural and natural areas (Parris, 2016). These effects of habitat fragmentation, UHI, and ALAN get stronger with increasing built-up cover (BUC) (Sutton, 2003; Merckx, Souffreau et al., 2018).

Urbanisation's effect of habitat fragmentation *sensu lato* is known to induce biodiversity loss and biotic homogenisation (McKinney, 2006), the process by which regional biotas become more similar over time (McKinney & Lockwood, 1999; Olden, Comte, & Giam, 2016; Olden, Comte, & Giam, 2018). Often, homogenisation involves more than the random loss of species (i.e. taxonomic homogenisation), with functional homogenisation happening when species invasions and extinctions are related to intrinsic life-history traits (Villéger, Grenouillet, & Brosse, 2014). Indeed, the relationship between change in taxonomic and functional similarity appears to be governed by trait redundancy (Baiser & Lockwood, 2011; Sonnier, Johnson, Amatangelo, Rogers, & Waller, 2014). Hence, functional homogenisation reflects a convergence of biotas over time associated with the establishment of species with similar functional 'roles' in the ecosystem (Olden, Poff, Douglas, Douglas, & Fausch, 2004).

An enhanced focus on understanding the patterns and drivers of functional homogenisation is needed (Olden et al., 2018). Within the context of urbanisation, functional homogenisation is set to favour generalist species due to a severe reduction in the types of habitat resources on offer within urbanised settings (Devictor, Julliard, Couvet, Lee, & Jiguet, 2007; Lizée, Mauffrey, Taton, & Deschamps-Cottin, 2011; Deguines, Julliard, Flores, & Fontaine, 2016; Knop, 2016). Moreover, the fragmentation *sensu stricto* of the remaining habitat types is expected to filter against low-mobility species (Sattler, Duelli, Obrist, Arlettaz, & Moretti, 2010; Rochat, Manel, Deschamps-Cottin, Widmer, & Joost, 2017), since mobility mitigates reduced resource connectivity (Parris, 2016; Cote et al., 2017). For instance, local filtering on traits known to covary with increased dispersal has been demonstrated for urban communities of vascular plants, carabid beetles and macro-moths (Concepción, Moretti, Altermatt, Nobis, & Obrist, 2015; Piano et al., 2017; Merckx, Kaiser, & Van Dyck, 2018). Additionally, the UHI-effect is expected to favour thermophilic, warm-adapted species, a process already observed for zooplankton and beetle communities (Brans, Govaert et al., 2017; Piano et al., 2017).

Here, we test for such urbanisation-driven biotic homogenisation, both taxonomically and functionally, by comparing communities of both butterflies and moths (Lepidoptera) along urbanisation gradients, in the first combined study of both groups, using a shared, replicated and nested sampling design. Specifically, we expect a loss of species that we predict to be vulnerable to urbanisation due to their low habitat generalism, mobility and warm-adaptedness. We expect such losses to exacerbate more general declines in abundance, species richness and Shannon diversity of both groups, which are known to be susceptible indeed to urbanisation (McGeoch, & Chown, 1997; Bates et al., 2014; Ramírez-Restrepo, & MacGregor-Fors, 2017).

Lepidoptera are one of the four most species-rich insect orders and are considered to be indicators for other flying insect groups (Merckx, Huertas, Basset, & Thomas, 2013). They are geographically widespread, occurring abundantly in all terrestrial ecosystems except glaciated and desert habitats. Given their abundance, they play important functional roles as prey items in food webs, as pollinators in diurnal and nocturnal pollination networks, and as herbivores in nutrient cycling (Merckx et al., 2013; van Langevelde et al., 2018), with population declines hence likely impacting ecosystem function (Noriega et al., 2018).

Our multi-scale (seven scales: 50-3200 m radii) analysis approach allows us to pin-point the spatial scales at which these homogenisation processes are happening. Although we predict homogenisation to affect both butterflies and macro-moths, we predict that homogenisation will be more pronounced for the nocturnal macro-moths than for the diurnal butterflies as ALAN is highly correlated with urbanisation (Sutton, 2003) and as nocturnally

active moth species have been shown to display stronger negative population trends than diurnal moth species in The Netherlands, which is affected by ALAN at a country-wide scale (van Langevelde et al., 2018). Also, we predict that homogenisation will be pronounced at larger spatial scales for macro-moths than for butterflies. This prediction follows from observations that –despite large variation among species– the macro-moth taxon appears to be on average more mobile than the butterfly taxon. While the majority of butterfly species are (relatively) sedentary (e.g. median dispersal ability of 145 Northwest European butterflies is 3 on a 1–9 scale from highly sedentary to highly mobile: Bink, 1992), a majority of common macro-moth species routinely perform wider landscape-scale movements (Nieminen, Rita, & Uuvana, 1999; Ricketts, Daily, Ehrlich, & Fay, 2001; Summerville & Crist, 2004; Merckx et al., 2009; Merckx et al., 2010; Betzholtz & Franzén, 2013; Slade et al., 2013) and can be labelled as mobile (Potocký, Bartoňová, Beneš, Zapletal, & Konvička, 2018). For instance, using a tethered flight technique, the large majority of all 24 tested common noctuid species covered mean overnight distances of several kilometres (Jones, Lim, Bell, Hill, & Chapman, 2016).

