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Urban moth communities suggest that life in the city favours thermophilic multi-dimensional generalists

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Biodiversity is challenged worldwide by exploitation, global warming, changes in land use and increasing urbanization. It is hypothesized that communities in urban areas should consist primarily of generalist species with broad niches that are able to cope with novel, variable, fragmented, warmer and unpredictable environments shaped by human pressures. We surveyed moth communities in three cities in northern Europe and compared them with neighbouring moth assemblages constituting species pools of potential colonizers. We found that urban moth communities consisted of multi-dimensional generalist species that had larger distribution ranges, more variable colour patterns, longer reproductive seasons, broader diets, were more likely to overwinter as an egg, more thermophilic, and occupied more habitat types compared with moth communities in surrounding areas. When body size was analysed separately, results indicated that city occupancy was associated with larger size, but this effect disappeared when body size was analysed together with the other traits. Our findings indicate that urbanization imposes a spatial filtering process in favour of thermophilic species characterized by high intraspecific diversity and multi-dimensional generalist lifestyles over specialized species with narrow niches.

1. Introduction

Earth is urbanizing rapidly, and this results in human-influenced environmental changes that can modify the conditions for life, and the patterns of biodiversity in urban as opposed to rural (non-urban) areas. Urbanization is an ongoing process and a driver of ecosystem change, and cities currently harbour more than half of the global human population [1,2]. Compared with rural areas, urban environments are characterized by elevated levels of air pollution, light pollution (likely of considerable relevance for nocturnal insects such as moths), different visual backgrounds (of relevance for protective coloration, whether via camouflage or warning signals), higher temperatures, fragmented and often monotonous green areas (such as lawns), and depauperate communities with strikingly different species compositions of plants and animals [3–5]. Thus, urbanization provides opportunities to study how species and communities respond to a wide range of environmental changes and rising human pressures [6,7]. Ultimately, this can inform about community assembly rules and the relative importance of stochastic events and deterministic processes in structuring species compositions [8–11].

Although plant species richness tends to increase in cities (mainly due to ornamental flowers in parks and gardens), many animal taxa seem to respond in the opposite way, and the processes underlying the patterns of biodiversity in cities are poorly understood [4,5,12]. Besides potentially influencing species richness, the environmental conditions that characterize urban environments may affect species composition in urban communities. Previous studies indicate that species in urbanized environments do not constitute a random sample of those available in surrounding rural areas [13–15]. This is likely because urban environments impose selection and constitute an ecological filtering process whereby species with certain traits might be favoured and better able to colonize and persist, whereas species with other traits are less likely to colonize and more likely to disappear [7,13,16,17]. More specifically, it can be hypothesized that urbanization imposes spatial sorting that is predictable, in that it favours species with high dispersal enhancing phenotypes, behavioural flexibility, bold and explorative personalities, broad niches, high intra-specific genetic and phenotypic diversity, and generalist lifestyles that buffer against environmental change, promote establishment success, and reduce extinction risk [7,13,16,18–22].

In agreement with the above reasoning, some previous studies suggest that large species and generalists are over-represented in urban environments compared with small and specialized species [3,7,14,17]. Another recent study reports that species with a high dispersal capacity (inferred from the functionality of the wings), and preference for high temperatures are disproportionately common in cities [23]. These findings are consistent with the notion that the contrasting environmental conditions in urban as opposed to rural areas impose selection and ecological filtering that drives intraspecific evolutionary modifications and induces shifts in community species composition.

However, for some traits the consequences of urbanization generate conflicting predictions. For example, the increased ambient temperatures in cities result in increased metabolic costs [24], particularly for larger species, and this is expected to drive shifts towards smaller body sizes. On the other hand, the higher dispersal capacity that comes with increased body size might enable larger individuals and species to better use the scarce and patchily distributed resources in cities [13,14,23]. To resolve this paradox, it is necessary to identify which specific species traits are key to success in urban environments. To determine the direction(s) of the filtering process on different traits (e.g. whether urbanization favours larger or smaller body size) also requires comparisons based on large numbers of species that differ in many attributes.

