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Urbanization hampers biological control of insect pests: A global meta-analysis



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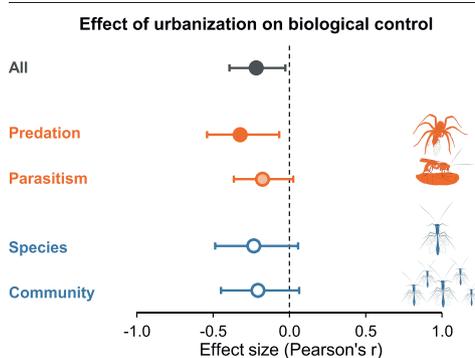
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HIGHLIGHTS

- Meta-analysis on the effects of cities on arthropods and biological control.
- Cities promoted the outbreaks of sap-feeding insect pests.
- Poor disperser arthropod natural enemies decreased towards urbanized areas.
- Overall biological control of insect pests declined with advancing urbanization.

GRAPHICAL ABSTRACT



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ABSTRACT

Biological control is a major ecosystem service provided by pest natural enemies, even in densely populated areas where the use of pesticides poses severe risks to human and environmental health. However, the impact of urbanization on this service and the abundance patterns of relevant functional groups of arthropods (herbivores, predators, and parasitoids) remain contested. Here, we synthesize current evidence through three hierarchical meta-analyses and show that advancing urbanization leads to outbreaks of sap-feeding insects, declining numbers of predators with low dispersal abilities, and weakened overall biological pest control delivered by arthropods. Our results suggest that sedentary predators may have the potential to effectively regulate sap-feeders, that are one of the most important pests in urban environments. A well-connected network of structurally diverse and rich green spaces with less intensive management practices is needed to promote natural plant protection in urban landscapes and sustainable cities.

1. Introduction

The expansion of cities is predicted to increase by 1.2 million km² in the coming decades (Seto et al., 2012). The global intensification of urban land use is a significant driver of landscape and habitat transformations (e.g. fragmentation, vegetation degradation), having substantial impacts on ecological assemblages and their associated ecosystem functions and services (Grimm et al., 2008). Arthropods are suitable indicators of anthropogenic

changes by having short generation times and representing a megadiverse group with a broad spectrum of trophic levels and functional traits that support key ecosystem functions (e.g. herbivory, decomposition, predation, and pollination) (McIntyre, 2000). Therefore, the number of studies examining how urban landscapes and urbanization processes (defined here as reduced vegetation cover and increasing proportion of impervious surfaces) affect arthropods has increased considerably in recent decades (Dale and Frank, 2018; Fenoglio et al., 2020). However, observations report inconsistent (positive, negative or neutral) effects of urbanization on the abundances of herbivores (Bergerot et al., 2010; Dale and Frank, 2014; Herrmann et al., 2012; Korányi et al., 2021; Liu et al., 2016; Long and

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Frank, 2020) and their natural enemies (Alarukka et al., 2002; Burks and Philpott, 2017; Dale and Frank, 2014; Rocha and Fellowes, 2020; Tamburini et al., 2016; Zolotarev and Belskaya, 2015).

The variety of responses may arise for many reasons. First, feeding guild of arthropods provides important information about ecological traits related to resource-acquisition, behavior and life-cycle (Raupp et al., 2010) and thus might influence their response to urbanization [e.g. positive effects on sap-feeders (Dale and Frank, 2014; Korányi et al., 2021), adverse effects on chewing folivores (Long and Frank, 2020; Moreira et al., 2019), and inconsistent effects on leaf miners (Denys and Schmidt, 1998; Dobrosavljević et al., 2020; Moreira et al., 2019)]. Second, arthropods from different taxonomic and functional groups have distinct sensitivities to the altered abiotic conditions of urban environments (e.g. urban heat island, air pollution) that may shape their adaptive abilities to urbanization (Fenoglio et al., 2020). For example, increased proportion of impervious surfaces filters arthropods based on dispersal ability, thus taxonomic groups with a high proportion of good dispersers are less affected by urbanization than those dominated by less mobile species (Korányi et al., 2021; Merckx et al., 2018a, 2018b; Merckx and Van Dyck, 2019; Vergnes et al., 2014). Third, the ecological level of organization may also influence the urbanization effects, because competition for limited resources in city centers increases within communities (Shochat et al., 2010). This may lead to different outcomes for arthropod communities compared to observations focusing on single species.

