Received: 24 September 2018 | Revised: 24 May 2019 | Accepted: 7 June 2019

DOI: 10.1111/geb.12969

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology WILEY

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

Thomas Merckx[1,2] | Hans Van Dyck[1]

[1]Behavioural Ecology and Conservation Group, Biodiversity Research Centre, Earth and Life Institute, UCLouvain, Louvain-La-Neuve, Belgium

[2]Department of Ecology and Genetics, University of Oulu, Oulu, Finland

Correspondence
Thomas Merckx, Department of Ecology and Genetics, University of Oulu, PO Box 3000, FI-90014 University of Oulu, Finland.
Email: th.merckx@gmail.com

Funding information
Federaal Wetenschapsbeleid, Grant/Award Number: IAP-grant P7/04

Editor: Nick Isaac

Abstract

Aim: We test whether urbanization drives biotic homogenization. We hypothesize that declines in abundance and species diversity of aerial insects are exacerbated by the urbanization-driven loss of species with low habitat generalism, mobility and warm-adaptedness. We predict this homogenization 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 urbanization 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 specialization, mobility and thermophily. Using linear regression models, variables are analysed in relation to site-specific urbanization values quantified at seven scales (50–3,200 m radii). At best-fitting scales, we test for taxonomic homogenization.

Results: With increasing urbanization, abundance, species richness and Shannon diversity severely declined, with butterfly and macro-moth declines due to local- versus landscape-scale urbanization (200 vs. 800–3,200 m radii, respectively). While taxonomic homogenization 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 urbanization 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 homogenization that follows urbanization at scales linked to taxon-specific mobility. Light pollution may explain why homogenization was more pronounced for the nocturnal taxon. We discuss that urbanization 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.

© 2019 John Wiley & Sons Ltd

KEYWORDS
ALAN, biotic homogenization, butterflies, community filtering, dispersal ability, habitat specialization, macro-moths, thermophily, urban ecology, urban green infrastructure

1 | INTRODUCTION

Urbanization 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 characterized 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) (Merckx, Souffreau, et al., 2018; Sutton, 2003).

Urbanization's effect of habitat fragmentation *sensu lato* is known to induce biodiversity loss and biotic homogenization (McKinney, 2006), the process by which regional biotas become more similar over time (McKinney & Lockwood, 1999; Olden, Comte, & Giam, 2016, 2018). Often, homogenization involves more than the random loss of species (i.e., taxonomic homogenization), with functional homogenization 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 homogenization 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 homogenization is needed (Olden et al., 2018). Within the context of urbanization, functional homogenization is set to favour generalist species due to a severe reduction in the types of habitat resources on offer within urbanized settings (Deguines, Julliard, Flores, & Fontaine, 2016; Devictor, Julliard, Couvet, Lee, & Jiguet, 2007; Knop, 2016; Lizée, Mauffrey, Tatoni, & Deschamps-Cottin, 2011). Moreover, the fragmentation *sensu stricto* of the remaining habitat types is expected to filter against low-mobility species (Rochat, Manel, Deschamps-Cottin, Widmer, & Joost, 2017; Sattler, Duelli, Obrist, Arlettaz, & Moretti, 2010), since mobility mitigates reduced resource connectivity (Cote et al., 2017; Parris, 2016). 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; Merckx, Kaiser, & Van Dyck, 2018; Piano et al., 2017). 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 urbanization-driven biotic homogenization, both taxonomically and functionally, by comparing communities of both butterflies and moths (Lepidoptera) along urbanization 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 urbanization 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 to urbanization (Bates et al., 2014; McGeoch & Chown, 1997; 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 (van Langevelde et al., 2018; Merckx et al., 2013), with population declines hence likely impacting ecosystem function (Noriega et al., 2018).

Our multi-scale (seven scales: 50–3,200 m radii) analysis approach allows us to pin-point the spatial scales at which these homogenization processes are happening. Although we predict homogenization to affect both butterflies and macro-moths, we predict that homogenization will be more pronounced for the nocturnal macro-moths than for the diurnal butterflies as ALAN is highly correlated with urbanization (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 homogenization 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 north-west 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 (Betzholtz & Franzén, 2013; Merckx et al., 2009, 2010; Nieminen, Rita, & Uuvana, 1999; Ricketts, Daily, Ehrlich, & Fay, 2001; Slade et al., 2013; Summerville & Crist, 2004) 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 not only 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.

2 | MATERIAL AND METHODS

2.1 | Sampling design

2.1.1 | Study sites

Sampling followed a nested design wherein a local urbanization gradient was repeatedly sampled within landscapes that also differed in urbanization degree. Butterflies were sampled in grassland habitat from 81 local-scale subplots (200 m × 200 m) located within 27 landscape-scale plots (3 km × 3 km) situated within a study area of 8,140 km^2 in northern Belgium. Woodland habitat within a subset of these plots was repeatedly sampled for macro-moths: twelve subplots within six plots (Figure 1). At the start of 2018, the average human population density of this urbanized area amounted to 700 inhabitants/km^2, with cities and urban sprawl embedded within an agricultural and semi-natural matrix (IBZ, 2018). As a proxy for urbanization 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 urbanized. 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 urbanization 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 urbanization 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 was carried out 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 was carried out randomly from the pool of subplots that contained woodland patches. This nested design for both taxa allowed sampling of a similar number of samples from each subplot category nested within each plot category, so that samples displayed a good spread of urbanization 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, 1,600 and 3,200 m radii around the sampling sites (Figure 1). The nested design meant that BUC values at small scales were not correlated with values at large scales, hence allowing us to pin-point the scale at which the effects of urbanization are most pronounced.

2.1.2 | Species sampling

Butterflies were sampled within 81 subplots by means of visual counts. For each subplot, this was done for 20 min 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 4,413 individual observations, which belonged to 23 butterfly species. Macro-moths were sampled within 12 subplots (see above) by means of full-night light-trapping with one Heath trap (6W actinic) per subplot. Each of these 12 sites was sampled 11 times during a total of 33 trap nights from August until 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, 3,067 individuals belonging to 202 macro-moth species were sampled.

2.2 | 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 (CWMs) and variation (standard deviation; *SD*) of a series of species-specific traits related to resource use specialization, mobility and thermophily. These traits were scored for each species based on scientific literature and distribution data (see Supporting Information Table S1.1). 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