At the proximate level, there are fundamental differences among diurnal butterflies and nocturnal moths relative to their thermal strategies, with consequences for their flight performance under different environmental conditions. Butterflies are ectothermic, which means that the major heat source to reach high body temperatures necessary for flight is external (Wickman, 2009). Hence, their flight performance (e.g. flight distance) can be strongly limited by ambient temperature, but also by wind chill and irradiation levels (Merckx, Van Dongen, Matthysen, & Van Dyck, 2008; Wickman, 2009). Nocturnal moths, on the other hand, do not rely on basking in the sun, but produce high body temperatures for flight in an endothermic way through their metabolism (Heinrich, 1974). Hence, we envisage the best-fitting models to occupy a range of smaller scales for butterflies than for macro-moths.

Material & Methods

Sampling design

Study sites – Sampling followed a nested design wherein a local urbanization gradient was repeatedly sampled within landscapes that also differed in urbanisation degree. Butterflies were sampled in grassland habitat from 81 local-scale subplots (200x200 m) located within 27 landscape-scale plots (3x3 km) situated within a study area of 8140 km² in northern Belgium. Woodland habitat within a subset of these plots was repeatedly sampled for macro-moths: twelve subplots within six plots (Fig. 1). At the start of 2018, the average human population density of this urbanised area amounted to 700 inhabitants/km², with cities and urban sprawl embedded within an agricultural and seminatural matrix (IBZ, 2018). As a proxy for urbanisation degree we used BUC, which was assessed using a vectorial layer with the precise contours of all buildings in a GIS, excluding roads and car parks (LRD, 2013). Given that only buildings are considered, 15% BUC can be considered highly urbanised. The location of the plots was established by moving them over this vectorial layer until their BUC-value fitted well with one of the three urbanisation classes, while making sure that the plots were more or less evenly spread out, and at the same time avoiding a clumped configuration for plots belonging to identical urbanisation classes. For butterflies, one urban (BUC>15%), one semi-urban (5%<BUC<10%) and one non-urban (BUC<3%) subplot was chosen within each of the nine urban (BUC>15%), nine semi-urban (5%<BUC<10%) and nine non-urban (BUC<3%) plots, and this randomly from the pool of subplots that contained grassland habitat patches. For macro-moths, one urban and one non-urban subplot were chosen within three urban and three non-urban plots, and this randomly from the pool of subplots that contained woodland patches. This nested design for both taxa allowed sampling a similar number of samples from each subplot category nested within each plot category, so that samples displayed a good spread of urbanisation values at both local and landscape scales. For increased precision in the data analysis we then moved away from having BUC as a class variable and instead quantified BUC as a continuous variable at seven spatial scales, namely at 50, 100, 200, 400, 800, 1600, and 3200 m radii around the sampling sites (Fig. 1). The nested design meant that BUC-values at small scales were not correlated with values at large scales, hence allowing to pinpoint the scale at which the effects of urbanisation are most pronounced.

Species sampling – Butterflies were sampled within 81 subplots by means of visual counts. For each subplot, this was done for 20 minutes while walking at slow pace through grassland habitat, with the occasional netting of

individuals to double-check species identifications. Sampling only took place when weather conditions allowed butterfly flight activity: sunny and non-windy conditions above 17°C (i.e. ‘Pollard walk’: Pollard, 1977). Two experienced researchers (TM and Aurélien Kaiser) sampled simultaneously –in different subplots– so that up to 18 subplots were sampled daily. In total, each subplot was sampled on three occasions between July and early September 2014. This resulted in 4413 individual observations; which belonged to 23 butterfly species. Macro-moths were sampled within twelve subplots (see above) by means of full-night light-trapping with one Heath trap (6W actinic) per subplot. Each of these twelve sites was sampled eleven times during a total of 33 trap nights from August till early September 2014 and in April, July and August 2015. Trapping was only performed during nights with suitable weather conditions for moth flight activity (Merckx, Marini, Feber, & Macdonald, 2012), and always involved simultaneous trapping at four sites from different plot/subplot categories. The identification of the within-trap samples during early mornings consistently reached species-level, except for the *Hoplodrina* and *Mesapamea* species complexes. All sampling and identifications were done by the same experienced researcher (TM). In total, 3067 individuals belonging to 202 macro-moth species were sampled.

Community-weighted variables

While we quantified taxonomic community composition using three key variables –abundance (N), species richness (S), and Shannon diversity (H)– functional community composition was quantified via two approaches: community-weighted means (CWM) and variation (standard deviation; SD) of a series of species-specific traits related to resource use specialisation, mobility and thermophily. These traits were scored for each species based on scientific literature and distribution data (see Table S1.1 in Supporting Information). Because our sampling involved species-specific count data, we opted for abundance-weighted CWMs, which for a given site are calculated as the average of species-specific trait values weighted by species abundances. This approach is indicative of functional dominance and summarizes shifts in mean trait values within communities due to environmental selection for certain traits. It allows measuring the rate of change in community composition based on community indices (sensu the community temperature index: Devictor, Julliard, Jiguet, & Couvet, 2008). Here, we use it to measure the rate of change in community composition for a given trait in response to urbanisation, as the CWM-indices reflect the relative composition of species in local communities regarding species-specific traits. On the other hand, our complementary SD-approach is a presence/absence-weighted approach and indicative of functional diversity, revealing patterns of trait convergence or divergence compared to a random expectation.