Moths have several features that make them suitable for investigations on this topic. They constitute a species rich and highly diverse group that contribute to ecosystem services and functional diversity by being important in food webs and as pollinators [25–27]. It has even been argued that species composition of moths can be used to assess both the functioning and health of urban ecosystems [28,29]. A number of studies that explore species-specific responses to urbanization among invertebrates across multiple traits have been published mainly from urban areas in central Europe [3,14,17]. Yet, little is known about whether multiple traits have an impact on urban community composition across larger spatial scales, and whether different traits interact to influence urban communities. This may lead to biased conclusions regarding what attributes enable species to cope with environmental change and conditions influenced by human activities, and ultimately hamper projections regarding future biodiversity responses to global change.

In this study, we surveyed moth communities in three cities in northern Europe and compared them with neighbouring moth assemblages that comprise species pools of potential colonizers. We analysed occurrence patterns and compared species traits using data for 858 species of moths. Based on predictions from theory and previous empirical findings on how species traits impact colonization and establishment, we expected that communities in urban environments were dominated by multi-dimensional generalist moth species characterized by large distribution ranges, varied habitat preferences, broad diets, variable colour patterns and a long reproductive season [3,7,13,15,16,18–22]. Because urban environments tend to be warm with patchy resource distributions, we also expected species in the cities to have a high thermal tolerance, and either a small (low energy demands) or large (high dispersal capacity) body size [13,14,17,23]. We had no *a priori* prediction regarding what overwintering stage(s) might be overrepresented in urban environments.

2. Material and methods

(a) Study areas and sampling

We studied 858 night active macro moths from the 14 families Brahmaeidae (1), Cossidae (4), Drepanidae (16), Endromidae (1), Erebidae (86), Geometridae (304), Hepialidae (5), Lasiocampidae (16), Limacodidae (2), Noctuidae (358), Nolidae (11), Notodontidae (36), Saturniidae (2) and Sphingidae (16) (see electronic supplementary material, table S1) in three cities and regions in Europe; Halle (Germany, Sachsen-Anhalt), Kalmar (Sweden, county of Kalmar) and Lund (Sweden, Skåne) (figure 1). The three cities varied somewhat in climate (mean annual temperature and precipitation) and with regard to light pollution, number of inhabitants, availability of green space and population size (table 1). To sample moths in the cities, we used one automatic light trap [32] equipped with a mercury vapour lamp that was in operation from April 2011 to October 2012 in each city. The traps were checked every 10–21 days throughout the season, and all macro moth species were determined to species level and registered. With this method, all species of macro moths caught by our light sources during 3570 light-hours (distributed over all dark hours during the year) were included in our dataset. The traps had a similar position in each city between the city centre and the outskirts with the exact trap locations; Halle: Viktor-Scheffel-Str. 8, 51°29′36.04″ N, 11°58′28.13″ E, Lund: Sölvegatan 37, 55°42′51.21″ N, 13°12′26.27″ E and Kalmar: Landgången 4, 56°39′31.24″ N, 16°21′45.97″ E.

To evaluate the consequences of ecological filtering, we compared the community composition and species traits of moths collected in the three urban environments with the moth assemblages of potential colonizers, as based on previous observations in the corresponding regions. The species composition of the neighbouring macro moth communities (858 species) was determined based on previously published records for the region/province to which each city belonged (electronic supplementary material, table S1). For Halle we used records for the province Sachsen-Anhalt [33], for Lund the province Skåne, and for Kalmar the county of Kalmar [34] was used. The data on the three regional species pools were all based on data from 1990 to 2011. The cities had a rather central position, with the exception of Kalmar that is situated on the coast, facing the Baltic sea in the east—an area that is unlikely to influence the composition of the species pool. Province records have a long lasting tradition, are continuously kept up to date and provide the most reliable information on species occurring in the surroundings of the surveyed cities [33,34]. Many moth species can disperse over long distances (greater than 10 km), and it was assumed that species previously recorded in each province constituted potential colonizers of the respective city [35–38].