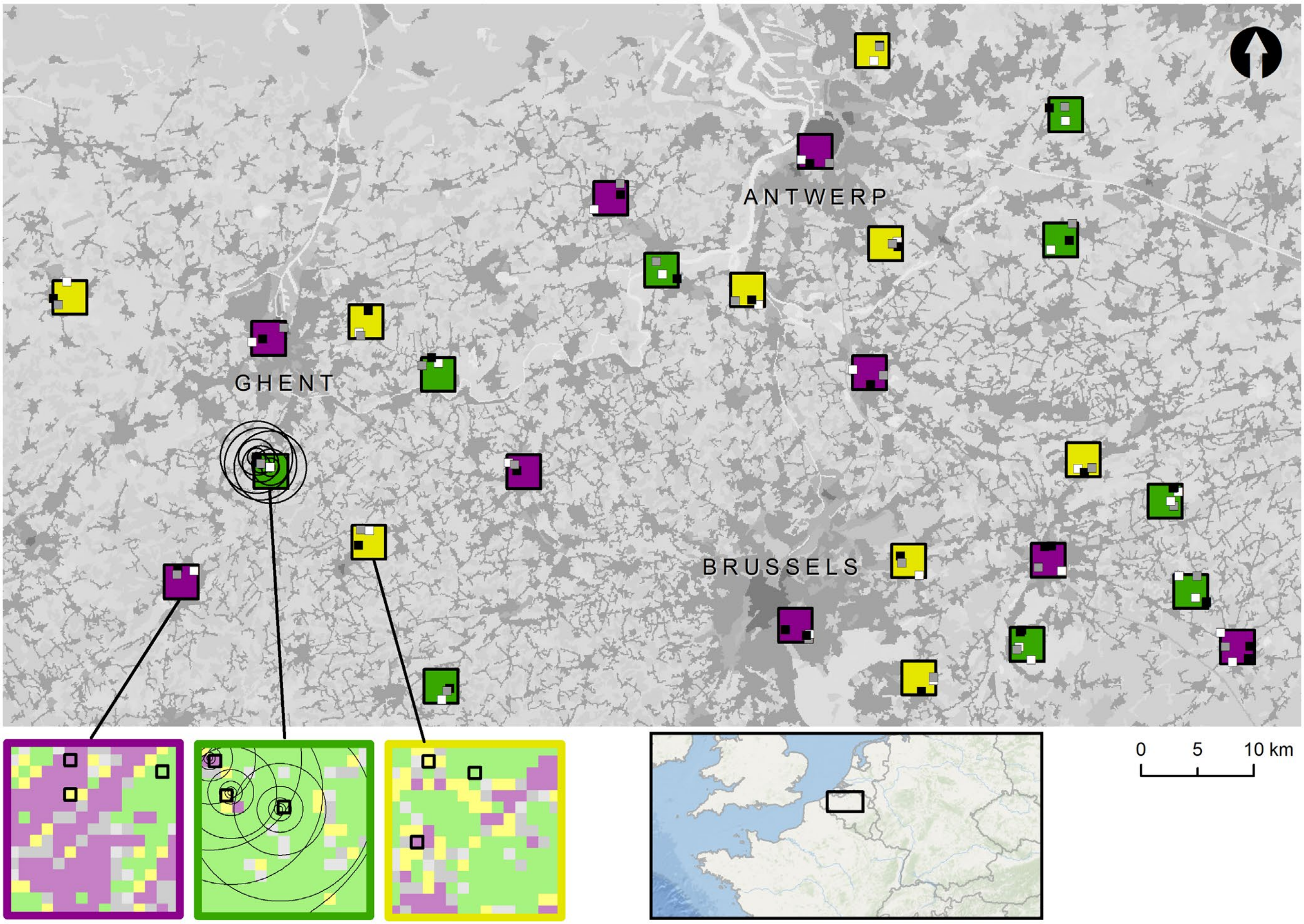

FIGURE 1 Spatial sampling design of the butterfly and macro-moth sampling. Depiction of the nested sampling configuration of local-scale subplots within 27 landscape-scale sampling plots on an urbanization background (CORINE Land Cover European Environment Agency) for northern Belgium (west Europe; Esri, Redlands, California). Urbanization 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 urbanization gradients at both the local and landscape scale. Three plots are enlarged and show the within-plot distribution of local subplot types. Urbanization (BUC) was quantified for each sample site at seven spatial scales (50–3,200 m radii), which on the zoom-in and map are depicted around the three sample sites of one non-urban plot. Note 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

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 urbanization, 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.

2.3 | Statistical analyses

N, *S* and *H* variables as well as CWMs and *SD*s of samples were all separately analysed as dependent variables—and each time separately so for butterflies and macro-moths—in relation to site-specific urbanization (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 (50–3,200 m radii). This approach allowed us to identify the spatial scale with the best-fitting model [best on corrected Akaike information criterion (AICc)] for each response variable (Burnham & Anderson, 2004; 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 homogenization 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.

3 | RESULTS

3.1 | Taxonomic homogenization

Abundance, species richness and Shannon diversity declined with increasing urbanization, both for butterflies and macro-moths (Table 1; Figure 2). When contrasting sites that differed by 25% BUC, the modelled extent of these declines—based on the modelled intercept and slope and at the spatial scale of the best-fitting model—amounted to −84% in abundance, −59% in species richness and −26% in diversity of butterflies. Moth declines were even more pronounced, and amounted to −89% in abundance, −82% in richness and −43% in diversity. While the butterfly models had their best fit when urbanization was quantified locally (i.e., within a 200 m radius around the centre of the sampling sites), and this consistently for the three variables, best fits appeared with urbanization quantified at

TABLE 1 Overview of mixed effect linear regression model output, showing the effect of urbanization (built-up cover, BUC) on key variables related to taxonomic and functional community composition, both for the community-weighted mean (CWM) and *SD* approaches, and separately for butterflies and macro-moths

	Butterflies		**Macro-moths**	
Taxonomic homogenization				
N	200: $F_{1,71.44} = 42.08$; $p < .0001$		3,200: $F_{1,4.01} = 52.64$; $p = .0019$	
S	200: $F_{1,69.74} = 54.18$; $p < .0001$		3,200: $F_{1,4.01} = 108.08$; $p = .0005$	
H	200: $F_{1,75.01} = 8.87$; $p = .0039$		800: $F_{1,5.22} = 55.81$; $p = .0006$	
Functional homogenization	**CWM**	***SD***	**CWM**	***SD***
Specialization				
Host plant specialization	n.s.	100: $F_{1,60.35} = 11.47$; $p = .0013$	200: $F_{1,6.93} = 38.04$; $p = .0005$	400: $F_{1,7.41} = 35.67$; $p = .0004$
Habitat use generalism	100: $F_{1,63.29} = 7.08$; $p = .0099$	n.s.	200: $F_{1,6.47} = 21.88$; $p = .0028$	n.s.
Distribution	100: $F_{1,65.06} = 8.85$; $p = .0041$	n.s.	800: $F_{1,4.91} = 20.77$; $p = .0063$	n.s.
Mobility				
Mobility	200: $F_{1,71.50} = 19.10$; $p < .0001$	n.s.	800: $F_{1,4.60} = 17.81$; $p = .010$	n.s.
Wing length	100: $F_{1,59.56} = 7.53$; $p = .0080$	n.s.	800: $F_{1,4.60} = 16.84$; $p = .011$	200: $F_{1,6.98} = 6.19$; $p = .042$
Thermophily				
Heat tolerance	100: $F_{1,60.18} = 32.10$; $p < .0001$	*100: $F_{1,58.40} = 4.72$; $p = .034$*		
Habitat openness	100: $F_{1,61.92} = 6.19$; $p = .016$	n.s.	200: $F_{1,8.11} = 12.74$; $p = .0071$	n.s.
Scale range	100–200		200–3,200	

Note: 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 specialization, mobility and thermophily (see Supporting Information 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 (BUC values were quantified at seven scales: 50–3,200 m radii). Non-significant output is given as n.s. ($p \geq .05$), while output with an effect direction opposite to the hypothesized direction is given in italics (one instance only). All other output is in line with the hypothesized directions.