Statistical analyses

N, S and H variables as well as CWMs and SDs of samples were all separately analysed as dependent variables – and each time separately so for butterflies and macro-moths– in relation to site-specific urbanisation (BUC) values (i.e. the independent variable) using mixed effect linear regression models (R-package lme4). For each model, the plot identifier (i.e. 27 classes) was consistently used as a random variable to account for potential spatial autocorrelation among sites belonging to the same landscape-scale plot. While the BUC variable was never transformed, we applied a transformation ($\log x + 1$) of dependent variables only in those instances where such a transformation was necessary for the residual plot to reach a homogeneous distribution (three instances only: $N_{\text{butterflies}}$, $N_{\text{macro-moths}}$ and $S_{\text{macro-moths}}$). For each dependent variable we followed a multi-scale approach, in which we separately ran models with BUC-values quantified at seven different spatial scales (50-3200 m radii). This approach allowed us to identify the spatial scale with the best-fitting model (best on AICc) for each response variable (Burnham & Anderson, 2003; R-package AICcmodavg). Next, P-values for the independent variable (BUC) of these best-fitting models were obtained using likelihood-ratio tests of nested models that were fitted with maximum-likelihood and parameter estimates from restricted maximum-likelihood models. Visual inspection of the residual plots always indicated good model fit.

We tested for taxonomic homogenisation by assessing differences in beta-diversity levels of non-urban and urban communities, and this at the best-fitting spatial scale, separately for butterflies and macro-moths. Beta-diversity was measured as the average dissimilarity from individual communities to their group centroid in multivariate space, using the turnover and nestedness partitions of the abundance-based Bray-Curtis dissimilarity measure (Anderson, Ellingsen, & McArdle, 2006; Baselga, 2010; R-packages betapart and vegan). Using ANOVA, we tested for statistically significant differences between non-urban and urban communities. All analyses were performed using R version 3.2.3 (R, 2015).

186

187 Results

188 Taxonomic homogenisation

189 Abundance, species richness and Shannon diversity declined with increasing urbanisation, both for butterflies
190 and macro-moths (Table 1; Fig. 2). When contrasting sites that differed by 25% BUC, the modelled extent of these
191 declines –based on the modelled intercept and slope and at the spatial scale of the best-fitting model– amounted
192 to -84% in abundance, -59% in species richness and -26% in diversity of butterflies. Moth declines were even
193 more pronounced, and amounted to -89% in abundance, -82% in richness and -43% in diversity. While the
194 butterfly models had their best fit when urbanisation was quantified locally (i.e. within a 200 m radius around
195 the centre of the sampling sites), and this consistently for the three variables, best fits appeared with
196 urbanisation quantified at the landscape scale for moths: 3200 m (for N and S) and 800 m radii (for H) around
197 the light-trap sites (Table 1; Fig. 2).

198 Both overall beta-diversity, as well as its turnover and nestedness components, were contrasted between non-
199 urban and urban communities, with urbanisation being quantified at these most relevant spatial scales. For
200 butterflies, all communities characterised by a <1% BUC at the 200 m radius scale (i.e. 19 non-urban sites) were
201 contrasted with a similar amount of the most urban communities (i.e. 19 sites with >14% BUC at the 200 m radius
202 scale); alpha-diversity (mean $\pm$ SE): 10.3 $\pm$ 0.4 vs. 5.0 $\pm$ 0.6 species; gamma-diversity: 23 vs. 18 species,
203 respectively. These urban and non-urban communities differed neither in overall beta-diversity ($F_{1,36} = 0.41$; $P =$
204 0.53) nor in turnover and nestedness ($F_{1,24} = 0.30$; $P = 0.59$; $F_{1,24} = 1.35$; $P = 0.26$, respectively). For macro-moths,
205 all six communities from non-urban sites were contrasted with the six urban communities (i.e. <3.5% vs. >7%
206 BUC at the 800 m radius scale); alpha-diversity (mean $\pm$ SE): 79.3 $\pm$ 6.4 vs. 36.7 $\pm$ 7.9 species; gamma-diversity:
207 191 vs. 102 species, respectively. While urban and non-urban communities did not differ in overall beta-diversity
208 ($F_{1,10} = 0.09$; $P = 0.78$), urban communities tended to display lower turnover and displayed higher levels of
209 nestedness than non-urban ones ($F_{1,10} = 3.63$; $P = 0.086$; $F_{1,10} = 6.92$; $P = 0.025$, respectively).