As part of sustainable pest management, biological control is one of the most important ecosystem services that arthropods provide, especially in cities where synthetic chemicals have major impacts on the environment and human health (Lowe et al., 2019). In addition to landscape and habitat characteristics, herbivorous pest suppression is influenced by other biotic

factors including natural enemy activity and prey density (Langellotto and Denno, 2004; Rusch et al., 2010). Thus, although landscape and habitat simplification can reduce biological control, similar to the aforementioned controversial responses of the involved trophic groups, the impact of urbanization on this service is difficult to predict (Egerer et al., 2018c; Fenoglio et al., 2009; Turrini et al., 2016).

In this study, we performed a set of global meta-analyses in the frame of systematic reviews to evaluate the effects of urbanization on arthropods and biological control (Fig. 1). More specifically, we posed the following questions: (1) Does urbanization affect the overall abundance of insect herbivores and arthropod natural enemies in a similar way? (2) Do arthropods from different groups (i.e. feeding guild of herbivores; functional and taxonomic group, and dispersal ability of natural enemies) respond similarly to urbanization? (3) Does urbanization affect the biological control of insect herbivores by arthropod natural enemies? (4) Is organization level (i.e. species vs. community) relevant to determine urbanization effects on arthropod abundances and biological control?

2. Material and methods

2.1. Literature search

We conducted a systematic literature survey using keyword searches in two major databases, Web of Science (SCI-EXPANDED index) and Scopus, for studies that examined the effect of urbanization on (1) abundance of insect herbivores and (2) arthropod natural enemies, and (3) biological control of herbivorous insects by arthropods (until 6th May 2020, for detailed search terms see Supplementary material). This resulted in a total number of 1415 potential publications. Moreover, we found