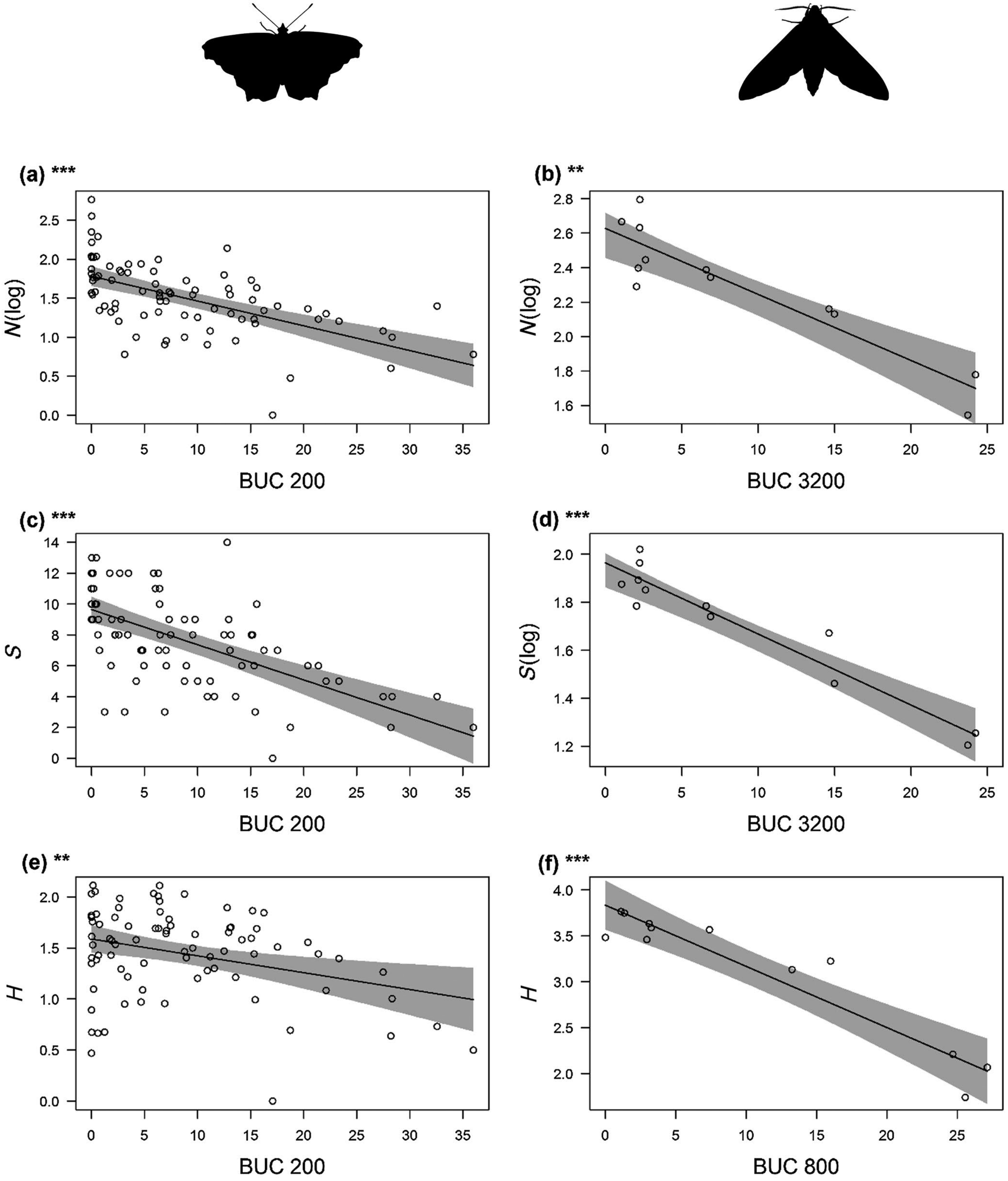

FIGURE 2 Taxonomic community composition. Declines in abundance (*N*, top row), species richness (*S*, middle row) and species diversity (*H*, bottom row) for butterflies (left) and macro-moths (right) as a function of increasing urbanization (built-up cover, BUC), with BUC numbers referring to the spatial scale of these best-fitting models (BUC values were quantified at seven scales: 50–3,200 m radii). Modelled linear regression slopes with 95% confidence intervals (shaded regions) are shown. Necessary log-transformations of dependent variables to improve residual fits are indicated. Star symbols refer to *p*-values (**$p \le .01$. ***$p \le .001$). 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

the landscape scale for moths: 3,200 m (for *N* and *S*) and 800 m radii (for *H*) around the light-trap sites (Table 1; Figure 2).

Both overall beta-diversity, as well as its turnover and nestedness components, were contrasted between non-urban and urban communities, with urbanization being quantified at these most relevant spatial scales. For butterflies, all communities characterized by a < 1% BUC at the 200 m radius scale (i.e., 19 non-urban sites) were contrasted with a similar amount of the most urban communities (i.e., 19 sites with > 14% BUC at the 200 m radius scale); alpha-diversity (mean ± *SE*): 10.3 ± 0.4 vs. 5.0 ± 0.6 species; gamma-diversity: 23 versus 18 species, respectively. These urban and non-urban communities differed neither in overall beta-diversity ($F_{1,36} = 0.41$; $p = .53$) nor in turnover and nestedness ($F_{1,24} = 0.30$; $p = .59$; $F_{1,24} = 1.35$; $p = .26$, respectively). For macro-moths, all six communities from non-urban sites were contrasted with the six urban communities (i.e., < 3.5 vs. > 7% BUC at the 800 m radius scale); alpha-diversity (mean ± *SE*): 79.3 ± 6.4 versus 36.7 ± 7.9 species; gamma-diversity: 191 versus 102 species, respectively. While urban and non-urban communities did not differ in overall beta-diversity ($F_{1,10} = 0.09$; $p = .78$), urban communities tended to display lower turnover and displayed higher levels of nestedness than non-urban ones ($F_{1,10} = 3.63$; $p = .086$; $F_{1,10} = 6.92$; $p = .025$, respectively).

3.2 | Functional homogenization

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

Urbanization also led to community-wide shifts in mobility for butterflies and macro-moths, showing a pattern of dominance of mobile species with increasing urbanization (Table 1; Figure 4). A comparison in CWM mobility for the direct species-specific mobility measure between sites differing by 25% BUC in their surroundings, revealed that urban communities are on average 23 and 66% more mobile than non-urban communities, for butterflies and macro-moths, respectively. This difference in the extent of the effect between the two taxa was also reflected in wing length, which is a proxy of mobility in Lepidoptera (Nieminen et al., 1999; Sekar, 2012; Slade et al., 2013). CWM forewing length was 7% larger for butterfly communities at urban than at non-urban sites (25 vs. 0% BUC, respectively), while CWM wingspan was 21% larger in urban than in non-urban moth communities. For moths, this shift in mean wingspan was accompanied by trait convergence: urban communities are characterized by smaller variance in wingspan than non-urban ones. For butterflies, there was a trend for a similar trait convergence, and this at the 200 m radius scale ($F_{1,75.29} = 3.54$; $p = .064$) (Table 1; Figure 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; Figure 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 urbanization 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).

4 | DISCUSSION

In line with the urbanization-driven biotic homogenization 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 urbanization 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 characterized 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 homogenized, urban macro-moth communities are both taxonomically and functionally homogenized. Such effects are poorly known for invertebrate groups (Olden et al., 2016, 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 homogenization of the on average more mobile macro-moth communities was more pronounced at larger scales (200–3,200 m radii) compared to the relatively less-mobile butterfly communities, which indeed responded to urbanization in the local surroundings (100–200 m radii) only. Additionally, although the butterfly community homogenization was clearly pronounced, homogenization was even stronger for the nocturnal macro-moth communities.