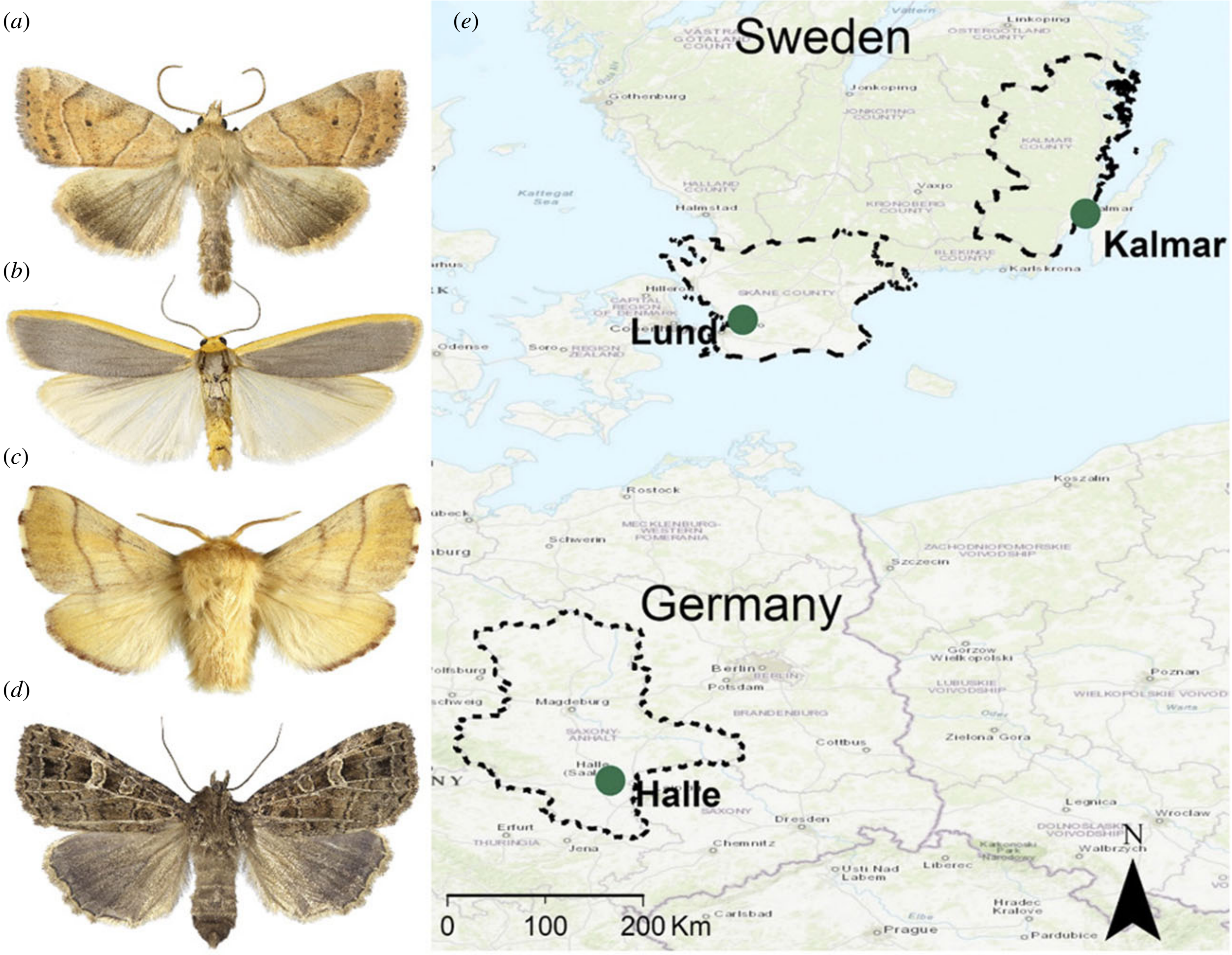

Figure 1. Examples of species with different frequency of occurrence in the three cities. From top to bottom, (*a*) *Cosmia trapezina* occurred in all three cities, (*b*) *Eilema complana* in two, (*c*) *Malacosoma neustria* in one and (*d*) *Naenia typica* was present in all three surrounding species pools of rural areas but did not occur in any of the studied cities. The three cities in northern Europe included in the present study (indicated by dots), and the three surrounding species pool of rural areas as delimited by dashed lines (*e*). Photos by Vladimir Kononenko. Map source from Esri. 'World Topographic Map', 29 September 2019. (Online version in colour.)

However, species that had not been recorded in the provinces in recent years (after 2010), and species known from only one relict population in the province, were excluded from the analyses, as they could not be expected to occur in the studied cities.

(b) Species traits

We extracted data on eight species traits (temperature preference, length of reproductive season, range size, body size, habitat use, dietary breadth, colour pattern variation and overwintering life stage) from the literature for all species studied (see electronic supplementary material, table S1). We used the most recent taxonomy ([39], see electronic supplementary material, table S1).

