Butterfly species' responses to urbanization: differing effects of human population density and built-up area

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Abstract

Good knowledge on how increasing urbanization affects biodiversity is essential in order to preserve biodiversity in urban green spaces. We examined how urban development affects species richness and total abundance of butterflies as well as the occurrence and abundance of individual species within the Helsinki metropolitan area in Northern Europe. Repeated butterfly counts in 167 separate 1-km-long transects within Helsinki covered the entire urbanization gradient, quantified by human population density and the proportion of built-up area (within a 50-m buffer surrounding each butterfly transect). We found consistently negative effects of both human population density and built-up area on all studied butterfly variables, though butterflies responded markedly more negatively to increasing human population density than to built-up area. Responses in butterfly species richness and total abundance showed higher variability in relation to proportion of built-up area than to human density, especially in areas of high human density. Increasing human density negatively affected both the abundance and the occurrence of 47% of the 19 most abundant species, whereas, for the proportion of built-up area, the corresponding percentages were 32% and 32%, respectively. Species with high habitat specificity and low mobility showed higher sensitivity to urbanization (especially high human population density) than habitat generalists and mobile species that dominated the urban butterfly communities. Our results suggest that human population density provides a better indicator of urbanization effects on butterflies compared to the proportion of built-up area. The generality of this finding should be verified in other contexts and taxonomic groups.

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Introduction

Urbanization is one of the most important causes of biodiversity decline worldwide (Seto et al. 2012). With an increasing proportion of the global human population living in cities (United Nations 2018), the preservation of urban biodiversity has become recognized as an important policy target which positively affects the well-being of people living in urban areas (Fuller et al. 2007; Dallimer et al. 2012; Aronson et al. 2017). Although many studies have demonstrated that species richness tends to decline with increasing urbanization, the responses differ between taxonomic groups as well as between species within taxonomic groups (McKinney 2008; Aronson et al. 2014; Ives et al. 2016; Piano et al. 2020). Some groups and species are better in coping with urbanization and increasing human density than others (McKinney 2008; Jones and Leather 2012; see also Tzortzakaki et al. 2019 for positive species responses to urbanization). For example, a high diversity of pollinating insects such as bees has

been found in cities (Baldock et al. 2019; Theodorou et al. 2020). A detailed understanding on how urbanization affects species assemblages is essential for preserving biodiversity in green spaces within cities (Grimm et al. 2008; Aronson et al. 2017; Lepczyk et al. 2017).

Several features of butterflies make them a useful and often used indicator group for biodiversity studies (Thomas 2005; Merckx et al. 2013) including research in human-dominated urban areas (Ramírez-Restrepo and MacGregor-Fors 2017). Butterflies are a relatively species-rich group with varying sensitivity to environmental disturbances between species, and they are generally easy to identify in the field without the need to collect samples (Thomas 2005; Merckx et al. 2013). Butterflies are positively valued and recognized by the general public (New 1991; Thomas 2005). Most importantly, butterflies quickly react to changes in their environment, because they tend to have subtle ecological habitat requirements and because they tend to produce at least one new generation every year (Erhardt and Thomas 1991; Thomas 2005).

In their review on butterfly research in urban areas, Ramírez-Restrepo and MacGregor-Fors (2017) reported that 28% of the published studies were conducted in Europe. However, only a few of these studies were conducted in northern Europe, and there were no publications on the effects of urbanization on butterfly diversity in the boreal zone. Earlier research has often focused on identifying the effect of local factors (such as patch area and local management; Melliger et al. 2017; Aguilera et al. 2019) and landscape context (such as habitat connectivity and the proportion of green vs. built-up area in different buffers surrounding the focal habitat patch; Lizée et al. 2012; Clark et al. 2007) on butterfly species richness in green habitat patches within cities. Focal habitat patches have included traditional parks (Öckinger et al. 2009; Lizée et al. 2012), ruderal areas (Melliger et al. 2017; Aguilera et al. 2019), gardens (Fontaine et al. 2016; Olivier et al. 2016) and nature reserves (Kadlec et al. 2008; Konvicka and Kadlec 2011).

Typically, studies have examined butterfly communities in a sample of 20–50 habitat patches located along an urbanization gradient, and as a rule they have found decreasing species richness with increasing urbanization (Ramírez-Restrepo and MacGregor-Fors 2017). In addition, local habitat quality (Aguilera et al. 2019) and connectivity (Öckinger et al. 2009; Lizée et al. 2012) affect butterfly species richness in urban settings. Several studies on urban butterfly diversity have linked the decrease in species richness with urbanization to species-specific traits, such as habitat specificity (Clark et al. 2007; Lizée et al. 2011; Merckx and Van Dyck 2019), mobility (Bergerot et al. 2011; Olivier et al. 2016; Merckx and Van Dyck 2019) and voltinism (Kitahara and Fujii 1994; Hogsden and Hutchinson 2004; Lizée et al. 2011). However, studies on how urbanization affects the occurrence of

individual species seem to be largely lacking (but see Hardy and Dennis 1999; Konvicka and Kadlec 2011; Leston and Koper 2017).

Among the numerous measures that have been used to quantify the degree of urbanization (McDonnell and Hahs 2008; Moll et al. 2019; Padilla and Sutherland 2019), the proportion of built-up area and human population density have often been used to measure the extent of human disturbance on various groups of organisms. Increasing proportions of built-up areas and human population densities have both been reported to have negative effects on butterfly species richness (Clark et al. 2007; Lizée et al. 2012). Human population density as an urbanization indicator has the strength that it can be measured simply and unambiguously by the number of inhabitants in a certain area, given that suitable register data with sufficiently detailed spatial resolution is available (Luck 2007). However, it is not clear by which mechanism human population density affects butterfly diversity (Kitahara and Fujii 1994; Clark et al. 2007).