Biotic homogenization due to urbanization is typically pronounced as urbanization 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

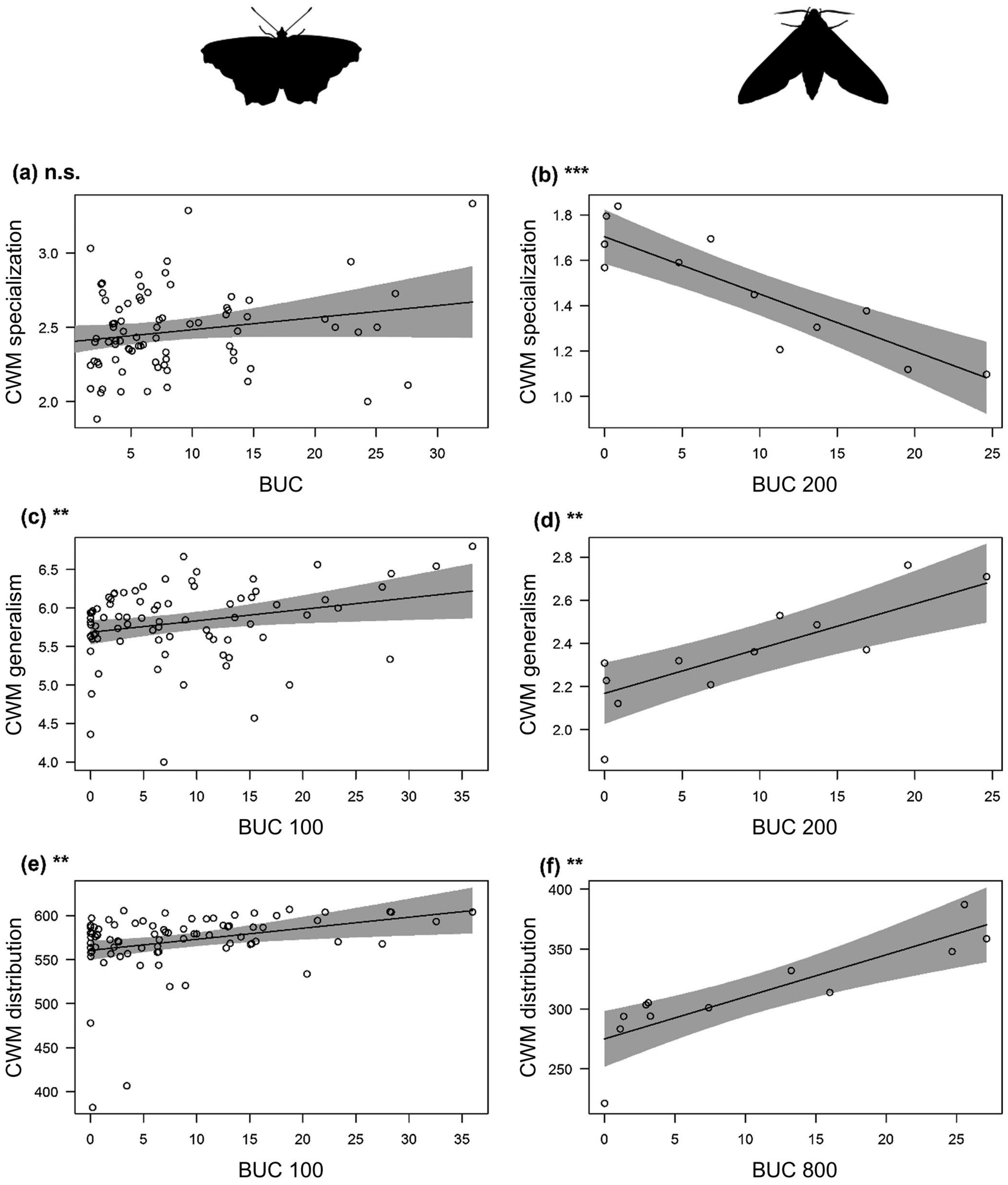

FIGURE 3 Decline in community-weighted mean (CWM) host plant specialization (top row) and increase in both CWM habitat use generalism (middle row) and CWM distribution (bottom row) (see Supporting Information Table S1.1 for a description of these variables) for butterflies (left) and macro-moths (right) as a function of increasing urbanization (built-up cover, BUC), with BUC numbers referring to the spatial scale of these best-fitting models (BUC values were quantified at seven scales: 50–3,200 m radii). Modelled linear regression slopes with 95% confidence intervals (shaded regions) are shown. Star symbols refer to *p*-values (n.s. $p > .10$. $^{**}p \leq .01$. $^{***}p \leq .001$). Image credits as in Figure 2

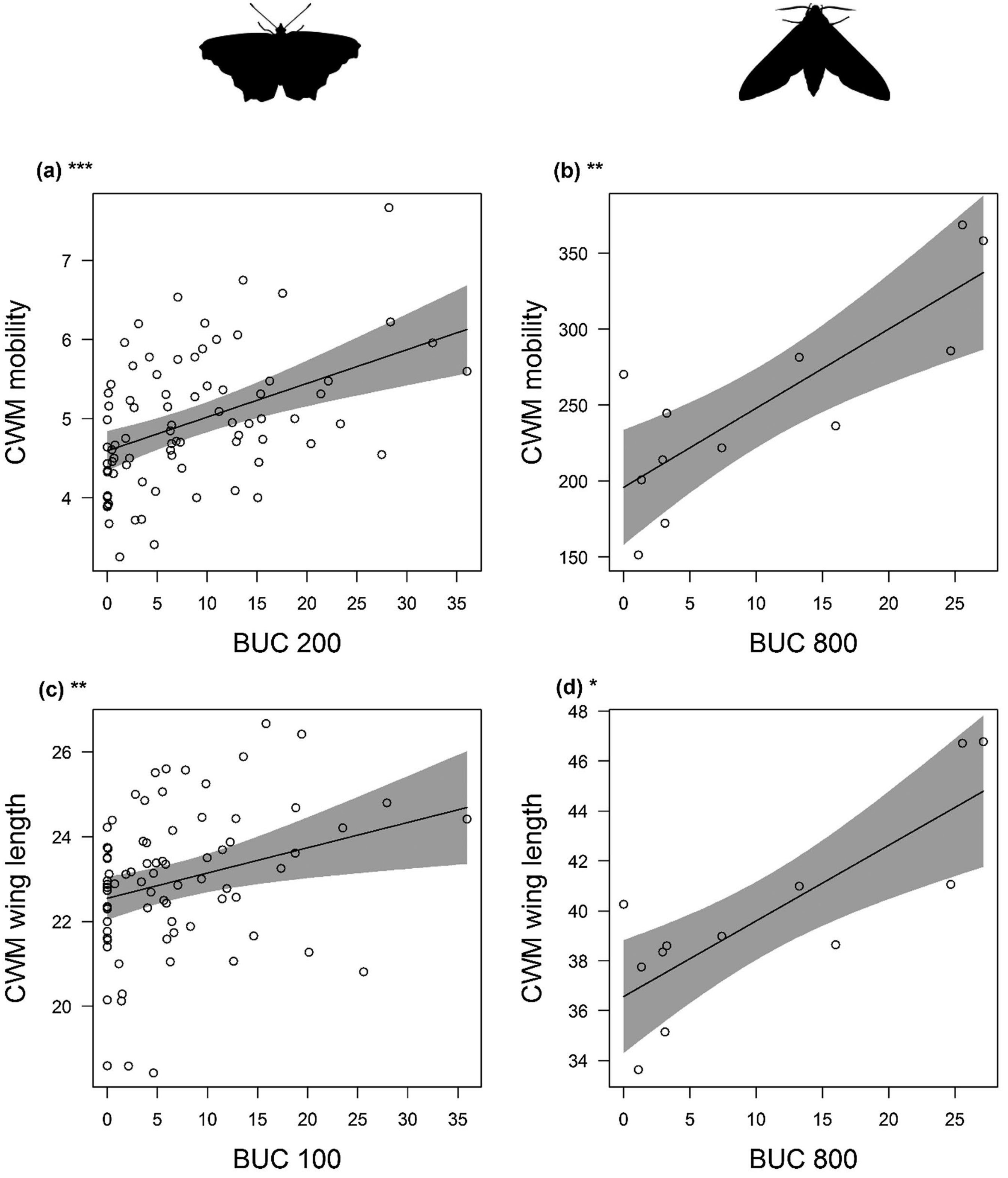

FIGURE 4 Increase in community-weighted means (CWMs) of mobility (top row) and wing length (bottom row) (see Supporting Information Table S1.1 for a description of these variables) for butterflies (left) and macro-moths (right) as a function of increasing urbanization (built-up cover, BUC), with BUC numbers referring to the spatial scale of these best-fitting models (BUC values were quantified at seven scales: 50–3,200 m radii). Modelled linear regression slopes with 95% confidence intervals (shaded regions) are shown. Star symbols refer to *p*-values ($*p \leq .05$. $**p \leq .01$. $***p \leq .001$). Image credits as in Figure 2

urbanization 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, 2008; McKinney & Lockwood, 1999). In particular, towns and cities are novel ecosystems characterized by extensive loss and fragmentation of (semi)