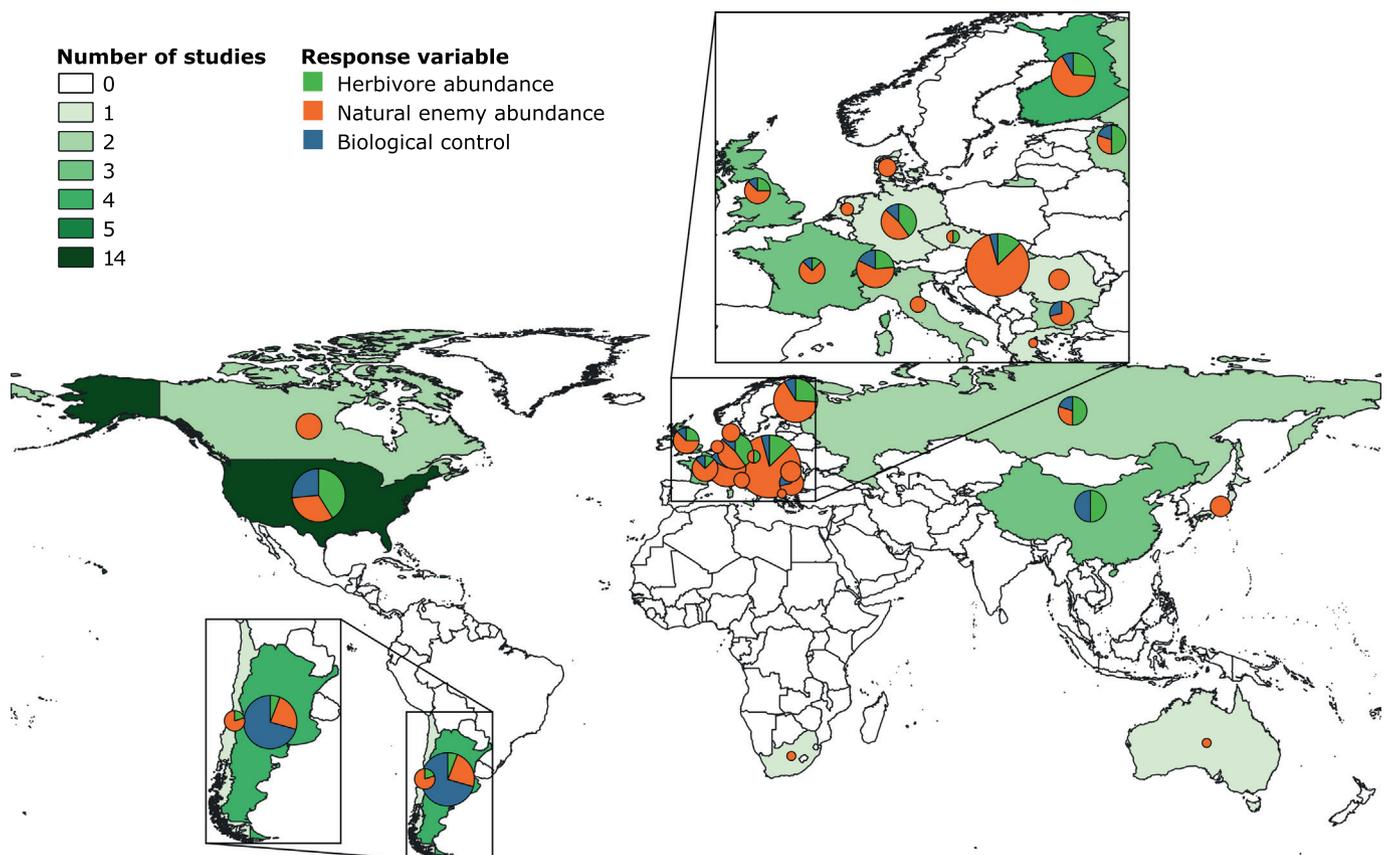


Fig. 1. Geographic distribution of studies and response variables in the meta-analyses. Countries where at least one study was carried out, are shaded according to the number of studies. The size of the pie charts is proportional to the number of outcomes for each country. Green, orange, and blue colors within charts respectively show the proportion of outcomes for herbivore, natural enemy abundance and biological control.

additional articles through cited references from primary studies and recent reviews (Fenoglio et al., 2020; Miles et al., 2019).

After filtering for duplicate hits located by both databases and screening papers by title and abstract, articles were screened based on a predefined set of inclusion and exclusion criteria (for the detailed selection process, see PRISMA flow diagram in Fig. S1). We applied the following inclusion criteria for study selection: studies that (1) investigated the abundance of herbivorous insects and/or arthropod natural enemies and/or biological control of herbivorous pest insects by arthropods in areas with contrasting levels of urbanization (e.g. urban vs. rural or urban vs. suburban vs. rural areas) or along a continuous urbanization gradient; (2) included at least three spatial replicates per urbanization category; and (3) reported mean, standard deviation, standard errors of mean or confidence interval (CI), and sample size for urbanization categories, or reported statistics (F , t , Chi-square, Pearson's r or R^2 values and sample size) on urbanization gradient effect. Studies that focused on (1) non-arthropod herbivores and natural enemies; (2) aquatic species; and (3) treatments under controlled environments (e.g. in greenhouse or laboratory) were excluded. We found 24 relevant papers comprising 54 observations for herbivore abundance, 36 papers comprising 144 observations for natural enemy abundance, and 16 papers with 50 observations for biological control (Tables S1, S2, and S3). A list of articles excluded during full-text filtering and reasons for exclusion is presented in Table S4.

The geographical distribution of the studies showed a quite unequal pattern. A relatively high proportion of the studies were performed in Europe (48.2%) and America (37.5%), whereas the rest of the studies were carried out in Asia (10.7%), Africa (1.8%), and Australia (1.8%). In the case of European studies, natural enemy abundance was the most frequent outcome (72.5%), whereas studies conducted in America provided observations primarily on biological control (40.1%) (Fig. 1).