210 Functional homogenisation

211 Overall, butterfly and macro-moth communities consisted on average of species characterized by lower habitat
212 resource specialisation with increasing urbanisation of the surroundings. They also displayed trait convergence
213 with increasing urbanisation, due to the observed lower variance in specialisation overall (Table 1; Fig. 3).
214 Although there was no shift in CWM host plant specialisation, a lower variance for this trait was present with
215 increasing urbanisation in butterfly communities. Moth communities on the other hand displayed both a
216 reduction in CWM host plant specialisation and trait convergence. In other words, they displayed a canalised
217 shift towards more polyphagous species. Also, with increasing urbanisation, both butterfly and moth
218 communities showed shifts towards species that on average occur in a larger set of habitat types and that are
219 more regionally widespread. These shifts in mean trait values are indicative of reduced specialisation (Table 1;
220 Fig. 3).

221 Urbanisation also led to community-wide shifts in mobility for butterflies and macro-moths, showing a pattern
222 of dominance of mobile species with increasing urbanization (Table 1; Fig. 4). A comparison in CWM mobility for
223 the direct species-specific mobility measure between sites differing by 25% BUC in their surroundings, revealed
224 that urban communities are on average 23% and 66% more mobile than non-urban communities, for butterflies
225 and macro-moths, respectively. This difference in the extent of the effect between both taxa was also reflected
226 in wing length, which is a proxy of mobility in Lepidoptera (Nieminen et al., 1999; Sekar, 2012; Slade et al., 2013).
227 CWM forewing length was 7% larger for butterfly communities at urban than at non-urban sites (25% versus 0%
228 BUC, respectively), while CWM wingspan was 21% larger in urban than in non-urban moth communities. For
229 moths, this shift in mean wingspan was accompanied by trait convergence: urban communities are characterised
230 by smaller variance in wing span than non-urban ones. For butterflies, there was a trend for a similar trait
231 convergence, and this at the 200 m radius scale ($F_{1,75.29} = 3.54$; $P = 0.064$) (Table 1; Fig. 4).

Regarding thermophily, we show that urban communities became increasingly dominated by heat-tolerant butterfly species, with this shift in mean trait value accompanied by trait divergence. Also, urban butterfly and moth communities became increasingly dominated by species that typically occur in more open habitat types (Table 1; Fig. 5).

In line with the results on abundance, species richness and Shannon diversity, the models for the functional traits consistently had their best fit when urbanisation was quantified at local scales (100-200 m radii) for butterfly communities, while their best fit occurred at local to landscape scales (200-800 m radii) for macro-moth communities (Table 1).

Discussion

In line with the urbanisation-driven biotic homogenisation hypothesis, and having used a replicated and nested sampling design, we demonstrate severe declines in overall abundance, species richness and Shannon diversity of Lepidoptera with increasing urbanisation around sample sites. These declines appear to be exacerbated by the loss of specialist, sedentary and non-thermophilic species, leading to trait convergence and shifts in CWMs of related functional traits. Additionally, when contrasting non-urban with urban communities, we show that urban macro-moth communities are not only characterised by lower alpha- and gamma-diversity, but also display higher nestedness and lower turnover. For butterfly communities, however, such beta-diversity differences were absent, with urban communities only displaying reduced alpha- and gamma-diversity. As a result, we show that while urban butterfly communities are functionally homogenised, urban macro-moth communities are both taxonomically and functionally homogenised. Such effects are poorly known for invertebrate groups (Olden et al. 2016; Olden et al., 2018), but there are well-known studies for plant and vertebrate communities (e.g. La Sorte, McKinney, & Pyšek, 2007; Luck & Smallbone, 2011; Morelli et al., 2016). As predicted, the homogenisation of the on average more mobile macro-moth communities was more pronounced at larger scales (200-3200 m radii) compared to the relatively less-mobile butterfly communities, which indeed responded to urbanisation in the local surroundings (100-200 m radii) only. Additionally, although the butterfly community homogenisation was clearly pronounced, homogenisation was even stronger for the nocturnal macro-moth communities.

Biotic homogenisation due to urbanisation is typically pronounced as urbanisation globally involves rapid and marked environmental changes for biota (Parris, 2016). Not only are the impacts on the environment strong, they are also predictable as urbanisation involves sets of similar drivers and stressors all over the world (Niemelä, 2011). Hence, it should be possible to predict which types of species are likely to 'win' and 'lose' during the urban environmental filtering process (McKinney & Lockwood, 1999; McKinney, 2008). In particular, towns and cities are novel ecosystems characterised by extensive loss and fragmentation of (semi)natural habitat types, man-induced disturbance regimes leading to swift spatial turnover of early successional habitats, high densities of man-made structures and impervious surfaces with strong heat-retaining abilities, few resource types at elevated levels, and high pollution levels (Hobbs et al., 2006; Niemelä, 2011; Aronson et al., 2014; Parris, 2016). Their combined impact is known to induce biodiversity loss and biotic homogenisation (e.g. Casner et al., 2014), favouring generalist species (Lizée et al., 2011; Knop, 2016).