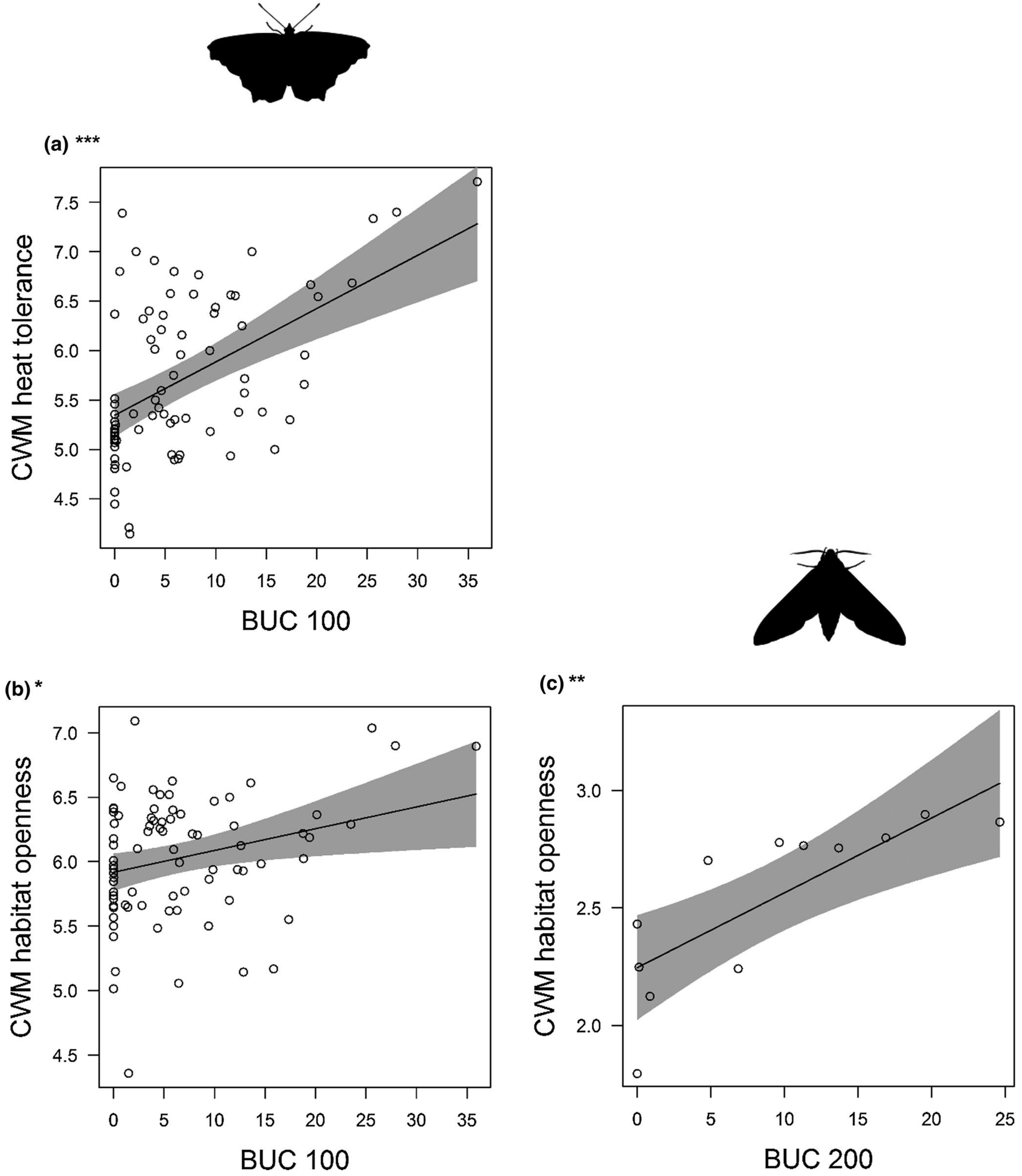

FIGURE 5 Increase in community-weighted means (CWMs) of heat tolerance (a) and habitat openness (b–c) (see Supporting Information Table S1.1 for a description of these variables) for butterflies (left) and macro-moths (right) as a function of increasing urbanization (built-up cover, BUC), with BUC numbers referring to the spatial scale of these best-fitting models (BUC values were quantified at seven scales: 50–3,200 m radii). Modelled linear regression slopes with 95% confidence intervals (shaded regions) are shown. Heat tolerance data are lacking for macro-moths. Star symbols refer to *p*-values (**p* ≤ .05. ***p* ≤ .01. ****p* ≤ .001). Image credits as in Figure 2

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 (Aronson et al., 2014; Hobbs et al., 2006; Niemelä, 2011; Parris, 2016). Their combined impact is known to induce biodiversity loss and biotic homogenization (e.g., Casner et al., 2014), favouring generalist species (Knop, 2016; Lizée et al., 2011).

One aspect of this generalization 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 (Piano et al., 2017; Rochat et al., 2017; Sattler et al., 2010). 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 (Olivier, Schmucki, Fontaine, Villemey, & Archaux, 2016; Rochat et al., 2017; Wood & Pullin, 2002). Moreover, the UHI-effect is expected to favour thermophilic, warm-adapted species (Brans, Govaert, et al., 2017; Piano et al., 2017), although adaptive thermal evolution to urbanization happens intraspecifically 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 characterized 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 of 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 urbanization (Merckx, Souffreau, et al., 2018). This multi-taxa study showed that butterfly and macro-moth communities become increasingly dominated by larger species with urbanization. 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; Slade et al., 2013; Stevens, Trochet, Van Dyck, Clobert, & Baguette, 2012). 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 instead to be 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, Merckx, & Van Dyck, 2016) and pose increased desiccation risks. In turn, insects' 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 homogenization 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, urbanization is also strongly associated with ALAN (Bennie, Duffy, Davies, Correa-Cano, & Gaston, 2015; Sutton, 2003). 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—although 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 (Grubisic, Van Grunsven, Kyba, Manfrin, & Hölker, 2018; Macgregor, Pocock, Fox, & Evans, 2015; 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 until 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 (Borges, 2018; Knop et al., 2017; Macgregor, Evans, Fox, & Pocock, 2017; 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 urbanization 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 homogenization 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 (Jones et al., 2016; Slade et al., 2013), 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 homogenization that we here observed for Lepidoptera in Belgium is a process that is likely to happen to aerial insect taxa in urbanized 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 (van Langevelde et al., 2018; Merckx et al., 2013). Their severe biotic homogenization as a response to urbanization, and the impacts of urbanization 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 homogenization 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, Tatoni, and 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 covariation 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 urbanized settings, for instance via insect-friendly, phased mowing regimes and via the replacement of exotic with native vegetation in urban parks (e.g., Buchholz, Hannig, Möller, & Schirmel, 2018; Čížek, Zámečník, Tropek, Kočárek, & Konvička, 2012; Mata et al., 2017; Threlfall et al., 2017). If such management were 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 urbanized, it is timely to understand current and future changes in community composition within urbanizing regions, especially also in terms of ecosystem function and ecosystem services. For example, by both narrowing and synchronizing the response diversity of communities, functional homogenization 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 another. 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).