2.2. Data extraction

We extracted data preferably on species-level abundance and biological control (i.e. control by certain natural enemy species) and used community-level data if species-level observations were not available. When the same study reported outcomes for more cities, host plants, arthropod taxa, and study years separately, each of them was considered as a separate observation ($n = 31$ studies). We considered outcomes on different sampling occasions as separate observations if cumulative temporal data was not provided ($n = 3$). In order to obtain meaningful quantitative responses, we excluded observations reported from less than 20% of the study sites along urbanization gradients within each study.

For the abundance of insect herbivores and arthropod natural enemies, we extracted data reported on the number and density of individuals and considered them as response variables. When abundance data were provided for more herbivore or natural enemy species within the same study, we considered species only, of which abundance exceeded 5% of the total sample. In a study ($n = 1$), where abundance data were reported for more development stages of the same species, we selected the stage with the highest density. We excluded community-level observations if species from different trophic levels were included (e.g. herbivorous or mycophagous species listed among predators) or it was unclear whether herbivores or predators were exclusively examined. We considered abundance data on each functional group of natural enemies (i.e. predators and parasitoids) as a separate observation.

Herbivores were categorized based on feeding guild (sap-feeders, leaf miners, wood borers, stem borers, defoliators, gall makers, and fruit feeders), and natural enemies were categorized based on the functional group (predators and parasitoids), dispersal ability (poor and good dispersers) and taxonomic group (earwigs, true bugs, carabids, coccinellids, rove beetles, net-winged insects, flies, wasps, mites, spiders, and harvestmen). For dispersal ability, we considered species-level observations and used data on wing morphology and flight capability for insects (poor dispersers: apterous, brachypterous, predominantly brachypterous species, and winged species with low flight capability; good dispersers:

macropterous and predominantly macropterous species with good flight capability) and ballooning propensity for spiders (poor dispersers: rarely or non-ballooning species; good dispersers: frequently ballooning species) (see Table S2 for the assigned dispersal categories and Table S5 for the expectations related to all moderators).

For biological control, we used observations on parasitism/predation rate ($n = 12$), predation-prey ratio ($n = 2$), number of parasitized prey ($n = 1$), number of attacks on prey ($n = 1$), and on the difference between the abundance of protected (i.e. caged) and predation-exposed prey ($n = 1$) as response variables. We considered data on each interaction type (i.e. predation and parasitism) as separate observations.

We used the proportion of impervious surfaces (e.g. buildings, roads, and other paving surfaces; $n = 13$), principal components analysis scores based on variables describing urbanization intensity such as distance from the city core, vegetation and impervious surface coverage ($n = 3$), distance to the city center ($n = 2$), and proportion of vegetation-free area ($n = 1$) as indices of urbanization for studies with the gradient-based approach. When a given study used several urbanization gradients ($n = 4$) or compared urban areas with others that were relatively similar in terms of urbanization ($n = 12$), we chose the gradient with the widest data range and comparison with the highest contrast.

2.3. Effect size calculation

We used Pearson's r correlation coefficient (and its variance) for an effect size measure, which was calculated in different ways depending on the urbanization approach: (1) from two-level categorical data (e.g. urban vs. rural comparison), we calculated Hedges' g (i.e. unbiased standardized mean difference) based on mean, standard deviation and sample size (number of spatial replicates) of abundance and biological control levels of urban and rural areas. Then, Hedges' g values were transformed to Pearson's r correlation coefficients; (2) from three-level categorical data (e.g. urban vs. suburban vs. rural comparisons), we calculated Hedges' g for urban-suburban and suburban-rural comparisons separately, then these were transformed to Pearson's r (Lajeunesse, 2013). Then, we computed the combined urban-suburban and suburban-urban effect sizes considering multiple comparisons within a study (Borenstein et al., 2009); (3) from continuous urbanization gradients, Pearson's r was calculated from F , t , χ^2 , or R^2 data (Lajeunesse, 2013). Finally, we transformed all Pearson's r values to Fisher's z for all analyses, but back-transformed for data visualization. A negative effect size indicated a decrease in abundance or weakening biological control from rural to urban areas.