(c) Statistical analysis

Given that we studied eight predictor traits, it was important to evaluate redundancy among these variables to avoid problems potentially associated with correlated predictors [40]. Redundancy among predictors can exist in two forms: pairwise correlation and multi-collinearity. While correlation measures the degree of association between pairs of variables, multi-collinearity refers to the situation when there is a concurrent relationship between multiple variables (i.e. when some variables can be predicted from a combination of other variables). We pre-processed the set of predictor variables by applying correlation and multi-collinearity analyses. Results did not point to any strong signatures of correlated predictors or multi-collinearity (electronic supplementary material, table S2, figure S1), and we therefore included all eight traits in the remaining statistical analyses [41].

We tested whether the moth species that were caught in the three cities could be characterized by any of the eight species traits or whether urban moth communities comprised species with random trait values. A species was denoted 'present' in a city if it had been caught in the city by our traps, and denoted 'absent' if it had not been caught in the city but was present in the regional species pool. We used a generalized linear mixed (GLMM) effects model with a binomial error distribution, a log-link function and treatment contrasts. We examined whether results and conclusions were robust or sensitive to alternative analytical approaches by analysing our data in three different ways. In all three analytical approaches, city occupancy (present or absent) was considered the dependent (response) variable, each species recorded in the region/province surrounding the city contributed with one observation, the species traits represented eight explanatory variables, and the three cities and their associated provinces were considered as separate samples (replicates). The sample sizes (number of species recorded in each region) were 853 for Halle, 718 for Lund and 695 for Kalmar.

In the first analysis, all traits were combined and analysed together in the same GLMM. In this approach, city occupancy (0/1) was treated as a binary response variable, and temperature preference, length of reproductive season, range size, body size, habitat use, dietary breadth, colour pattern variation and overwintering life stage were treated as fixed explanatory variables (see above). Region was included as a fixed explanatory factor to account for variation in community composition among the three

Table 1. Characteristics of the three studied cities. The proportion green spaces was measured based on the CORINE land cover data from the year 2000 [30] and light pollution data were based on the artificial light pollution data [31]. Climate data is based on the yearly average data from 1980 to 2010.

city	species richness[a]	species/urban km^2	human population	size (km^2)	proportion green spaces	light pollution (m/ha)	temperature °C (annual average)	precipitation mm yr^{-1}	longitude	latitude
Halle	853 (268)	1.99	236 991	135	22%	26.9	9.1	483	11.973°	51.497°
Lund	718 (215)	8.27	88 788	26	19%	13.1	9.0	666	13.207°	55.714°
Kalmar	695 (178)	8.9	36 392	20	11%	11.7	7.7	484	16.362°	56.659°

[a] Species richness of moths in the region and species present in the city in brackets.

cities and regions. We did not evaluate the contributions of two-way and higher-order interactions between the explanatory traits, to avoid problems associated with over-parametrizing statistical models. Species nested in region and species nested in taxonomic family were included as random terms in the model to partially account for greater similarity in the response variable among species that are more similar in general ecology and life history because they are more closely related [42–45]. The models were built based on AIC (Akaike's information criterion), by comparing all possible models with different combinations of the explanatory variables. We present the model with the lowest AIC as it is considered the model that best fit our data. We used the glmer function in the lme4 package for the GLMMs and the Anova function in the car package to test each main effect after the other main effects (type II) in the GLMMs. We used the function r.squaredGLMM described in Nakagawa & Schielzeth [46] to obtain values for the explained variance in the final GLMMs.

Second, we evaluated whether results and conclusions regarding the roles of the eight species traits were similar or varied among the different cities. To that end, we performed a separate GLMM for each city/region. In these analyses, all eight species traits were included as fixed explanatory variables, taxonomic family was included as a random term and model selection was performed as described above. Third, we evaluated whether and how results and conclusions regarding city occupancy changed depending on whether species traits were analysed together in one model or one at a time in separate models. For that purpose, we performed eight separate GLMs, one for each trait. City was included as a fixed factor to account for variation in community composition among the three cities and regions. Because we analysed each trait separately, significant associations may occur by chance. Adjusting critical significance levels for multiple tests has problems [47,48]. Nevertheless, we indicate in the results sections whether the reported test results remained statistically significant after sequential Bonferroni corrections, thereby enabling readers to judge for themselves.