The proportion of built-up area is technically easy to measure based on any available land cover data using Geographical Information Systems (McDonnell and Hahs 2008), and perhaps because of that, it has been a more popular urbanization measure in butterfly studies than human population density (e.g. Melliger et al. 2017; Merckx and van Dyck 2019; Tzortzakaki et al. 2019). A weakness of built-up area as an indicator is that any specific land cover classes included in the total built-up area as well as their detailed definitions often vary between studies (McDonnell and Hahs 2008), which complicates a direct comparison of results on the effects of built-up area between studies (Moll et al. 2019; Padilla and Sutherland 2019). As an example, the amount of natural vegetation (and thus potentially suitable habitat for butterflies) may vary within the built-up land cover measure between empirical studies, compromising the explanatory power of the urbanization indicator and its effects on urban butterfly diversity. One can therefore expect that the less ambiguously measured human population density could be a more reliable and more readily comparable indicator of butterfly diversity than built-up area in urban settings.

In this study, our specific aim was to compare the efficiency of two urbanization measures, the proportion of built-up area and human population density, in explaining patterns of butterfly occurrence and species richness. Using an intensive sampling based on 167 separate one kilometre transects that systematically covered the existing urbanization gradient within the Helsinki metropolitan area in Finland, we examined the effects of urbanization both on species richness and total abundance of butterflies as well as on the occurrence and abundance of individual species. Based on the large dataset, we were able to evaluate which one of the two urbanization measures would be a better indicator of urban butterfly diversity. Our second aim was to investigate whether our results

support the prediction that urban development leads to homogenization of species communities as urbanization increases (McKinney 2006; Knop 2016; Merckx and Van Dyck 2019). We tested whether habitat specialists and sedentary species were more negatively affected by increasing proportion of built-up area and human population density than habitat generalists and mobile butterfly species.

Methods

Study area and design

The study was conducted within the Helsinki metropolitan area in Finland (Fig. 1a) in the summer of 2001. Helsinki, the largest city in Finland, is located at the coast of the Baltic Sea (60° 10′ 15″ N, 24° 56′ 15″ E). The city was founded in its present location in 1640, but it remained small until it became the capital city of the Grand Duchy of Finland in 1827 (at that time part of the Russian empire). Since then, Helsinki rapidly grew, especially during the 20th century. In the year 2001, there were ca. 560 000 inhabitants in the city of Helsinki, and ca. 960 000 inhabitants in the Helsinki metropolitan area, which is characterized by hemiboreal and south boreal forests, agricultural areas and suburbs surrounding the city (Vähä-Piikkiö et al. 2004). Butterflies were surveyed in 167 transects that were relatively evenly placed within a ca. 150-km^2 study area that covered an urbanization gradient. The urbanization gradient peaked in the Helsinki city centre and gradually declined towards the edges of the city as indicated in Fig. 1 (b, c), showing the distribution of transects in relation to human population density and proportion of built-up area, respectively.

Butterfly survey

We surveyed butterflies using standardized transect counts (Pollard and Yates 1993). Each transect was walked at a

steady speed, and every butterfly observed within 5 m ahead and 2.5 m on either side of the surveyor was recorded. The transects were approximately 1 km long, with some variation between individual transects (mean = 1.0, sd = 0.2, range 0.7–2.7 km, n = 167). Following the recommendations of Pollard and Yates (1993) counts were not made when the temperature was below 13 °C in sunny and below 17 °C in overcast weather, or when wind speed exceeded four on the Beaufort scale. Each transect was conducted four times during the summer at 3- or 4-week intervals (ranging between 26 May and 27 August 2001) to cover the flight periods of different species. A total of 12 surveyors participated in the butterfly survey, and each transect was always surveyed by the same surveyor. The observations for the four counts were summed up for each species and their total abundances were used in the analyses.

Species traits

Previously published measures of habitat specificity and mobility were used in the species traits analyses. Habitat specificity was quantified as adult habitat breadth, an inverse measure of habitat specificity, according to Komonen et al. (2004). The values ranged from 1 to 4, indicating the number of habitat types typically used by adult butterflies. Butterfly female wingspan (Marttila et al. 1990) was used as a proxy for dispersal capacity. Butterfly wingspan has been shown to significantly correlate with species mobility (Sekar 2012; Kuussaari et al. 2014). Habitat specificity and mobility were analysed separately, i.e. in a univariate manner, although they are known to relate to each other: species with poor dispersal capacity tend to be habitat specialists while mobile species are often generalists (Warren et al. 2001).

Measures of urbanization

The effects of urban development on butterflies were examined based on two measures of urbanization: human population
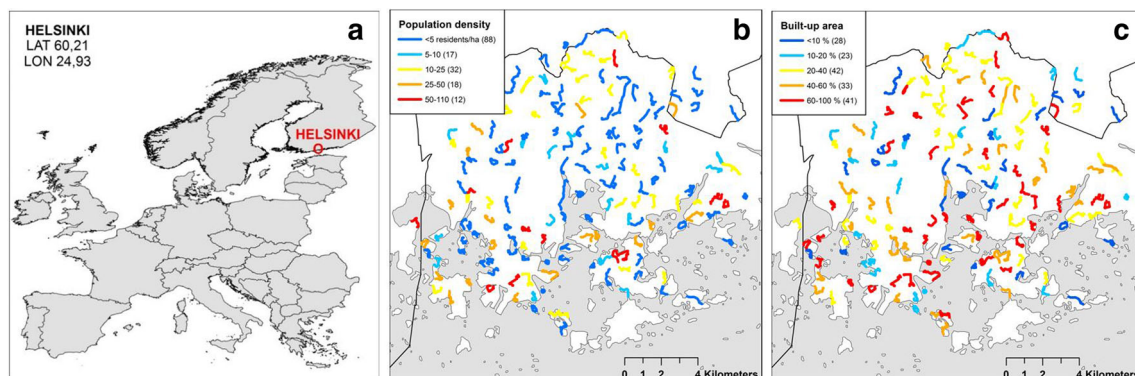