One aspect of this generalisation process is the decline of rare native species with restricted regional distributions (Kühn & Klotz, 2006). For instance, butterfly sampling in and around Boston, Massachusetts, USA, showed that while increased urbanization is associated with decreased butterfly species richness, regionally rare and specialized butterflies are most affected, disappearing 2.9–4.5 times faster than ubiquitous and generalist species (Clark, Reed, & Chew, 2007). Simultaneously, the fragmentation of the remaining habitat types is expected to filter for mobile species (Sattler et al., 2010; Piano et al., 2017; Rochat et al., 2017). For instance, it has been shown for butterflies that the increased costs associated with investment in higher dispersal ability eventually result in enhanced chances of survival in urban environments (Wood & Pullin, 2002; Rochat et al., 2007; Olivier, Schmucki, Fontaine, Villemey, & Archaux, 2016). Moreover, the UHI-effect is expected to favour thermophilic, warm-adapted species (Brans, Govaert et al., 2017; Piano et al., 2017), though adaptive thermal evolution to urbanization happens intra-specifically too (Brans, Jansen et al., 2017). For instance, when exposed to high limiting temperatures, leaf-cutter ants from urban Sao Paulo colonies took about 20% longer to lose mobility than did those from rural colonies (Angilletta et al., 2007). At the community level, ant species

assemblages in more open and hence warmer urban environments of Raleigh, North Carolina, are disproportionately characterised by warmer (0.5–1 °C) and drier (10–20 mm) distribution ranges within North America. This finding illustrates that their natural climatic range may predispose species to thrive in urban settings, while cities may accelerate climate change driven range shifts of species pre-adapted to the urban landscape (Menke et al., 2011). Here, we show functional responses in line with all three these drivers: urban communities of Lepidoptera become increasingly dominated by generalist species (in casu polyphagous species, habitat generalists and regionally ubiquitous species), thermophilic species (in casu species that are heat-tolerant and that prefer open habitat types) and mobile species.

The pattern of dominance of mobile species with increasing urbanization is a result fully in line with recent findings on body-size shifts due to urbanisation (Merckx, Souffreau et al., 2018). This multi-taxa study showed that butterfly and macro-moth communities become increasingly dominated by larger species with urbanisation. The body-size shift was interpreted as a shift towards increased mobility since body size is positively linked to mobility in Lepidoptera (Nieminen et al., 1999; Sekar, 2012; Stevens et al., 2012; Slade et al., 2013). Rather than by the UHI-effect which would have caused shifts towards smaller body size for metabolic reasons (Merckx, Souffreau et al., 2018), the body size of the urban communities of butterflies and moths appeared indeed shaped mainly by the high degree of habitat fragmentation. It is obvious that the typically severe fragmentation of ecological resources in urban settings constitutes an effective filter on mobility, so that mainly the more mobile species are retained within urban communities (Sattler et al., 2010). Moreover, urbanized sites have lower relative humidity (e.g. Kaiser et al., 2016) and pose increased desiccation risks. In turn, the insect's water balance can be important for continuous flight under warm and dry anthropogenic conditions (Chown, Sørensen, & Terblanche, 2011).

For animal groups where being mobile means being large, as is the case for Lepidoptera, urban fragmentation hence results in shifts towards increased body size, as the mobile, larger-sized species will have a less difficult time dealing with the low functional connectivity typical for urban areas. Here, we provide evidence for this explanation, not only via the proxy measure of wing length, but now also via direct estimates of species-specific mobility. In line with the proxy measure, the direct mobility measure too points towards urban communities that are more mobile than non-urban ones. For instance, macro-moth communities from urban sites with a 25% BUC in the surrounding 800 m radius consist of species that on average move a net distance of 326 m/week, compared to only 196 m/week in non-urban communities. This translates into a 66% increase in mobility.

While homogenisation was present for both butterflies and macro-moths, it was clearly more pronounced in the latter. Although butterflies are merely one small group, phylogenetically placed in between several other groups of macro-moths and Lepidoptera (Mutanen, Wahlberg, & Kaila, 2010), a salient characteristic of nearly all butterflies is that they are active during the day, whereas most macro-moths are nocturnal. Here, all sampled butterfly species are diurnal and all sampled macro-moth species are nocturnal given the latter were all sampled with light-traps at nights. Hence, it is possible that this characteristic, which sets the studied groups of macro-moths and butterflies apart, explains the stronger effects for macro-moths. Indeed, apart from habitat loss, fragmentation and the UHI-effect, urbanisation is also strongly associated with ALAN (Sutton, 2003; Bennie, Duffy, Davies, Correa-Cano, & Gaston, 2015). Because ALAN disrupts the perception of circadian cycles of darkness and light, it has been shown to strongly affect both diurnal and nocturnal organisms as they all evolved responses to these cycles (Gaston, Bennie, Davies, & Hopkins, 2013). Consequently, ALAN could be an important driver of global environmental change as its ecological impacts –though largely overlooked until recently– could be huge (Davies & Smyth, 2018; van Langevelde et al., 2018).