(d) Non-metric multidimensional scaling for visualization of results

Besides the approaches outlined above that were used to evaluate the statistical significance of associations of species traits with city occupancy, we used an additional, separate statistical method based on ordination to generate plots that enabled visualization of results. To illustrate and describe the trait composition that characterizes moth species collected in urban environments and how they differ from moth assemblages in neighbouring areas we used non-metric multidimensional scaling (NMDS) [49]. For this, we used a species by trait matrix that included presence/absence and the number of cities occupied by each species. The NMDS was performed with the R package vegan [50] using the Bray–Curtis dissimilarity measure.

3. Results

Of the 858 moth species recorded in the combined species pool, 392 species were caught in at least one of the cities, 196 species were caught in one city only and 90 species were caught in all three cities. In Halle, we caught 286 of the 853 species that were included in the species pool, in Lund 215 of the 718, species in the species pool, and in Kalmar we caught 178 of the 695 species (electronic supplementary material, table S1).

When data for all three cities and all eight trait variables were analysed together, the final best fitting model included all traits except body size (AIC = 2276, table 2), and provided

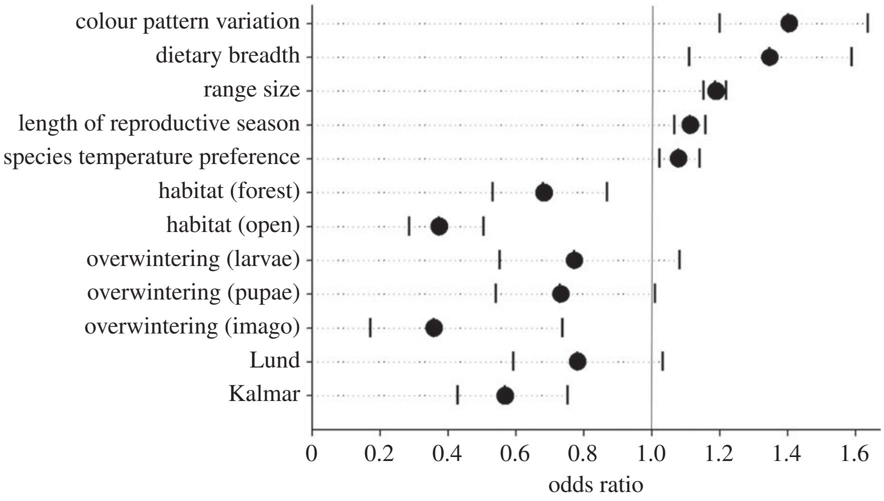

Figure 2. Odds ratios (dots ± 95% CI denoted by vertical lines) for the relationship between moths present in the cities (compared with a species pool of surrounding rural areas) and the seven species traits that remained in the model with the lowest AIC value (table 2). The vertical line shows the odds ratio of 1.0. Each of the categorical variables are compared to a reference category i.e. habitat (open, forest species to generalist species), overwintering (larvae, pupae, imago to egg) and Lund/Kalmar to Halle.

Table 2. Estimates from the final best-fitting generalized linear mixed effect model (lowest AIC) for the relationship between moths present in the cities (compared with a species pool of surrounding rural area) and eight species traits. The proportion of the variance explained by the fixed factor alone was 0.30, and the proportion of the total variance explained by fixed and random factors together was 0.36.

source of variation	d.f.	χ^2	*p*-value
range size	1	136.78	<0.001
colour pattern variation	1	18.320	<0.001
length of reproductive season	1	26.580	<0.001
habitat	2	45.790	<0.001
dietary breadth	1	9.630	0.002
species temperature preference	1	7.980	0.005
overwintering	3	9.262	0.026
city	2	18.918	<0.001

a better representation of the data compared to the null model that only included the random terms (AIC = 2661.6). Results thus provide strong evidence for urban filtering across multiple species traits. Overall, species in the cities had significantly larger distribution ranges, more variable colour patterns, a longer reproductive season, higher temperature preferences, broader diets and were more inclined to be habitat generalists (table 2, figure 2). Further, species in the cities were more likely to overwinter as an egg compared to imago, larvae and pupae (table 2, figure 2). Species recorded in the surrounding regions were also more likely to occur in the city of Halle, compared to both Lund and Kalmar (table 2, figure 2).