Fig. 1 (a) Location of the study area in Northern Europe. (b-c) Locations of the studied butterfly transects (n = 167; the black line indicating the boundary of the city of Helsinki) and variation of (b) human population density (residents / ha) and (c) proportion of built-up area within a 50- meter buffer area around each transect in the Helsinki metropolitan area at the coast of the Baltic Sea. The number of transects for each human population density and built-up area class is shown in parentheses after the explanation of each class

density (residents / ha) and the percentage of built-up area of all land area in the close surroundings of the butterfly transects. We calculated urbanization using seven polygon buffers of different widths (20, 50, 100, 200, 500, 1000 and 2000 m) centred along the butterfly transects using ArcGIS 10 (Esri 2011). High-resolution population density data were derived from the Finnish National Population Register System which contains information on the number of residents at the level of separate buildings. Population densities in the surroundings of the butterfly transects were calculated using the human population data from the year 2001 (Finnish Population Register Centre 1/2001), i.e. from the year when the empirical butterfly data were collected. Data on built-up area were in turn derived from the Urban Atlas 2006 database (European Environment Agency 2015). Our measure of built-up area was a mixture of many kinds of built-up land use classes generally uninhabitable for butterflies, including all terrestrial land cover types of the Urban Atlas except forest, agricultural and semi-natural areas, wetlands and urban green areas (Table S1). Urban green areas included green recreational areas such as city parks, more or less frequently mown lawns as well as relatively natural forest patches neighboured by urban areas which are common and typical semi-natural habitats for urban areas in Helsinki and other cities in the boreal climatic zone.

Statistical analyses

The relationships between the two urbanization measures (human population density and built-up land cover) calculated for differing buffer widths (20, 50, 100, 200, 500, 1000 and 2000 m) surrounding the butterfly transects and butterfly species richness and total abundance were analysed using Pearson's correlation analysis. The buffer width with the strongest correlation to the two butterfly variables was selected as the focal scale for the main statistical analyses (Steffan-Dewenter et al. 2002). Correlation between the two urbanization measures was also tested.

Generalized linear mixed models were used to analyse the effects of human population density and built-up land cover in the selected buffer on butterfly species richness, total abundance and the abundance and occurrence of those 19 individual species that were observed in at least 10 transects. The responses of butterflies to the two urbanization measures were analysed separately using univariate models. All models included the surveyor identity as a categorical random factor and transect length (log$_e$-transformed) as an offset variable. Poisson distribution was used for the models explaining species richness. To model total butterfly abundance and the abundances of individual species, negative binomial distribution was selected, because the data were over-dispersed and, in many cases, contained a large number of zeros. In addition, negative binomial models fitted the data as well as, or better than, zero-inflated Poisson models as evaluated by Akaike

Information Criterion (AIC) values. Accounting for spatial autocorrelation by adding coordinates as predictors did not qualitatively change our results concerning butterfly species richness or total abundance (data not shown). To model occurrence probability of individual species, binomial distribution with a logit link function was used.

The models were fitted using the function glmmTMB() of the R package glmmTMB (Brooks et al., 2017). Model estimates were used to calculate predicted changes (%) in butterfly species richness, abundances and occurrence probabilities when human population density increased with 10 residents per hectare, or built-up land cover increased with 10% of the total buffer area. In addition, differences in AIC values (ΔAIC) between the models with human population density and built-up land cover as explanatory variables were used to facilitate the comparison of the two measures of urbanization. If ΔAIC was less than 2, the models were considered to be equally good (Burnham and Anderson 2002).

The effects of human population density and built-up land cover on habitat specificity and mobility of butterfly communities were analysed using linear regression models. Response variables in the models were mean habitat breadth (a proxy for habitat specificity) and wing span (a measure of mobility) of butterfly species, calculated as the community-weighted mean on the basis of observed species-specific abundances (i.e. the recorded numbers of butterfly individuals of each species) for each transect following Merckx and Van Dyck (2019). The models were fitted using the function lm() of the R package stats (R Core Team 2017).

All statistical analyses were conducted using the statistical software R 3.4.1 (R Core Team 2017).

Results

Altogether 7 753 individuals of 36 species of butterflies were recorded in the 167 sampling transects (Table S2). There was a large variation in the number of recorded individuals (mean = 46.4, sd = 47.9, range 0–247) and species (mean = 7.2, sd = 3.8, range 0–17) between the transects. A total of 19 butterfly species were recorded in at least 10 transects.

Correlations between the urbanization measures and butterfly species richness and total abundance were strongest within the 50-m buffer (Fig. 2), and therefore this buffer width was selected for the main statistical analyses. Human population density and percentage of built-up area were positively correlated in the 50-m buffer (r_S = 0.62, $p < 0.001$, $n = 167$, Fig. S1). Both measures captured wide urbanization gradients surrounding the studied transects in the 50-m buffer (human population density: mean = 13.3, sd = 20.6 and range 0.0–109.2 inhabitants/hectare; percentage of built-up area: mean = 40.0, sd = 28.0 and range 0.0–100.0% of the total buffer area).
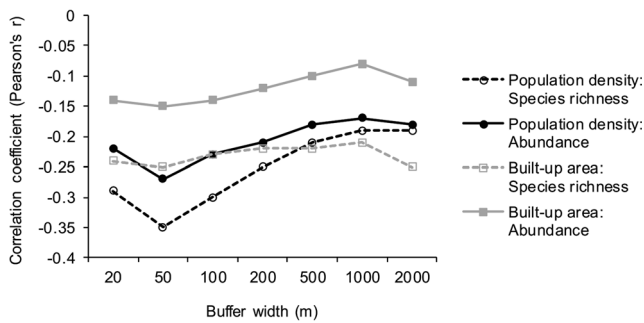
Fig. 2 Correlations of the human population density and built-up land cover with butterfly species richness and total abundance in landscape buffers of different width