2.4. Meta-analysis

We used the 'rma.mv' function of the 'metafor' package (Viechtbauer, 2010) of R 3.5.0 statistical software (R Core Team, 2018) for all analyses. We performed hierarchical meta-analysis models separately for herbivore and natural enemy abundance and biological control, which allowed the incorporation of random and fixed effects (moderators) and the specification of nesting factors. As we often extracted more data points from a single article, we included a publication-level random effect as a nesting factor to consider the non-independence of observations within the same study. For the biological control analyses, where the studied plant species were provided for all observations (Table S3), we also considered the dependency of herbivores and herbivore-natural enemy interactions on the same plant species by including plant species as the second nesting factor in the models (see Supplementary material for model codes).

First, we performed random-effects summary meta-analyses to calculate the overall mean effect size for herbivore and natural enemy abundance data and biological control data separately. The output of each statistical test consisted of the mean effect size for the analysis with accompanying 95% CIs, and the total heterogeneity statistic (Q). The heterogeneity statistic is a weighted sum of squares tested against a χ^2 distribution. Estimates of the effect size were considered to be significantly different from zero if their 95% CIs did not include zero (Borenstein et al., 2009).

Second, we performed categorical meta-analyses. We used the following explanatory variables as moderators for the effects of urbanization: (1) level of organization (species and community) for all response variables; (2) feeding guild (sap-feeders, leaf miners, and wood borers) for herbivore abundance; (3) functional group (predators and parasitoids), (4) dispersal ability (poor and good), and (5) taxonomic group (carabids, coccinellids, true bugs, wasps, and spiders) for natural enemy abundance; and (6) type of interaction (predation and parasitism) for biological control (for the expectations, see Table S5). In case of each moderator, we ran separate models and excluded levels with less than five observations, thus four feeding guilds of herbivores (defoliators [$n = 1$], stem borers [$n = 1$], gall makers [$n = 2$], and fruit feeders [$n = 2$]) and six taxonomic groups of natural enemies (flies [$n = 1$], mites [$n = 1$], earwigs [$n = 4$], net-winged insects [$n = 2$], rove beetles [$n = 1$], and harvestmen [$n = 1$]) in order to obtain meaningful quantitative responses (Table S1 and S2). In the case of analysis on the dispersal ability, we used the taxon-level random effect as a second nesting factor. The total heterogeneity in the categorical meta-analysis is partitioned into variance explained by the categorical factor in the model (between-group heterogeneity) and residual error variance (within-group heterogeneity) with χ^2 tests indicating their significance. A significant between-group heterogeneity indicated that abundance or bio-control responses to urbanization differed based on the moderator categories (Borenstein et al., 2009).

2.5. Publication bias and sensitivity analysis

Since studies with larger effect sizes may be more likely to be published than studies with lower effect sizes (Rothstein et al., 2005), we explored the possibility of publication bias graphically (funnel plot) and statistically (Kendall's rank correlation test). The correlation test for funnel plot asymmetry examines the relationship between the standardized effect size and sample size across the studies. A significant p value may indicate publication bias, whereby studies with a small sample size are only published if they show large effect sizes. We also tested the robustness of the analyses by removing individually the studies providing more than 5% of each dataset (4 studies with 29 observations for herbivore abundance, 3 studies with 57 observations for natural enemy abundance, and 3 studies with 30 observations for biological control).

3. Results

We found a positive, but non-significant effect of urbanization on the abundance of insect herbivores and no overall effect of urbanization on arthropod natural enemies (Table 1; Figs. 2 and 3). However, the average level of biological control decreased significantly in more urbanized areas (Fig. 4). Feeding guild modulated the responses of herbivores to urbanization, as we found a strong positive effect of urbanization on sap-feeder abundance, but no significant effects on leaf miner and wood borer densities (Fig. 2). For natural enemy abundance, there was no marked moderation effect of functional group (predator or parasitoid) (Fig. 3). However, studies examining predation rates showed a significant negative effect of urbanization on biological control and a marginally significant negative effect on parasitism (Fig. 4). In addition, we found a strong contrast between species- and community-level observations for both herbivore and natural enemy abundances with a significant positive effect of urbanization on herbivore species and a marginally significant negative effect on natural enemy communities with marked between-group heterogeneities (Table 1; Figs. 2 and 3). For biological control, there was no significant moderation effect of organization level (Fig. 4). When considering dispersal abilities of natural enemies, we found that urbanization had a significant negative effect on the abundance of poorly dispersing species and no effect on species with good dispersal ability. Finally, we found substantial differences in reaction to urbanization between taxonomic groups with stronger positive effects on coccinellids and true bugs than carabids (Table 1; Fig. 3).