ACKNOWLEDGMENTS

We thank Hans Matheve for his help in selecting (sub)plots, calculating BUC values, and designing the map of the study area. We thank Aurélien Kaiser for his help with the butterfly sampling, and we also thank two anonymous referees for their role in improving the manuscript's quality. This research is part of the 'SPEEDY'-project funded by the Interuniversity Attraction Poles program (IAP-grant P7/04) of the Belgian Science Policy Office (Belspo). The authors declare no conflicts of interest.

DATA ACCESSIBILITY

A dataset containing the *N*, *S* and *H* variables as well as CWMs and *SD*s of butterfly and macro-moth samples, and their respective site-specific urbanization (BUC) values, is available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k2d45c2.

ORCID

Thomas Merckx https://orcid.org/0000-0002-6195-3302

REFERENCES

Altermatt, F., & Ebert, D. (2016). Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biology Letters*, *12*, 20160111. https://doi.org/10.1098/rsbl.2016.0111

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, *9*, 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Angilletta, M. J., Jr., Wilson, R. S., Niehaus, A. C., Sears, M. W., Navas, C. A., & Ribeiro, P. L. (2007). Urban physiology; city ants possess high heat tolerance. *PLoS ONE*, *2*(2), e258.

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1780), 20133330. https://doi.org/10.1098/rspb.2013.3330

Aronson, M. F. J., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., … Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. *Frontiers in Ecology and the Environment*, *15*(4), 189–196. https://doi.org/10.1002/fee.1480

Baiser, B., & Lockwood, J. L. (2011). The relationship between functional and taxonomic homogenization. *Global Ecology and Biogeography*, *20*(1), 134–144. https://doi.org/10.1111/j.1466-8238.2010.00583.x

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Bates, A. J., Sadler, J. P., Grundy, D., Lowe, N., Davis, G., Baker, D., … Young, H. (2014). Garden and landscape-scale correlates of moths of differing conservation status: Significant effects of urbanization and habitat diversity. *PLoS ONE*, *9*, e86925. https://doi.org/10.1371/journal.pone.0086925

Bennie, J., Duffy, J. P., Davies, T. W., Correa-Cano, M. E., & Gaston, K. J. (2015). Global trends in exposure to light pollution in natural terrestrial ecosystems. *Remote Sensing*, *7*, 2715–2730. https://doi.org/10.3390/rs70302715

Betzholtz, P. E., & Franzén, M. (2013). Ecological characteristics associated with high mobility in night-active moths. *Basic and Applied Ecology*, *14*(3), 271–279. https://doi.org/10.1016/j.baae.2013.01.004

Bink, F. A. (1992). *Ecologische atlas van de dagvlinders van Noordwest-Europa*. Haarlem, The Netherlands: Schuyt & Co.

Borges, R. M. (2018). Dark matters: Challenges of nocturnal communication between plants and animals in delivery of pollination services. *The Yale Journal of Biology and Medicine*, *91*(1), 33.

Bowden, J. (1982). An analysis of factors affecting catches of insects in light-traps. *Bulletin of Entomological Research*, *72*, 535–556. https://doi.org/10.1017/S0007485300008579

Brans, K. I., Govaert, L., Engelen, J. M., Gianuca, A. T., Souffreau, C., & De Meester, L. (2017). Eco-evolutionary dynamics in urbanized landscapes: Evolution, species sorting and the change in zooplankton body size along urbanization gradients. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160030. https://doi.org/10.1098/rstb.2016.0030

Brans, K. I., Jansen, M., Vanoverbeke, J., Tüzün, N., Stoks, R., & De Meester, L. (2017). The heat is on: Genetic adaptation to urbanization mediated by thermal tolerance and body size. *Global Change Biology*, *23*, 5218–5227. https://doi.org/10.1111/gcb.13784

Buchholz, S., Hannig, K., Möller, M., & Schirmel, J. (2018). Reducing management intensity and isolation as promising tools to enhance ground-dwelling arthropod diversity in urban grasslands. *Urban Ecosystems*, *21*, 1139–1149. https://doi.org/10.1007/s11252-018-0786-2

Burnham, K. P., & Anderson, D. R. (2004). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer.

Casner, K. L., Forister, M. L., O'brien, J. M., Thorne, J., Waetjen, D., & Shapiro, A. M. (2014). Contribution of urban expansion and a changing climate to decline of a butterfly fauna. *Conservation Biology*, *28*, 773–782. https://doi.org/10.1111/cobi.12241

Chown, S. L., Sørensen, J. G., & Terblanche, J. S. (2011). Water loss in insects: An environmental change perspective. *Journal of Insect Physiology*, *57*, 1070–1084. https://doi.org/10.1016/j.jinsphys.2011.05.004

Čížek, O., Zámečník, J., Tropek, R., Kočárek, P., & Konvička, M. (2012). Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. *Journal of Insect Conservation*, *16*(2), 215–226. https://doi.org/10.1007/s10841-011-9407-6

Clark, P. J., Reed, J. M., & Chew, F. S. (2007). Effects of urbanization on butterfly species richness, guild structure, and rarity. *Urban Ecosystems*, *10*(3), 321–337. https://doi.org/10.1007/s11252-007-0029-4

Concepción, E. D., Moretti, M., Altermatt, F., Nobis, M. P., & Obrist, M. K. (2015). Impacts of urbanisation on biodiversity: The role of species mobility, degree of specialisation and spatial scale. *Oikos*, *124*, 1571–1582. https://doi.org/10.1111/oik.02166

Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D., & Baguette, M. (2017). Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography*, *40*, 56–73. https://doi.org/10.1111/ecog.02538

Davies, T. W., & Smyth, T. (2018). Why artificial light at night should be a focus for global change research in the 21st century. *Global Change Biology*, *24*, 872–882. https://doi.org/10.1111/gcb.13927

Deguines, N., Julliard, R., Flores, M., & Fontaine, C. (2016). Functional homogenization of flower visitor communities with urbanization. *Ecology and Evolution*, *6*, 1967–1976. https://doi.org/10.1002/ece3.2009

Devictor, V., Julliard, R., Couvet, D., Lee, A., & Jiguet, F. (2007). Functional homogenization effect of urbanization on bird communities. *Conservation Biology*, *21*, 741–751. https://doi.org/10.1111/j.1523-1739.2007.00671.x

Devictor, V., Julliard, R., Jiguet, F., & Couvet, D. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 2743–2748.

Gaston, K. J., Bennie, J., Davies, T. W., & Hopkins, J. (2013). The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biological Reviews*, *88*, 912–927. https://doi.org/10.1111/brv.12036

Grubisic, M., Van Grunsven, R. H. A., Kyba, C. C. M., Manfrin, A., & Hölker, F. (2018). Insect declines and agroecosystems: Does light pollution matter? *Annals of Applied Biology*, *173*(2), 180–189. https://doi.org/10.1111/aab.12440

Heinrich, B. (1974). Thermoregulation in endothermic insects. *Science*, *185*, 747–756. https://doi.org/10.1126/science.185.4153.747

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., … Zobel, M. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, *15*, 1–7. https://doi.org/10.1111/j.1466-822X.2006.00212.x

IBZ. (2018). *FOD binnenlandse zaken, algemene directie instellingen en bevolking, rijksregister*. Retrieved from http://www.ibz.rrn.fgov.be/fileadmin/user_upload/fr/pop/statistiques/population-bevolking-20180101.pdf

Jones, H. B., Lim, K. S., Bell, J. R., Hill, J. K., & Chapman, J. W. (2016). Quantifying interspecific variation in dispersal ability of noctuid moths using an advanced tethered flight technique. *Ecology and Evolution*, *6*, 181–190. https://doi.org/10.1002/ece3.1861

Kaiser, A., Merckx, T., & Van Dyck, H. (2016). The Urban Heat Island and its spatial scale dependent impact on survival and development in butterflies of different thermal sensitivity. *Ecology and Evolution*, *6*, 4129–4140. https://doi.org/10.1002/ece3.2166

Knop, E. (2016). Biotic homogenization of three insect groups due to urbanization. *Global Change Biology*, *22*, 228–236.

Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., & Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature*, *548*(7666), 206–209. https://doi.org/10.1038/nature23288

Kühn, I., & Klotz, S. (2006). Urbanization and homogenization—Comparing the floras of urban and rural areas in Germany. *Biological Conservation*, *127*(3), 292–300. https://doi.org/10.1016/j.biocon.2005.06.033

La Sorte, F. A., McKinney, M. L., & Pyšek, P. (2007). Compositional similarity among urban floras within and across continents: Biographical consequences of human-mediated biotic interchange. *Global Change Biology*, *13*, 913–921.

Lizée, M.-H., Mauffrey, J. F., Tatoni, T., & Deschamps-Cottin, M. (2011). Monitoring urban environments on the basis of biological traits. *Ecological Indicators*, *11*, 353–361. https://doi.org/10.1016/j.ecolind.2010.06.003

Lizée, M.-H., Tatoni, T., & Deschamps-Cottin, M. (2016). Nested patterns in urban butterfly species assemblages: Respective roles of plot management, park layout and landscape features. *Urban Ecosystems*, *19*, 205–224. https://doi.org/10.1007/s11252-015-0501-5

LRD. (2013). *Large-scale reference database, an object-oriented reference map of Flanders*. Retrieved from https://www.agiv.be/international/en/products/grb-en

Luck, G. W., & Smallbone, L. T. (2011). The impact of urbanization on taxonomic and functional similarity among bird communities. *Journal of Biogeography*, *38*, 894–906. https://doi.org/10.1111/j.1365-2699.2010.02449.x

Macgregor, C. J., Evans, D. M., Fox, R., & Pocock, M. J. (2017). The dark side of street lighting: Impacts on moths and evidence for the disruption of nocturnal pollen transport. *Global Change Biology*, *23*, 697–707. https://doi.org/10.1111/gcb.13371

Macgregor, C. J., Pocock, M. J., Fox, R., & Evans, D. M. (2015). Pollination by nocturnal Lepidoptera, and the effects of light pollution: A review. *Ecological Entomology*, *40*, 187–198. https://doi.org/10.1111/een.12174

Macgregor, C. J., Pocock, M. J., Fox, R., & Evans, D. M. (2019). Effects of street lighting technologies on the success and quality of pollination in a nocturnally pollinated plant. *Ecosphere*, *10*, e02550. https://doi.org/10.1002/ecs2.2550

Mata, L., Threlfall, C. G., Williams, N. S., Hahs, A. K., Malipatil, M., Stork, N. E., & Livesley, S. J. (2017). Conserving herbivorous and predatory insects in urban green spaces. *Scientific Reports*, *7*, 40970. https://doi.org/10.1038/srep40970

McGeoch, M. A., & Chown, S. L. (1997). Impact of urbanization on a gall-inhabiting Lepidoptera assemblage: The importance of reserves in urban areas. *Biodiversity and Conservation*, *6*, 979–993.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, *11*, 161–176. https://doi.org/10.1007/s11252-007-0045-4

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Menke, S. B., Guenard, B., Sexton, J. O., Weiser, M. D., Dunn, R. R., & Silverman, J. (2011). Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants. *Urban Ecosystems*, *14*, 135–163. https://doi.org/10.1007/s11252-010-0150-7

Merckx, T., Feber, R. E., Dulieu, R. L., Townsend, M. C., Parsons, M. S., Bourn, N. A. D., … Macdonald, D. W. (2009). Effect of field margins on moths depends on species mobility: Field-based evidence for landscape-scale conservation. *Agriculture, Ecosystems and Environment*, *129*, 302–309. https://doi.org/10.1016/j.agee.2008.10.004

Merckx, T., Feber, R. E., Mclaughlan, C., Bourn, N. A. D., Parsons, M. S., Townsend, M. C., … Macdonald, D. W. (2010). Shelter benefits less mobile moth species: The field-scale effect of hedgerow trees. *Agriculture, Ecosystems and Environment*, *138*, 147–151. https://doi.org/10.1016/j.agee.2010.04.010

Merckx, T., Huertas, B., Basset, Y., & Thomas, J. (2013). A global perspective on conserving butterflies and moths and their habitats. In D. W. Macdonald & K. J. Willis (Eds.), *Key topics in conservation biology 2* (pp. 237–257). Oxford, UK: Wiley.

Merckx, T., Kaiser, A., & Van Dyck, H. (2018). Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Global Change Biology*, *24*, 3837–3848. https://doi.org/10.1111/gcb.14151

Merckx, T., & Macdonald, D. W. (2015). Landscape-scale conservation of farmland moths. In D. W. Macdonald & R. E. Feber (Eds.), *Wildlife conservation on farmland. Volume 1: Managing for nature on lowland farms* (pp. 147–166). UK: Oxford University Press.

Merckx, T., Marini, L., Feber, R. E., & Macdonald, D. W. (2012). Hedgerow trees and extended-width field margins enhance macro-moth diversity: Implications for management. *Journal of Applied Ecology*, *49*, 1396–1404. https://doi.org/10.1111/j.1365-2664.2012.02211.x

Merckx, T., & Slade, E. M. (2014). Macro-moth families differ in their attraction to light: Implications for light-trap monitoring programmes. *Insect Conservation and Diversity*, *7*, 453–461. https://doi.org/10.1111/icad.12068

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., … Van Dyck, H. (2018). Body-size shifts in aquatic and terrestrial urban communities. *Nature*, *558*, 113–116. https://doi.org/10.1038/s41586-018-0140-0

Merckx, T., Van Dongen, S., Matthysen, E., & Van Dyck, H. (2008). Thermal flight budget of a woodland butterfly in woodland versus agricultural landscapes: An experimental assessment. *Basic and Applied Ecology*, *9*, 433–442. https://doi.org/10.1016/j.baae.2007.03.009

Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Jokimäki, J., Mänd, R., Tryjanowski, P., & Møller, A. P. (2016). Evidence of evolutionary homogenization of bird communities in urban environments across Europe. *Global Ecology and Biogeography*, *25*, 1284–1293. https://doi.org/10.1111/geb.12486

Mutanen, M., Wahlberg, N., & Kaila, L. (2010). Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 2839–2848.

Niemelä, J. (2011). *Urban ecology: Patterns, processes, and applications*. UK: Oxford University Press.