Negative effect of urbanization on butterfly species richness and total abundance

Butterfly species richness and total abundance significantly decreased with increasing human population density and built-up land cover (Table 1; Fig. 3). The effect of human population density on species richness and total abundance remained significant also if human population density was $\log_e$-transformed. Butterfly species richness and abundance incrementally decreased 11% and 12%, respectively, as human population density increased with 10 residents per hectare. Similarly, with every 10% increase in built-up land cover, species richness decreased 5% and abundance 6% (Table 1). Variation in butterfly species richness and total abundance

were better explained by human population density than percentage built-up area based on model comparisons (ΔAIC > 10), which indicates a stronger response of butterflies to increasing human population density than to built-up area.

Varying sensitivity of butterfly species to urbanization

In all examined butterfly species, the highest abundances and occurrence probabilities were observed in landscapes with low human population density, and for most species, in landscapes with low cover of built-up areas (Figs. S2–S5). The abundance and occurrence probability of two butterfly species, *Aphantopus hyperantus* and *Ochlodes sylvanus* decreased statistically significantly with both increasing human population density and built-up land cover (Table 1 and 2). Abundance of nine butterfly species decreased statistically significantly with increasing human population density, whereas abundance of six species decreased significantly with increasing built-up area (Table 1). Different sets of species responded significantly to the two urbanization measures: *Coenonympha glycerion*, *Thymelicus lineola*, *Gonepteryx rhamni*, *Aglais io*, *Pieris brassicae*, *P. napi* and *P. rapae* responded negatively only to human population density, whereas *Brenthis ino*, *Lycaena virgaureae* and *L. phlaeas* only to proportion of built-up area (Table 1). The results were qualitatively similar for butterfly occurrence probability,

Fig. 3 Observed species richness and abundance of butterflies in relation to human population density and built-up land cover in the 50-m buffer with lines depicting predicted values based on the generalized linear mixed models
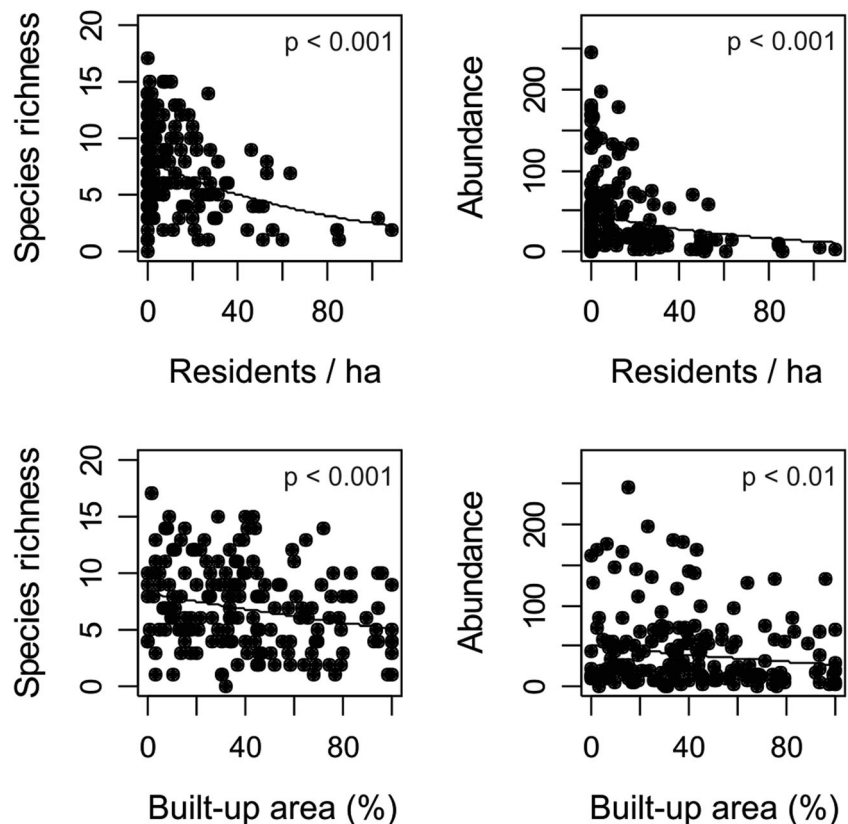
Table 1 The effects of human population density and built-up land cover in the 50-m buffer on butterfly species richness and total abundance as well as abundance of individual species, and the model predicted changes when population density or built-up land cover increases 10 units

	n	Population density (residents / ha)		Change (%) when population density increases 10 residents/ha	Built-up area (% of land area)		Change (%) when built-up area increases 10%
		Estimate	Std. error		Estimate	Std. error	
Community level results							
Species richness	166	-0.011***	0.002	-10.7	-0.005***	0.001	-4.7
Total abundance	166	-0.013***	0.003	-12.1	-0.006**	0.002	-6.2
Species level results							
Coenonympha glycerion	14	-0.096*	0.047	-61.5	-0.005	0.010	-5.3
Lycaena virgaureae	14	-0.083	0.046	-56.6	-0.034*	0.013	-28.6
Erebia ligea	18	-0.058	0.030	-44.1	-0.020	0.010	-17.8
Nymphalis antiopa	14	-0.037	0.025	-31.0	-0.019	0.011	-17.2
Lycaena phlaeas	33	-0.029	0.015	-24.8	-0.017*	0.008	-15.9
Ochlodes sylvanus	66	-0.026**	0.009	-22.6	-0.012*	0.005	-11.0
Aphantopus hyperantus	76	-0.025**	0.009	-21.9	-0.013**	0.005	-12.6
Polyommatus icarus	22	-0.022	0.017	-19.9	-0.003	0.008	-2.7
Polyommatus semiargus	49	-0.021	0.011	-19.1	0.001	0.005	1.3
Thymelicus lineola	95	-0.019*	0.007	-17.1	-0.006	0.004	-5.6
Brenthis ino	27	-0.018	0.014	-16.9	-0.020*	0.009	-18.5
Pieris brassicae	70	-0.017*	0.008	-15.5	-0.003	0.005	-2.8
Gonepteryx rhamni	57	-0.015*	0.007	-13.5	-0.005	0.004	-4.5
Vanessa atalanta	51	-0.014	0.008	-12.7	-0.008	0.005	-7.6
Pieris napi	143	-0.011**	0.004	-10.6	-0.005*	0.003	-5.3
Aglais io	127	-0.011*	0.005	-10.2	-0.005	0.003	-5.3
Polyommatus amandus	26	-0.010	0.013	-9.5	-0.009	0.008	-8.8
Pieris rapae	141	-0.010*	0.004	-9.3	0.000	0.003	0.2
Aglais urticae	108	-0.007	0.005	-6.4	-0.003	0.003	-2.7