Validating the robustness of our study, we found no skewness in the funnel plots of effect size vs. sample size (Fig. S2), indicating no evidence of

Table 1

Summary table of hierarchical meta-analysis models showing total heterogeneity ("all," only effects of urbanization without moderators), and heterogeneities explained by moderators (level of organization [species and community] for all response variables; feeding guild [sap-feeders, leaf miners, and wood borers] of herbivores; functional group [predators and parasitoids], dispersal ability [poor and good], and taxonomic group [carabids, coccinellids, true bugs, wasps, and spiders] of natural enemies; and type of interaction [predation and parasitism] for biological control) with corresponding residual heterogeneities.

	<i>df</i>	<i>Q</i>	<i>p</i>
Abundance of herbivores			
All	53	289.599	<0.001
Feeding guild	2	4.639	0.098
Residual	40	143.329	<0.001
Level of organization	1	4.059	0.044
Residual	52	280.897	<0.001
Abundance of natural enemies			
All	143	1372.621	<0.001
Functional group	1	1.803	0.179
Residual	141	1367.372	<0.001
Level of organization	1	5.378	0.020
Residual	142	1357.412	<0.001
Dispersal ability	1	7.056	0.008
Residual	84	928.186	<0.001
Taxonomic group	4	14.670	0.005
Residual	123	1258.943	<0.001
Biological control			
All	49	201.012	<0.001
Type of interaction	1	1.435	0.231
Residual	48	191.415	<0.001
Level of organization	1	0.019	0.892
Residual	48	200.865	<0.001

publication bias in our dataset. Furthermore, Kendall's rank correlation tests did not show significant relationships between effect sizes and sample sizes in the meta-analysis models. Finally, our sensitivity analysis revealed that removing studies providing more than 5% of each dataset did not significantly change the model outputs (Table S6).

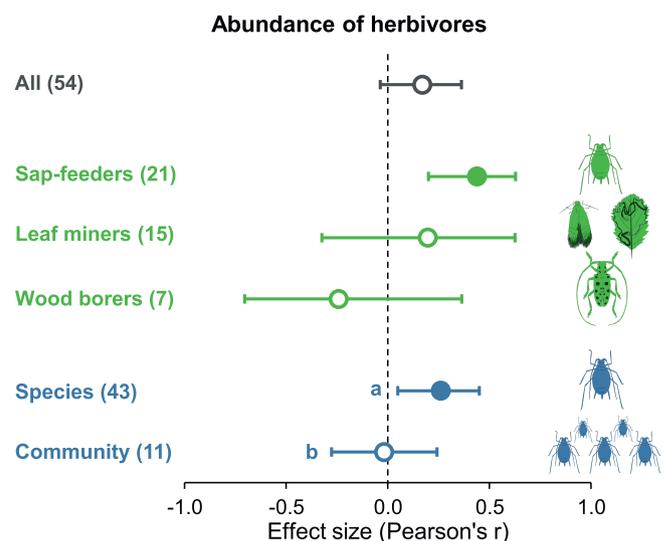


Fig. 2. The effects of urbanization on the abundance of herbivores depending on the feeding guild (sap feeders, leaf miners, and wood borers) and level of organization (species and community). Mean effect sizes and 95% CIs are shown. Filled symbols indicate a significant ($p < 0.05$) effect of urbanization (within-group heterogeneity). Significant differences between moderator levels are indicated by different letters (Table 1). Numbers in parentheses indicate the sample size.