The results and conclusions regarding the roles of the explanatory species traits for city occupancy were largely robust to choice of analytical approach (tables 2–4). Although statistically important variables, coefficient estimates and parameter values varied somewhat between the statistical models, the results were surprisingly similar. However, the results for body size and temperature preference varied depending on whether they were analysed together with other traits in the same model or analysed alone (table 4). The association of city occupancy with overwintering stage did not remain statistically significant when adjusting for multiple comparisons (table 4). Comparisons of mean body sizes showed that, when the contributions of all other traits were not taken into consideration, species occurring in the city were larger on average compared with species in the region (table 4). However, this effect of body size did not manifest when all traits were analysed together (tables 2 and 3). The conclusion was opposite for temperature preferences. When all traits were analysed together in the multivariate GLMM, the results indicated that moth species caught in the city were more likely to be thermophilic (tables 2 and 3), but temperature preference was not significant in the univariate GLMs (table 4). The results for the remaining six traits were qualitatively similar (had the same direction) when analysed separately and together with the other traits (tables 2–4).

The results generated by the NMDS illustrated and confirmed that urban moth communities were structured based on species traits (electronic supplementary material, figure S2). The results further indicated that urban communities differed from the regional species pool. This was evident for each of the three cities/regions and also for the number of cities the species occupied (from zero to three, see electronic supplementary material, figure S2).

4. Discussion

(a) Traits characterizing urban communities

We explored whether moth communities in urban areas primarily included generalist species with broad niches that are able to cope with more novel, variable, fragmented, warmer and unpredictable environments shaped by human activities. Results showed that urban moth communities consisted largely of multi-dimensional generalists with larger distribution ranges, more variable colour patterns, longer reproductive seasons, broader diets, tended to occupy more habitat types, were

Table 3. Comparisons of results from the final best-fitting generalized linear mixed effect model (lowest AIC) based on separate analyses of data for each of the three cities. The analyses evaluated which of the eight species traits were associated with city occupancy (compared with a species pool of surrounding rural area). Asterisk indicates that the association remained significant after sequential Bonferroni correction. AIC values for the models were for Halle = 926.8, Kalmar AIC = 649.6, Lund AIC = 689.0.

	Halle		*Kalmar*		*Lund*	
variable	χ^2	*p*-value	χ^2	*p*-value	χ^2	*p*-value
range size	79.80	<0.001*	13.02	<0.001*	53.28	<0.001*
length of reproductive season	9.56	0.002*	10.71	0.001*	9.82	0.002*
colour pattern variation	17.19	<0.001*			2.81	0.093
dietary breadth			8.14	<0.001*	11.23	<0.001*
species temperature preference	2.15	0.143	9.97	0.002*		
body size	2.69	0.101				
habitat use	13.27	0.001*	20.13	<0.001*	22.57	<0.001*
overwintering	5.16	0.160			6.27	0.099

more likely to overwinter as an egg, and were also more thermophilic compared with species of moths recorded in surrounding areas. From a long-term eco-evolutionary perspective, cities may be thought of as offering novel habitats and resources ready to be colonized and used by species that have the capacity to do so [51,52]. On average, only about one third of the moth species that made up the pool of potential colonizers available in surrounding rural areas were present (caught) in the three cities included in our study. Urban environments thus seem to impose a filtering process that negatively influences species richness. This finding is in agreement with studies of butterfly and bird communities [15,53], and moth communities that were reduced by 82% in urban areas compared to rural areas in Belgium [17].

Another key finding that emerged from our analyses is that moth communities in the three cities studied here did not constitute random subsamples of the species that made up the pool of potential colonizers recorded in the surrounding rural areas. Instead, results from the comparisons of species characteristics between city exploiters and moth species in rural areas pointed to an important role of spatial sorting and species filtering, thus suggesting an important role of deterministic processes rather than stochastic events for community assembly [8–11]. Specifically, our results suggest that urbanization imposes a strong filtering process in favour of multi-dimensional generalist species characterized by large range size, habitat and diet generalists, and a high intraspecific diversity (table 4; electronic supplementary material, table S3 and figure S2). As a result of continued urbanization and biotic homogenization [17], future communities are expected to comprise fewer species and an overrepresentation of species having broader niches and more generalized lifestyles, and a lower incidence of specialized species. This is likely to apply across spatial scales, taxonomic groups and trophic levels, based on the finding that results seem to be general among birds [54] and several groups of invertebrates [17,23].