*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$

n indicates the number of transects in which the species was observed. The species have been ordered according to the sensitivity of their abundance to human population density (based on the model estimate). Species recorded in less than 10 transects were excluded from species-specific analyses

although slightly different species responded significantly to human population density and built-up area (Table 2). Only four out of the 19 species tested showed no relationships between abundance or the probability of occurrence and either of the two urbanization measures (Table 1 and 2).

Although none of the examined butterfly species showed positive responses to increasing urbanization, there was much variation in the sensitivity of the species to our two measures of urbanization (Table 1, and 2, Figs. S2–S5). The abundance of 12 out of 19 species was better explained by human population density than by the cover of built-up area ($\Delta AIC > 2$), whereas built-up area was a better predictor for only one species ($\Delta AIC > 2$). The abundance of six species was equally well explained by the two urbanization measures ($\Delta AIC < 2$). Different sensitivity of species to urbanization is illustrated in Fig. 4 by the results of four selected example species. *Lycaena virgaureae* and *C. glycerion* represented highly sensitive species completely absent from the more urbanized areas, whereas *Aphantopus hyperantus* was a less sensitive intermediate case

and *Pieris napi* was one of the few species seen even in the most heavily urbanized areas. In three of these species we found a similar difference in their response to the two urbanization measures: human population density was a better predictor of their abundance and occurrence probability than the proportion of built-up area. However, in *L. virgaureae* built-up area was a better predictor than human population density (Fig. 4).

Species traits

The responses of butterfly communities to increasing urbanization were significantly associated with community weighted means of habitat specificity (measured by habitat breadth) and mobility (measured by wingspan; Fig. 5, Table S3). Mean habitat specificity of recorded individuals significantly decreased with increasing human population density, indicating that the butterfly communities became more dominated by habitat generalists with increasing urbanization. However, this relationship was not significant when urbanization was measured by the

Table 2 The effects of human population density and built-up land cover in the 50-m buffer on the occurrence probability of butterfly species, and the model predicted changes when population density or built-up land cover increases 10 units

	n	Population density (residents / ha)		Change (%) in probability of occurrence when population density increases 10 residents / ha	Built-up area (% of land area)		Change (%) in probability of occurence when built-up area increases 10%
		Estimate	Std. error		Estimate	Std. error	
Lycaena virgaureae	14	-0.093	0.051	-60.4	-0.039**	0.015	-32.5
Coenonympha glycerion	14	-0.084	0.046	-56.8	-0.009	0.012	-9.0
Erebia ligea	18	-0.061*	0.031	-45.9	-0.020	0.011	-18.2
Nymphalis antiopa	14	-0.041	0.027	-33.6	-0.020	0.012	-18.5
Aphantopus hyperantus	76	-0.040**	0.013	-33.0	-0.019*	0.007	-17.0
Pieris brassicae	70	-0.035*	0.014	-29.4	-0.010	0.007	-9.7
Ochlodes sylvanus	66	-0.034**	0.012	-29.1	-0.016*	0.007	-14.6
Polyommatus semiargus	49	-0.032*	0.014	-27.6	0.000	0.007	0.5
Lycaena phlaeas	33	-0.029	0.016	-25.2	-0.017	0.009	-16.0
Thymelicus lineola	95	-0.029**	0.011	-24.9	-0.014*	0.007	-12.8
Gonepteryx rhamni	57	-0.025*	0.011	-21.8	-0.009	0.007	-8.7
Vanessa atalanta	51	-0.024*	0.012	-21.4	-0.015*	0.007	-14.2
Polyommatus icarus	22	-0.024	0.018	-21.3	-0.002	0.009	-1.7
Pieris rapae	141	-0.022*	0.010	-19.6	0.000	0.008	-0.3
Brenthis ino	27	-0.019	0.016	-17.6	-0.023*	0.010	-20.4
Polyommatus amandus	26	-0.014	0.015	-12.7	-0.010	0.010	-9.5
Aglais urticae	108	-0.012	0.009	-11.2	-0.008	0.007	-7.7
Aglais io	127	-0.011	0.009	-10.5	-0.005	0.007	-5.3
Pieris napi	143	-0.011	0.010	-10.3	-0.005	0.008	-4.8

*** = p < 0.001; ** = p < 0.01; * = p < 0.05

n indicates the number of transects in which the species was recorded. The species have been ordered according to the sensitivity of their occurrence probability to human population density (based on the model estimate). Species observed in less than 10 transects were excluded from the analyses

proportion of built-up area (Fig. 5, Table S3). Average mobility of butterfly individuals significantly increased with increasing urbanization based on both studied urbanization measures (Fig. 5, Table S3). Thus, butterfly communities tended to increasingly consist of mobile individuals in more densely populated areas and increasingly built-up areas.