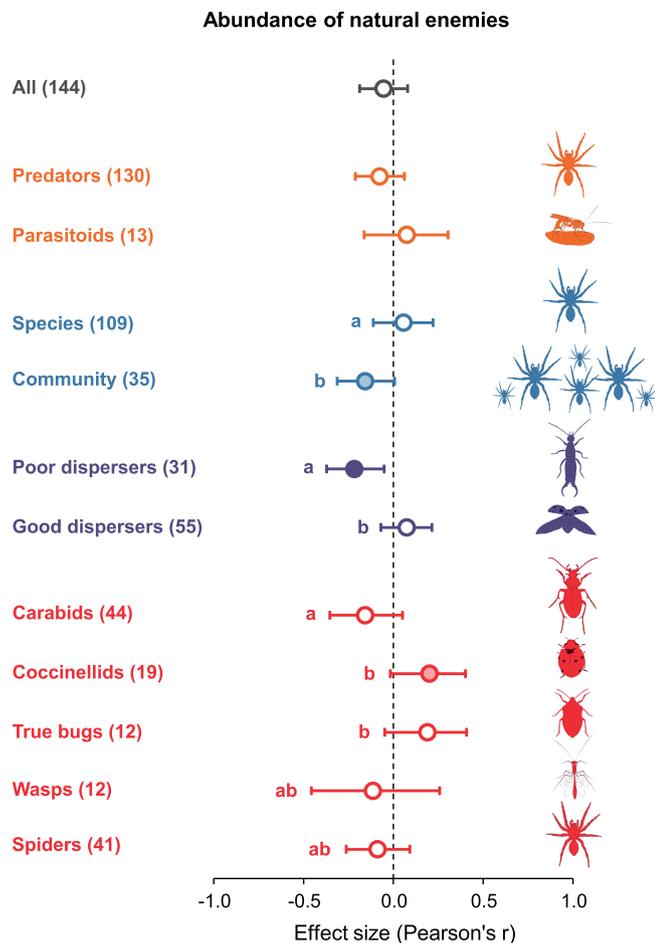


Fig. 3. The effects of urbanization on the abundance of natural enemies depending on the functional group (predators and parasitoids), level of organization (species and community), dispersal ability (poor and good dispersers), and taxonomic group (carabids, coccinellids, true bugs, wasps, and spiders). Mean effect sizes and 95% CIs are shown. The filled symbol indicates a significant ($p < 0.05$), transparently filled symbols indicate marginally significant ($0.05 \leq p < 0.1$) effect of urbanization (within-group heterogeneity). Significant differences between moderator levels are indicated by different letters (Table 1). Numbers in parentheses indicate the sample size.

4. Discussion

Studies investigating arthropods in urban environments are multiplying but no consensus exists about the actual effect of urbanization on herbivore and natural enemy densities and biological control. Our meta-analysis shows that although urbanization does not strongly affect the overall abundances of herbivores and natural enemies, it does reduce levels of biological control. Importantly, effects of urbanization were modulated by feeding guild, dispersal abilities and levels of organization; urbanization benefits sap-feeding insects and limits predator communities with poor dispersal abilities.

We found no evidence that urbanization uniformly enhances herbivore densities. Nevertheless, the abundance of each feeding guild showed different response patterns to urbanization. Increasing level of urbanization is associated with reduced vegetation cover and an increasing proportion of impervious surfaces making cities warmer than the surrounding areas (Grimm et al., 2008). Temperature is a crucial factor for the development of sap-feeder insects like aphids and scale insects, as warmer environments can contribute to their increased fecundity and faster development (Dale and Frank, 2014; Harrington et al., 2007). In addition, plant management