For range size, length of reproductive season and habitat use, the results regarding how different phenotypic traits responded to the urbanization filtering process were qualitatively very similar across the three cities. Body size was only important in one city. For the other traits the model fit improved in two out of the three cities (table 3). The reasons for these minor discrepancies are probably mainly due to the lower statistical power when data are analysed separately for each city. Further, the discrepancies they might reflect differences in human population size, area, proportion of green space, annual average temperature, precipitation, and light pollution. Nevertheless, that results were comparable for most traits across the three cities (table 4; electronic supplementary material, table S3), suggests that the community assembly rules [8–11] that influenced species composition of moths were similar, and further indicates that deterministic ecological and environmental filtering processes were more important than stochastic events. This adds an important layer of generalization to the issue under investigation, and suggests that the effects that the fundamental ecological processes involved (e.g. dispersal, colonization and extinction) have on species with different characteristics are predictable, at least in the sense that they are repeatable in space. Species traits have also been found to be reliable predictors of spatial trends and temporal dynamics across several taxonomic groups [3,38,55–59].

(b) Traits targeted by the ecological and environmental filtering that shapes urban moth communities

The smallest city (in terms of both human population size and area) had the lowest species number and the lowest proportion of the species pool present (and vice versa for the results for the largest city). This is a surprising finding as the opposite could be expected if the regional species pool represents the source of potential colonizers, and if urbanization can be seen as a filtering process *per se*. The equilibrium theory of island biogeography [60] posits that species richness should be higher in larger cities. That species richness increased with city size might reflect in part that more habitats are available in larger cities, but independent of the city the species in the cities are characterized by multi-dimensional generalists. That the number of species per urban square kilometre was highest in the smallest city might reflect in part that trapping effort per city area decreased with increasing city size (table 1).

A reassuring finding (from a methodological perspective) was that results and conclusions regarding the associations of different species traits with city occupancy were largely

Table 4. Comparison of the number of species and the mean (±s.d.) for each continuous trait variable (n.a. for categorical variables) of moth species present in urban and surrounding rural areas for three cities in northern Europe. χ^2, *p*-values and d.f. from univariate linear regressions for presence/absence in each city in relation to each trait one by one, while treating city/region as a fixed factor in the model. *N* = number of species. For frequency distribution of the categorical variables see electronic supplementary material, table S3. Asterisk indicates that the association remained significant after sequential Bonferroni correction.

city	**Halle**		**Kalmar**		**Lund**				
N	**286**	**567**	**178**	**518**	**215**	**503**			
traits	**present**	**absent**	**present**	**absent**	**present**	**absent**	**d.f.**	χ^2	***p*-value**
range size	28.97 (±3.96)	25.13 (±5.57)	28.89 (±4.47)	26.62 (±4.70)	29.54 (±3.24)	25.86 (±5.15)	1	259.467	<0.001*
colour pattern variation	0.64 (±0.72)	0.41 (±0.61)	0.58 (±0.73)	0.48 (±0.64)	0.63 (±0.70)	0.44 (±0.64)	1	35.205	<0.001*
length of reproductive season	7.84 (±3.18)	6.86 (±2.85)	7.76 (±3.01)	6.55 (±2.39)	7.69 (±2.97)	6.47 (±2.34)	1	81.285	<0.001*
habitat	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	2	104.855	<0.001*
dietary breadth	2.57 (±0.65)	2.35 (±0.71)	2.74 (±0.52)	2.41 (±0.67)	2.74 (±0.52)	2.35 (±0.71)	1	103.767	<0.001*
body size	35.27 (±11.29)	33.97 (±11.82)	36.59 (±10.10)	32.93 (±11.29)	34.97 (±8.35)	33.10 (±11.87)	1	18.41	<0.001*
overwintering	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	3	9.417	0.024
species temperature preference	6.91 (±2.76)	6.84 (±2.41)	6.60 (±3.31)	6.95 (±2.42)	6.37 (±2.56)	6.94 (±2.39)	1	0.366	0.545

independent of whether the traits were analysed one at a time or together, except for body size and temperature preference. This suggests that variation among species in at least six of the eight analysed traits contribute in important ways to the ability of moth species to colonize, cope with and persist in challenging urban environments. That species with large geographical range distributions were overrepresented in the cities was expected, as they occur across larger regions, including urban areas and cities, compared to species with restricted ranges [17,61]. That species with a high colour pattern variation were overrepresented in cities is consistent with previous evidence that more variable colour patterns in moths is associated with larger intraspecific trait variation also in other (morphological, behavioural, and life history) phenotypic dimensions [62], and with increased colonization success, more stable population dynamics, and decreased extinction risk [42,43,45]. Moreover, light pollution [63] and non-native plant species [5] might create more heterogeneous and novel visual backgrounds in cities that are more suitable for species with variable colour patterns [64]. Altered predator communities in cities have been found in a previous study [23], and this might favour species with variable colour patterns. A longer reproductive season may be favourable in cities as it extends the possibilities to use and find resources over time and space, compared to species with a short reproductive season.