Discussion

We found consistently negative effects of both human population density and built-up area on species richness, abundance and the occurrence of most butterfly species. Our results generally agree with previous studies on the effects of urbanization on butterflies (Blair and Launer 1997; Stefanescu et al. 2004; Clark et al. 2007; Bergerot et al. 2011; Konvicka and Kadlec 2011; Lizée et al. 2012; Melliger et al. 2017; Ramírez-Restrepo and MacGregor-Fors 2017; Merckx and Van Dyck 2019; Tzortzakaki et al. 2019) and other flower-visiting insects (Bates et al. 2011; Geslin et al. 2016; Lagucki et al. 2017). However, our study highlighted three important and less studied aspects. First, we found that the negative effect of high human population density was markedly stronger than the

effect of built-up area. Second, we found considerable variation in the sensitivity of individual butterfly species to urban development, and third, this variation was systematically associated with species traits reflecting habitat specificity and mobility, leading to homogenization of butterfly communities with increased urbanization. Thus, butterfly communities dominated by habitat generalists and large, highly mobile species characterized the most urbanized areas. Below we discuss the implications of these findings separately.

Differing effects of human population density and built-up area

Thus far, few studies have simultaneously evaluated effects of increasing human population density and proportion of built-up area on butterfly assemblages in urban contexts (Blair and Launer 1997; Clark et al. 2007; Concepción et al. 2016), and these studies have shown inconsistent effects of the two drivers. Compared to some earlier studies, our study captured a wider range in both human population density and proportion built-up area, which may explain why we found clear effects of both urbanization gradients (cf. Concepción et al. 2016). In our study, human population density explained
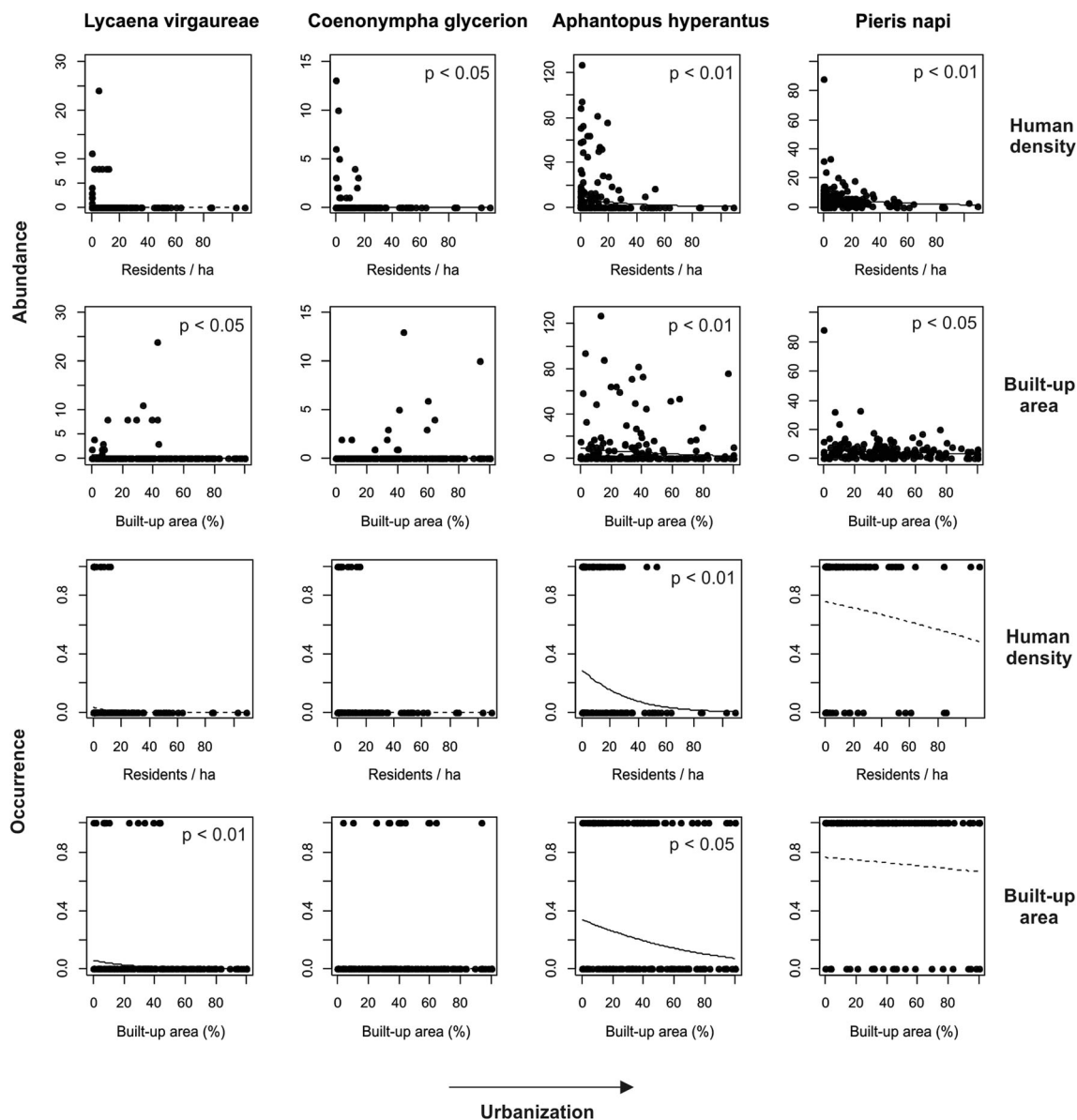
Fig. 4 Responses of four butterfly species to increasing human population density and cover of built-up area. These species were selected to represent the observed variation in the sensitivity to urbanization between the 19 butterfly species that were analysed individually. Solid and dashed lines depict statistically significant and non-significant predicted responses of the species based on the fitted generalized linear mixed models (Table 1 and 2)