Nocturnal taxa are likely to be even more strongly affected. Indeed, many nocturnal moth species are well-known for their flight-to-light behaviour, which disrupts flight activity, hence impacting food and mate resource allocation. This mechanism could be one of the factors driving moth declines (Macgregor, Pocock, Fox, & Evans, 2015; Grubisic, van Grunsven, Kyba, Manfrin, & Hölker, 2018; Wilson et al., 2018), as the attraction to artificial light sources makes them lose valuable energy and/or time and is often fatal. Individuals either remain inactive for nights on end, often under a high predation risk due to forced settling on substrates not conducive to their camouflaged wing patterns, or fly around the light source till exhaustion or predation by insectivores lured to these light sources (Macgregor et al., 2015). Also, the typically sophisticated behaviours that moths have evolved to escape or disrupt detection by bat sonars, appear reduced under artificial lighting (e.g. Wakefield, Stone, Jones, & Harris, 2015). Moreover, even low-intensity ALAN may affect the production and composition of female

sex pheromones as well as male attraction to them, disrupting adult reproductive behaviour of moths (Macgregor et al., 2015; van Geffen, Groot, et al., 2015; van Geffen, van Eck, et al., 2015), while larval life-histories and pupal diapause may be affected too, all impacting biological fitness (van Geffen, van Grunsven, van Ruijven, Berendse, & Veenendaal, 2014).

Because of these strong pressures on survival and reproduction, rapid evolutionary adaptations to ALAN are to be expected. So far, this has been demonstrated for one ermine moth species, where offspring from urban, light-polluted populations displayed reduced flight-to-light behaviour compared with offspring from pristine populations (Altermatt, & Ebert, 2016). Although such evolutionary reduced attraction to light sources may hence directly increase survival and reproduction, the authors anticipated that it comes with reduced mobility, negatively affecting foraging and thus indirectly their role in pollination too. ALAN's direct effects on moths are indeed expected to trigger cascading impacts on ecosystem functioning, for instance with disrupted nocturnal pollination networks –as moths are globally important pollinators– causing negative consequences for plant reproductive success (Macgregor, Evans, Fox, & Pocock, 2017; Knop et al., 2017; Borges, 2018; Macgregor, Pocock, Fox, & Evans, 2019).

As sky glow reduces sampling efficiency of light-traps (Bowden, 1982), we opted to consistently sample in woodland habitat because these relatively dark environments shield traps to a large extent from sky glow (Merckx & Slade, 2014). Nevertheless, since this shielding may not be complete, the urbanisation effects we here show for moth abundance, richness and diversity might be slightly overestimated, at least if attraction efficiency of the light-traps would have been reduced in the urban settings. However, this would not have affected the functional homogenisation measures as these are based on a community-weighted means approach. At the same time, it is likely that our findings for these relatively dark habitats are conservative compared to more open habitats, such as grasslands, where light pollution is much more pronounced. But then again, the macro-moth taxon is mobile, with individuals often moving at the landscape scale (Slade et al., 2013; Jones et al., 2016), which means that individuals from urban settings –even when sampled at relatively dark sites– typically will have been exposed to more light-polluted conditions than non-urban individuals.

Since our planet is urbanizing rapidly with associated environmental change that is both profound and predictable (Niemelä, 2011; Seto et al., 2012), and since Lepidoptera are bio-indicators of other flying insect taxa (Merckx et al., 2013), the strong biotic homogenisation which we here observed for Lepidoptera in Belgium is a process that is likely to happen to aerial insect taxa in urbanised settings all over the world. Butterflies and moths occur in basically all terrestrial ecosystems, and given their abundance and diversity they play important functional roles as prey items in food webs, as pollinators in diurnal and nocturnal pollination networks, and as herbivores in nutrient cycling (Merckx et al., 2013; van Langevelde et al., 2018). Their severe biotic homogenisation as a response to urbanisation, and the impacts of urbanisation on other flying insect taxa, are hence likely to impact ecosystem function and ecosystem services provision in towns and cities across the globe (Noriega et al., 2018).

Mitigation of these impacts is to be achieved via the provision of habitat resources, such as native host and nectar plants, within urban green infrastructure. As our multi-scale analysis allows to pin-point the spatial scales at which this homogenisation is happening, we suggest that management of green infrastructure is likely to be more effective for less-mobile taxa, such as butterflies, than for mobile taxa, such as macro-moths, when applied at the local scale only. Contrastingly, Lizée, Taton, & Deschamps-Cottin (2016) showed a dominant effect of landscape-scale features on urban species assemblages of butterflies within the Mediterranean metropolitan area of Marseille, although they also highlighted important co-variation of features from the local to the landscape scale in their interaction with the community structure of urban butterflies. Mitigation management should involve increasing both the spatial heterogeneity (Sattler et al., 2010) and the quantity and quality of green infrastructure within urbanised settings, for instance via insect-friendly, phased mowing regimes and via the replacement of exotic with native vegetation in urban parks (e.g. Čížek, Zámečník, Tropek, Kočárek, & Konvička, 2012; Mata et al., 2017; Threlfall et al., 2017; Buchholz, Hannig, Möller, & Schirmel, 2018). In case such management is to be scaled up over whole districts at a landscape scale, then such a multi-scale management is likely to benefit not only butterflies and other less-mobile taxa but also on average more mobile taxa, such as macro-moths (Merckx & Macdonald, 2015). Nonetheless, additional research is needed to balance human needs and perceptions with increased biodiversity and improved ecological processes within urban green infrastructure management plans (Aronson et al., 2017).

As the Earth is getting more and more urbanised, it is timely to understand current and future changes in community composition within urbanising regions, especially also in terms of ecosystem function and ecosystem services. For example, by both narrowing and synchronising the response diversity of communities, functional homogenisation could compromise the potential for buffering of ecosystems to disturbance (Olden et al., 2004). Moreover, studying these changes should ideally be done within the overarching framework of global climatic change, as both processes are likely to interact with one each other. For instance, city heat waves are predicted to intensify over the next decades due to the combination of the UHI-effect and global warming (Wouters et al. 2017).