Nieminen, M., Rita, H., & Uuvana, P. (1999). Body size and migration rate in moths. *Ecography*, *22*, 697–707. https://doi.org/10.1111/j.1600-0587.1999.tb00519.x

Noriega, J. A., Hortal, J., Azcárate, F. M., Berg, M. P., Bonada, N., Briones, M. J. I., … Santos, A. M. C. (2018). Research trends in ecosystem services provided by insects. *Basic and Applied Ecology*, *26*, 8–23. https://doi.org/10.1016/j.baae.2017.09.006

Olden, J. D., Comte, L., & Giam, X. (2016). Biotic Homogenisation. In: *Encyclopedia of Life Sciences*. Chichester, UK: John Wiley & Sons Ltd. https://doi.org/10.1002/9780470015902.a0020471.pub2

Olden, J. D., Comte, L., & Giam, X. (2018). The Homogocene: A research prospectus for the study of biotic homogenisation. *NeoBiota*, *37*, 23–36. https://doi.org/10.3897/neobiota.37.22552

Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, *19*, 18–24. https://doi.org/10.1016/j.tree.2003.09.010

Olivier, T., Schmucki, R., Fontaine, B., Villemey, A., & Archaux, F. (2016). Butterfly assemblages in residential gardens are driven by species' habitat preference and mobility. *Landscape Ecology*, *31*, 865–876. https://doi.org/10.1007/s10980-015-0299-9

Parris, K. M. (2016). *Ecology of urban environments*. Chichester, UK: Wiley-Blackwell.

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., … Hendrickx, F. (2017). Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, *23*, 2554–2564. https://doi.org/10.1111/gcb.13606

Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biological Conservation*, *12*(2), 115–134. https://doi.org/10.1016/0006-3207(77)90065-9

Potocký, P., Bartoňová, A., Beneš, J., Zapletal, M., & Konvička, M. (2018). Life-history traits of Central European moths: Gradients of variation and their association with rarity and threats. *Insect Conservation and Diversity*, *11*, 493–505. https://doi.org/10.1111/icad.12291

Ramírez-Restrepo, L., & MacGregor-Fors, I. (2017). Butterflies in the city: A review of urban diurnal Lepidoptera. *Urban Ecosystems*, *20*, 171–182. https://doi.org/10.1007/s11252-016-0579-4

Ricketts, T. H., Daily, G. C., Ehrlich, P. R., & Fay, J. P. (2001). Countryside biogeography of moths in a fragmented landscape: Biodiversity in native and agricultural habitats. *Conservation Biology*, *15*, 378–388. https://doi.org/10.1046/j.1523-1739.2001.015002378.x

Rochat, E., Manel, S., Deschamps-Cottin, M., Widmer, I., & Joost, S. (2017). Persistence of butterfly populations in fragmented habitats along urban density gradients: Motility helps. *Heredity*, *119*, 328–338. https://doi.org/10.1038/hdy.2017.40

Sattler, T., Duelli, P., Obrist, M. K., Arlettaz, R., & Moretti, M. (2010). Response of arthropod species richness and functional groups to urban habitat structure and management. *Landscape Ecology*, *25*, 941–954. https://doi.org/10.1007/s10980-010-9473-2

Sekar, S. (2012). A meta-analysis of the traits affecting dispersal ability in butterflies: Can wingspan be used as a proxy? *Journal of Animal Ecology*, *81*, 174–184. https://doi.org/10.1111/j.1365-2656.2011.01909.x

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences USA*, *109*, 16083–16088.

Slade, E. M., Merckx, T., Riutta, T., Bebber, D. P., Redhead, D., Riordan, P., & Macdonald, D. W. (2013). Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology*, *94*, 1519–1530. https://doi.org/10.1890/12-1366.1

Sonnier, G., Johnson, S. E., Amatangelo, K. L., Rogers, D. A., & Waller, D. M. (2014). Is taxonomic homogenization linked to functional homogenization in temperate forests? *Global Ecology and Biogeography*, *23*, 894–902. https://doi.org/10.1111/geb.12164

Stevens, V. M., Trochet, A., Van Dyck, H., Clobert, J., & Baguette, M. (2012). How is dispersal integrated in life histories: A quantitative analysis using butterflies. *Ecology Letters*, *15*, 74–86. https://doi.org/10.1111/j.1461-0248.2011.01709.x

Summerville, K. S., & Crist, T. O. (2004). Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography*, *27*, 3–12. https://doi.org/10.1111/j.0906-7590.2004.03664.x

Sutton, P. C. (2003). A scale-adjusted measure of “urban sprawl” using nighttime satellite imagery. *Remote Sensing of Environment*, *86*, 353–369. https://doi.org/10.1016/S0034-4257(03)00078-6

Threlfall, C. G., Mata, L., Mackie, J. A., Hahs, A. K., Stork, N. E., Williams, N. S., & Livesley, S. J. (2017). Increasing biodiversity in urban green spaces through simple vegetation interventions. *Journal of Applied Ecology*, *54*, 1874–1883. https://doi.org/10.1111/1365-2664.12876

van Geffen, K. G., Groot, A. T., Van Grunsven, R. H., Donners, M., Berendse, F., & Veenendaal, E. M. (2015). Artificial night lighting disrupts sex pheromone in a noctuid moth. *Ecological Entomology*, *40*, 401–408. https://doi.org/10.1111/een.12202

van Geffen, K. G., van Eck, E., de Boer, R. A., van Grunsven, R. H., Salis, L., Berendse, F., & Veenendaal, E. M. (2015). Artificial light at night inhibits mating in a Geometrid moth. *Insect Conservation and Diversity*, *8*, 282–287. https://doi.org/10.1111/icad.12116

van Geffen, K. G., van Grunsven, R. H., van Ruijven, J., Berendse, F., & Veenendaal, E. M. (2014). Artificial light at night causes diapause inhibition and sex-specific life history changes in a moth. *Ecology and Evolution*, *4*, 2082–2089. https://doi.org/10.1002/ece3.1090

van Langevelde, F., Braamburg-Annegarn, M., Huigens, M. E., Groendijk, R., Poitevin, O., Deijk, J. R., … WallisDeVries, M. F. (2018). Declines in moth populations stress the need for conserving dark nights. *Global Change Biology*, *24*, 925–932. https://doi.org/10.1111/gcb.14008

Villéger, S., Grenouillet, G., & Brosse, S. (2014). Functional homogenization exceeds taxonomic homogenization among European fish assemblages. *Global Ecology and Biogeography*, *23*, 1450–1460. https://doi.org/10.1111/geb.12226

Wakefield, A., Stone, E. L., Jones, G., & Harris, S. (2015). Light-emitting diode street lights reduce last-ditch evasive manoeuvres by moths to bat echolocation calls. *Royal Society Open Science*, *2*, 150291. https://doi.org/10.1098/rsos.150291

Wickman, P.-O. (2009). Thermoregulation and habitat use in butterflies. In J. Settele, T. Shreeve, M. Konvička, & H. Van Dyck (Eds.), *Ecology of butterflies in Europe* (pp. 55–61). UK: Cambridge University Press.

Wilson, J. F., Baker, D., Cheney, J., Cook, M., Ellis, M., Freestone, R., … Young, H. (2018). A role for artificial night-time lighting in long-term changes in populations of 100 widespread macro-moths in UK and Ireland: A citizen-science study. *Journal of Insect Conservation*, *22*, 189–196. https://doi.org/10.1007/s10841-018-0052-1

Wood, B. C., & Pullin, A. S. (2002). Persistence of species in a fragmented urban landscape: The importance of dispersal ability and habitat availability for grassland butterflies. *Biodiversity and Conservation*, *11*, 1451–1468.

Wouters, H., De Ridder, K., Poelmans, L., Willems, P., Brouwers, J., Hosseinzadehtalaei, P., … Demuzere, M. (2017). Heat stress increase under climate change twice as large in cities as in rural areas: A study for a densely populated midlatitude maritime region. *Geophysical Research Letters*, *44*, 8997–9007. https://doi.org/10.1002/2017GL074889

BIOSKETCHES

Thomas Merckx is a postdoctoral researcher focusing on ecology and evolution of Lepidoptera and their landscape-scale conservation 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.

SUPPORTING INFORMATION

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

How to cite this article: Merckx T, Van Dyck H. Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects. *Global Ecol Biogeogr*. 2019;28:1440–1455. https://doi.org/10.1111/geb.12969