species richness and abundance of butterflies particularly well in areas with high human density, whereas in areas with low human density there was much more variability in the two butterfly measures (Fig. 3). A probable explanation for the latter observation is that areas with low human density in our study may have been dominated either by (semi-)natural habitats potentially suitable for butterflies or by densely built-up industrial or commercial areas largely unsuitable for butterfly breeding (cf. Fig. 1b, c). In contrast, the predictive power of the cover of built-up area did not differ much between transects situated in areas with either low or high proportion of built-up area (Fig. 3). Similarly, the explanatory power of human population density tended to

be higher compared to the proportion of built-up area regarding the occurrence and abundance of individual butterfly species. These results suggest that human population density is a better indicator of butterfly diversity than built-up area especially in areas where human density is high (cf. Clark et al. 2007; Concepción et al. 2016). At first glance, this may seem counter-intuitive, because truly built-up areas should be unsuitable habitat for butterflies by definition, whereas the presence of humans *per se* should not necessarily be harmful at all for butterflies (but see Kitahara and Fujii 1994). We suggest that at least three, potentially interacting causes, can influence the predictive capacity of these two broad urbanization measures.

Fig. 5 Mean habitat breadth (inverse measure of habitat specificity) and wingspan (measure of mobility) of butterfly individuals recorded for each of the 167 transects in relation to human population density and built-up land cover within the 50-m buffer. Lines depicting predicted values based on the linear models are shown for traits with a statistically significant response to the urbanization gradient
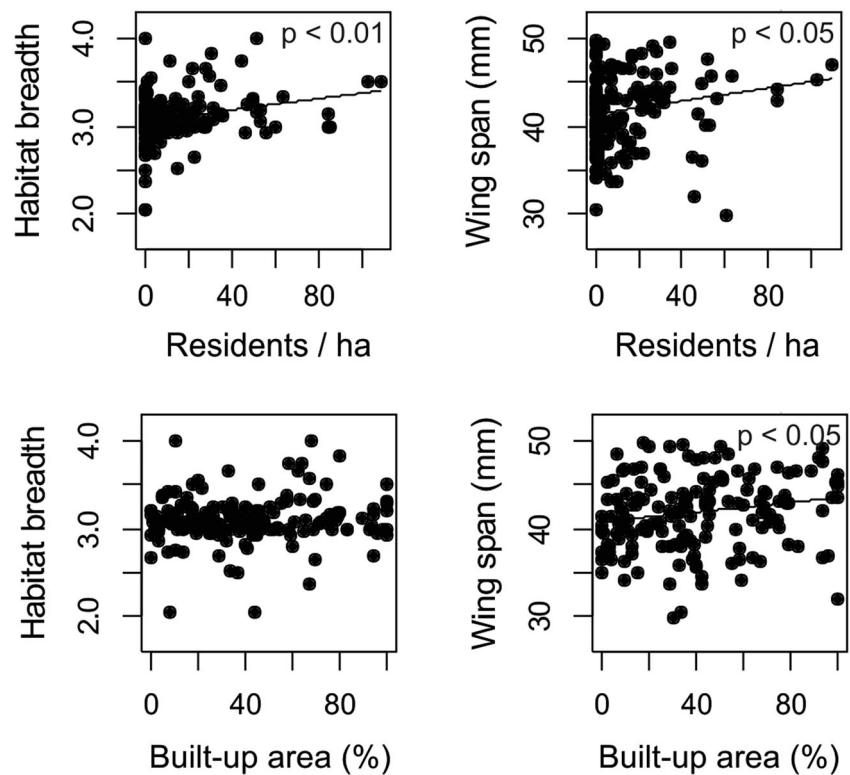
First, our measure of built-up area provided a coarse proxy of unsuitable habitat for butterflies, as it contained a variety of built-up habitat classes including varying extents of associated natural or semi-natural vegetation, such as private gardens and road verges with vegetation strips. Small urban green areas embedded in heavily built-up areas may nevertheless contain relatively rich butterfly assemblages, given that local habitat quality is sufficiently high (Aguilera et al. 2019). The availability of high-resolution satellite imagery has improved and allows for more detailed distinction between measures of built-up and urban green spaces. However, a single urbanization measure that attempts to cover a broad range of built-up areas is likely to include habitat heterogeneity caused by variation in the amount of natural vegetation between various kinds of built-up areas (McDonnell and Hahs 2008). Second, high human population density is usually associated with high intensity of habitat management of urban green spaces in the neighbourhood (Beninde et al. 2015; Olivier et al. 2016; Aronson et al. 2017). Butterflies negatively respond to intensive habitat management, such as frequent mowing of lawns (Öckinger et al. 2009; Aguilera et al. 2019). Third, human population density may be a better indicator of negative human disturbance (Kitahara and Fujii 1994) than built-up area from the butterflies' viewpoint especially in the most densely populated areas. This is because human disturbance may increase sharply from relatively low-density residential areas to very densely populated city areas with high multi-storey buildings (and thus cause a decrease in butterfly

habitat quality) although at the same time the proportion of built-up area may show only a modest increase. As a result of the combination of the three above-mentioned causes, human population densities may better reflect critical habitat conditions in urban green areas than proportions of built-up areas. Further studies with appropriate spatial sampling designs are needed to examine what kind of mechanisms directly affecting butterflies can explain the differing effects of human population density and built-up area that we found in the current study.