That diet and habitat generalists were overrepresented in the cities may be reflective of that food and habitat resources are novel, diverse, and only temporarily available [5,12,17,52]. Species associated to open habitats were less likely to be present in the cities (odds ratio 0.37 to generalist species), probably reflecting that most open habitats in cities are strictly managed lawns and parks with low overall species richness of plants [51]. In contrast to our results, a recent study reports that open habitat species are overrepresented in urban areas, and speculate that this could be an effect of the increased heat tolerance among open habitat species [17]. In view of these last findings, a change in cities towards less intensively managed areas may allow for a richer biodiversity [12,51,65]. It remains to be explored whether the declining species richness and biotic homogenization observed in this study allows for accurate predictions regarding dominating species traits in urban moth communities in other areas, on other continents, and in urban communities of other types of organisms.

(c) Body size and temperature preference responses depend on analytical approach

Our conclusion regarding the role of body size differed depending on analytical approach. Several previous studies report that urbanization favours larger species, possibly because larger size is associated with a superior dispersal and greater ability to use fragmented habitats and patchily distributed resources [3,7,14,23]. For example, Merckx *et al.* [13] report on community-level shifts in body size (forewing length) based on data for 23 species of butterflies and 202 species of macro-moths (wing span). Similarly, other studies report on both community-level and intra-specific shifts towards larger species and individuals in urban communities, based on individual measures and community weighted wing length data [14,17].

Community weighted variables used in previous studies might potentially suffer from the drawback that it is difficult to combine multiple community traits and taxonomic levels in the same statistical model [13,66]. In agreement with this conjecture, we found that when body size was analysed alone, moth species that occurred in the city were larger on average compared with species in the surrounding rural areas. However, when the role of body size was evaluated together with the other seven traits, the city, and taxonomic family, the association between city occupancy and large body size disappeared. This may be reflective of that larger size, while perhaps not being very important in itself, may be an adequate proxy for ecological generalization, and for taxonomic groups and traits that are well suited for life in urban environments. For temperature preferences the pattern was opposite, an association of city occupancy with thermophily was indicated by the multivariate but not by the univariate analyses. This emphasizes the importance of using both univariate and multivariate analytical approaches in ecological studies to better understand the importance of different predictor traits on species occurrence patterns.

5. Conclusion

The depauperate urban moth communities, with only about one-third of the species in rural areas occurring also in urban environments, is an alarming finding. Considering that moths contribute with many important ecosystem services [25–29], this points to a severe future biodiversity decline and biotic homogenization that may have far reaching implications for the functioning of communities and ecosystems. We found that urban moth communities were not random subsamples of neighbouring communities. Instead, our results point to the conclusion that urbanization imposes a spatial sorting filtering process that reduces species richness and results in biotic homogenization, favouring thermophilic and multi-dimensional generalist species characterized by high intraspecific diversity. The associations between species traits and city occupancy were mostly qualitatively robust and repeatable across the three regions (albeit with some exceptions). This is indicative of generality and predictability of the ecological and evolutionary drivers involved in the community assembly process. Future investigations of cities across other latitudes and with higher population densities will reveal whether our results are more broadly applicable, and whether the mechanistic drivers that structure urban communities may continue to inform about eco-evolutionary consequences and biodiversity responses to global environmental change. It can be hypothesized that species possessing those trait value combinations that enable them to cope with life in the city will also be particularly successful in the future when urbanization continues.

Data accessibility. Data are provided in the electronic supplementary material.

Authors' contributions. M.F. and L.B.P. conceived the study. M.F., L.B.P. and P.-E.B. collected data from the field and information on species traits, M.F. analysed the data. A.F. and M.F. wrote the first draft. All authors contributed to the final version and approved the submitted manuscript.

Competing interests. We declare we have no competing interests.

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