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Biosketch

Thomas Merckx is a postdoctoral researcher focusing on ecology and evolution of Lepidoptera and their landscape-scale conservation, and this within various frameworks: ecotypic differentiation, agri-environment policy, rewilding and urbanization.

Hans Van Dyck is professor in behavioural ecology and conservation at UCLouvain, Belgium. He has a strong interest in both basic and applied ecology and evolution, with a particular emphasis on the study of animal behaviour and life-history traits in rapidly changing landscapes under multiple anthropogenic impacts.

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619

620 Data Accessibility Statement

621 A dataset containing the N, S and H variables as well as CWMs and SDs of butterfly and macro-moth samples,
622 and their respective site-specific urbanisation (BUC) values, is available at the public data depository DRYAD.

623

Table 1 Overview of mixed effect linear regression model output, showing the effect of urbanisation (BUC) on key variables related to taxonomic and functional community composition, both for the CWM and SD approach, and separately for butterflies and macro-moths. Taxonomic community composition was quantified using abundance (N), species richness (S), and species diversity (Shannon index H), while functional community composition was quantified using a series of species-specific trait variables related to resource use specialisation, mobility and thermophily (see Table S1.1 for an overview of these variables). Numbers at the start of each output refer to the spatial scale of this best-fitting model (built-up cover values were quantified at seven scales: 50-3200 m radii). Non-significant output is given as NS ($P \geq 0.05$), while output with an effect direction opposite the hypothesised direction is given in *italics* (one instance only). All other output is in line with the hypothesised directions.

BUTTERFLIES			MACRO-MOTHS	
TAXONOMIC HOMOGENISATION				
N	200: $F_{1,71.44} = 42.08$; $P < .0001$		3200: $F_{1,4.01} = 52.64$; $P = 0.0019$	
S	200: $F_{1,69.74} = 54.18$; $P < .0001$		3200: $F_{1,4.01} = 108.08$; $P = 0.0005$	
H	200: $F_{1,75.01} = 8.87$; $P = 0.0039$		800: $F_{1,5.22} = 55.81$; $P = 0.0006$	
FUNCTIONAL HOMOGENISATION	CWM	SD	CWM	SD
Specialisation				
Host plant specialisation	NS	100: $F_{1,60.35} = 11.47$; $P = 0.0013$	200: $F_{1,6.93} = 38.04$; $P = 0.0005$	400: $F_{1,7.41} = 35.67$; $P = 0.0004$
Habitat use generalism	100: $F_{1,63.29} = 7.08$; $P = 0.0099$	NS	200: $F_{1,6.47} = 21.88$; $P = 0.0028$	NS
Distribution	100: $F_{1,65.06} = 8.85$; $P = 0.0041$	NS	800: $F_{1,4.91} = 20.77$; $P = 0.0063$	NS
Mobility				
Mobility	200: $F_{1,71.50} = 19.10$; $P < .0001$	NS	800: $F_{1,4.60} = 17.81$; $P = 0.010$	NS
Wing length	100: $F_{1,59.56} = 7.53$; $P = 0.0080$	NS	800: $F_{1,4.60} = 16.84$; $P = 0.011$	200: $F_{1,6.98} = 6.19$; $P = 0.042$
Thermophily				
Heat tolerance	100: $F_{1,60.18} = 32.10$; $P < .0001$	100: $F_{1,58.40} = 4.72$; $P = 0.034$		
Habitat openness	100: $F_{1,61.92} = 6.19$; $P = 0.016$	NS	200: $F_{1,8.11} = 12.74$; $P = 0.0071$	NS
SCALE RANGE	100-200		200-3200

Fig. 1 Spatial sampling design of the butterfly and macro-moth sampling. Depiction of the nested sampling configuration of local-scale subplots within 27 landscape-scale sampling plots on an urbanisation background (CORINE Land Cover EEA) for northern Belgium (West-Europe; Esri). Urbanisation was quantified as built-up cover (BUC), assessed using a reference map with building contours (LRD, 2013). Urban (sub)plots are depicted in black/magenta ($BUC > 15\%$), semi-urban (sub)plots in grey/yellow ($5\% < BUC < 10\%$), and non-urban (sub)plots in white/green ($BUC < 3\%$). The nested design allowed sampling to cover urbanisation gradients at both the local and landscape scale. Three plots are enlarged and show the within-plot distribution of local subplot types. Urbanisation (BUC) was quantified for each sample site at seven spatial scales (50-3200 m radii), which on the zoom-in and map are depicted around the three sample sites of one non-urban plot. Remark that macro-moth sampling took place in urban and non-urban subplots of six south-eastern urban and non-urban plots only, which hence display up to five subplots each as macro-moth sampling sometimes happened in other subplots than those selected for the butterfly sampling.