Notably, built-up area (sometimes referred to as impermeable or impervious areas; often also including roads and parking areas) has been a more commonly used measure of urbanization than human population density (for recent reviews see Moll et al. 2019; Padilla and Sutherland 2019). Built-up area (or its opposite measure, proportion of urban green spaces) was used to measure urbanization in 15 previously published relevant urban butterfly studies examining butterfly communities along an urbanization gradient outside the tropics, whereas the effects of human population density were included only in three of these studies (Blair and Launer 1997; Clark et al. 2007; Concepción et al. 2016). Our results suggest that using human population density as an indicator of urbanization is more advisable compared to built-up area, because the former is a more reliable indicator of butterfly diversity in urban areas. In addition, using human population density as an urbanization measure makes results of different studies on the effects of urbanization more readily comparable

which is a highly desired characteristic of an urban biodiversity study (McDonnell and Hahs 2008; Moll et al. 2019). However, further studies comparing the two broad urbanization gradients are needed to confirm the generality of our findings.

Varying sensitivity of butterfly species to urbanization and species traits

Most previous butterfly studies on the effects of urbanization have focused on species richness and community composition (e.g. Olivier et al. 2016; Melliger et al. 2017; Merckx and Van Dyck 2019; Tzortzakaki et al. 2019), but only rarely on species-specific responses (Hardy and Dennis 1999; Konvicka and Kadlec 2011; Leston and Koper 2017). In our study, the large number of 167 sampled butterfly transects of sufficient length (roughly 1 km) enabled also species-specific analyses on the effects of the two urbanization measures. Even though none of the 19 recorded species responded positively to increasing urbanization in terms of their abundance or probability of occurrence, we found a wide variation in how strongly individual butterfly species suffered from urbanization. The species-specific occurrence patterns ranged from otherwise relatively common species that were almost completely lacking from the most heavily urbanized areas to species persisting even in some of the most densely populated areas in Helsinki. Interestingly, abundances of three of the least sensitive species to urbanization (*A. io*, *P. napi* and *P. rapae*) showed significant decreases with increasing human population density but no significant decreases with built-up area.

As predicted, the studied species traits, habitat specificity and mobility, were significantly associated with the butterfly responses to urbanization at the community level. Species with high habitat specificity and low mobility (small size), such as *C. glycerion* and *L. virgaureae*, showed higher sensitivity to urbanization than habitat generalists and mobile (large-sized) species, such as *P. napi* and *A. io*. Individuals of the latter group of species dominated the butterfly communities in the most urbanized areas (see also Merckx and Van Dyck 2019). These species are characterized by an open population structure (Hanski and Kuussaari 1995; Thomas 1995), with relatively continuous populations over large areas and individuals typically moving long distances during their adulthood. Such species are capable of utilizing small habitat patches, which probably helps them to occur in urban landscapes characterised by often highly scattered resources for both adults and larvae. Species with an open population structure were also reported to dominate butterfly communities of the most urbanized areas in the greater Paris area in France (Bergerot et al. 2011). Our observation that the occurrence of butterflies correlated most strongly with urbanization measured in the close surroundings of the butterfly transects (i.e.

the 50 m buffer) is well in agreement with the findings by Merckx and Van Dyck (2019) and further highlights the local filtering effect of species' mobility in shaping butterfly communities (Krauss et al. 2003; Cozzi et al. 2008).

An additional mechanism that may potentially favour large-sized, mobile butterfly species in urban areas is higher nitrogen deposition in urban compared to rural areas (Bettez and Groffman 2013). This increases both the dominance of nitrophilous plant species and nitrogen content (and thus nutritional value) of plants, which both are positively related to butterfly size (Pöyry et al. 2017). Soil nitrogen enrichment and increasing plant nitrogen content have been shown to benefit large-bodied but harm small-bodied lepidopteran species (Pöyry et al. 2017). Combined with the higher dispersal ability of large species, nitrogen enrichment may thus further enhance the occurrence of large mobile species in urban areas. A good example of a butterfly species group benefitting from nitrogen deposition in urban areas are the mobile nettle-feeding species such as *Aglais urticae*, *A. io* and *Vanessa atalanta* (Merckx et al. 2015).

Finally, our results support the hypothesis that increasing urbanization drives biotic homogenization of butterfly communities (McKinney 2006), a process that has previously been shown for intensively cultivated agricultural landscapes (Ekroos et al. 2010) and recently also for urban areas (Merckx and Van Dyck 2019). It is notable that also some earlier urban butterfly studies have reported that species with low mobility (Bergerot et al. 2011; Olivier et al. 2016) and narrow habitat requirements (Clark et al. 2007; Lizée et al. 2011) tend to be lacking from more urbanized areas, suggesting the impoverishment of urban butterfly communities and biotic homogenization. Hence, the heavily urbanized environment is particularly hostile to sedentary habitat specialist butterflies that need large areas of well-connected suitable habitat for long-term persistence. In a recent study, Knop (2016) reported biotic homogenization due to urbanization also in three other groups of insects (true bugs, leafhoppers and beetles) living in birch trees in six cities in Switzerland.

Conclusions

Detailed understanding on how urbanization affects biodiversity is needed to secure biodiversity and the well-being of the growing human population living in cities (Fuller et al. 2007; Beninde et al. 2015). Here, we have reported the results of an exceptionally intensive sampling of butterflies along the urbanization gradient in the city of Helsinki, including a comparison of two widely used measures of urbanization – human population density and the proportion of built-up areas – in their effects on butterfly species richness and the occurrence of individual butterfly species. The results suggest that human population density is a more reliable indicator of the negative

effects of urbanization on butterflies than the proportion of built-up area, especially in densely populated areas. Thus, using human population density as an indicator is preferable when suitable data on its spatial variation are available. Similar comparisons of the two urbanization measures are needed in other groups of organisms in order to test the generality of our finding. Besides reduced species richness and abundance, urbanized butterfly communities suffer from community impoverishment and biotic homogenization, because most habitat specialist and sedentary butterfly species tend to disappear when urban development proceeds and human population density increases. Further studies are needed to examine to what extent the same species suffer from different kinds of human disturbance. For example, it could be predicted that species with similar species traits would suffer from intensifying land use both in agricultural and urban areas.

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