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Fig. 2 Taxonomic community composition. Declines in abundance (N, top row), species richness (S, middle row) and species diversity (H, bottom row) for butterflies (left) and macro-moths (right) as a function of increasing urbanisation (BUC), with BUC-numbers referring to the spatial scale of these best-fitting models (BUC-values were quantified at seven scales: 50-3200 m radii). Necessary log-transformations of dependent variables to improve residual fits are indicated. Star symbols refer to P-values (** $P \leq 0.01$; *** $P \leq 0.001$). Butterfly (left) and macro-moth (right) silhouettes are from PhyloPic (<http://www.phylopic.org>) and fall under CC-BY 3.0 licences; credits: Gareth Monger.

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666 Fig. 3 Decline in CWM host plant specialisation (top row) and increase in both CWM habitat use generalism
 667 (middle row) and CWM distribution (bottom row) (see Table S1.1 for a description of these variables) for
 668 butterflies (left) and macro-moths (right) as a function of increasing urbanisation (BUC), with BUC-numbers
 669 referring to the spatial scale of these best-fitting models (BUC-values were quantified at seven scales: 50-3200
 670 m radii). Star symbols refer to P-values (ns $P > 0.10$; ** $P \leq 0.01$; *** $P \leq 0.001$). Image credits as in Fig. 2.

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Fig. 4 Increase in CWMs of mobility (top row) and wing length (bottom row) (see Table S1.1 for a description of these variables) for butterflies (left) and macro-moths (right) as a function of increasing urbanisation (BUC), with BUC-numbers referring to the spatial scale of these best-fitting models (BUC-values were quantified at seven scales: 50-3200 m radii). Star symbols refer to P-values (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$). Image credits as in Fig. 2.

Fig. 5 Increase in CWMs of heat tolerance (a) and habitat openness (c–d) (see Table S1.1 for a description of these variables) for butterflies (left) and macro-moths (right) as a function of increasing urbanisation (BUC), with BUC-numbers referring to the spatial scale of these best-fitting models (BUC-values were quantified at seven scales: 50–3200 m radii). Heat tolerance data are lacking for macro-moths. Star symbols refer to P-values (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$). Image credits as in Fig. 2.

Supporting Information: Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects

Table S1.1 Taxon-specific overview of the functional community composition variables related to resource use specialization, mobility and thermophily in Lepidoptera. The data source column specifies the sources based on which the species-specific traits were scored.

Taxon	Trait group	Trait	Description	Data source
BUTTERFLIES	Specialization	Host plant specialization	Species are classified on a scale of increasing larval host plant use specialization, from highly polyphagous to strictly monophagous (1: feeding on more than two plant families; 2: two families; 3: one family; 4: one genus; 5: one species) (<i>Gonepteryx rhamni</i> scored 3.5 as it feeds only on two species from the same family).	Bink, 1992
		Habitat use generalism	Species are classified on a scale of decreasing adult habitat use specialization, from specialist species occurring in three habitat types only (3) to generalist species occurring in eight habitat types (8).	Bink, 1992
		Distribution	Species are labelled according to the number of 5x5 km plots within Flanders and Brussels that contain observation records during the four-year period 2012-2015.	www.waarnemingenn.be
	Mobility	Mobility	Species are classified on a scale of increasing adult mobility, from highly sedentary species (1) to highly mobile species (9).	Bink, 1992
		Wing length	Mean forewing length (mm), from wing base till tip; means were used for species with sexual (<i>Papilio machaon</i> , <i>Maniola jurtina</i>) or seasonal (<i>Araschnia levana</i>) dimorphism.	Bink, 1992
	Thermophily	Heat tolerance	Species are classified on a scale (1-9) of increasing tolerance to temperature extremes.	Bink, 1992
		Habitat openness	Mean openness value for the range of habitat types used, from wooded to open habitat conditions (4-8).	Bink, 1992
MACRO-MOTHS	Specialization	Host plant specialization	Species are classified on a scale of increasing larval host plant use specialization, from polyphagous to monophagous (1: polyphagous, feeding on two or more plant families; 2: oligophagous, feeding on several genera within one family (or rarely on two host plant species from two families); 3: monophagous, feeding on one genus only).	Waring & Townsend, 2009; www.vlindernet.nl
		Habitat use generalism	Species are classified on a gradient scale of decreasing adult habitat use specialization, from specialist species occurring in a narrow habitat range (1), over species occurring in an average range of habitats (2), to generalist species occurring in a broad range of habitats (3).	Waring & Townsend, 2009; www.vlindernet.nl
		Distribution	Species are labelled according to the number of 5x5 km plots within Flanders and Brussels that contain observation records during the four-year period 2012-2015.	www.waarnemingenn.be
	Mobility	Mobility	Model-predicted mean distances (m) moved in seven days, calculated from the coefficients of a regression model with trait values wingspan, wing shape, adult feeding, larval feeding guild and forest affinity as predictive variables.	Slade et al., 2013
		Wing length	Mean wingspan (mm); means were used for species with seasonal or sexual dimorphism; for species with wingless females, wingspan refers to males only.	Manley, 2008
	Thermophily	Habitat openness	Species are classified on a scale of decreasing forest affinity (1: in woodlands only; 2: mainly in woodlands; 3: mainly in open biotopes).	Waring & Townsend, 2009; www.vlindernet.nl

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