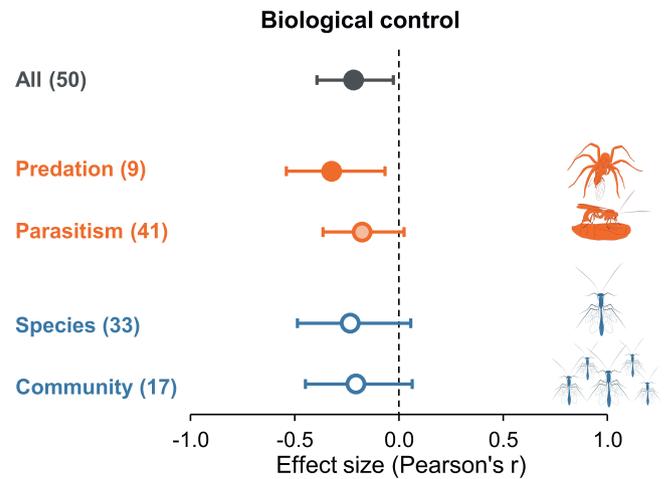


Fig. 4. The effects of urbanization on biological control depending on the type of interaction (predation and parasitism) and level of organization (species and community). Mean effect sizes and 95% CIs are shown. Filled symbols indicate a significant ($p < 0.05$), transparently filled symbol indicates marginally significant ($0.05 \leq p < 0.1$) effect of urbanization (within-group heterogeneity) (Table 1). Numbers in parentheses indicate the sample size.

practices in cities, including intensive pruning, irrigation, and fertilization have the potential to exacerbate sap-feeder infestations through improved host plant quality or weakened natural defenses of plants (Raupp et al., 2010). Such bottom-up effects combined with potential phenological mismatch between herbivores and their natural enemies may result in pest outbreaks in highly urbanized areas (Korányi et al., 2021; Meineke et al., 2014; Raupp et al., 2010). Although endophagous insects such as leaf miners and wood borers generally have a narrow host range and restricted movement in their early developmental stages, they may be less affected against altered local and landscape-level factors. For instance, in contrast to ectophagous species, by feeding inside the plant tissues, they are more protected against extreme microclimatic conditions (e.g. warm and dry environments) especially in small habitat fragments (Rossetti et al., 2017). However, wood borers were relatively underrepresented in our dataset (seven observations), which could also be a reason for missing effects of urbanization on this group.

In a meta-analysis on terrestrial arthropods, Fenoglio et al. (2020) found a negative effect of urbanization on natural enemies. However, they were interested in the effects of urbanization at the community level and not considered species-level observations, in which case we observed more positive responses. In addition, some of these community-level observations involved species from various functional groups [e.g. predators with mycophagous coccinellids (Egerer et al., 2018a) or herbivorous carabids (Niemelä et al., 2002)] which may also explain this different outcome. The lack of detection of overall natural enemy responses to urbanization in our study might be due to the major variabilities in responses across dispersal abilities or taxonomic groups. Indeed, abundance of natural enemies with limited dispersal abilities was significantly lower in urban than rural areas, in turn, good dispersers were unaffected by urbanization. Urban landscapes comprise patches of fragmented habitats immersed in a matrix of paved surfaces and artificial structures that act as physical barriers for arthropods making their dispersal to suitable resources difficult and risky (Raupp et al., 2010). Therefore, it is not surprising that urbanization filters arthropods based on mobility, and poor disperser species at higher trophic levels cannot reach great numbers in city centers (Korányi et al., 2021; Merckx et al., 2018b; Piano et al., 2017; Vergnes et al., 2014). In line with this, most of the studied carabid species were poor dispersers (64% of all species) compared to coccinellids and true bugs, which can explain the observed heterogeneity between

these taxonomic groups. Indeed, given that many species spread by walking, the dispersal of ground-dwelling arthropods is quite limited within an urban matrix (Vergnes et al., 2014). In contrast, associated features of urban environments (e.g. built-up areas, warmer temperatures, and artificial illumination) can result in increased activity and reduced site fidelity of coccinellids contributing to their increased numbers in highly urbanized areas (Egerer et al., 2018b). Moreover, coccinellids have a great tendency to aggregate on plants with large prey colonies (Honek et al., 2017; Piñol et al., 2009), therefore, the availability of aphids could promote their presence in cities. Our results suggest that urbanization has a similar effect on predatory true bugs.

Urbanization had more favorable effects on some species than overall herbivore communities indicating a high variance in herbivore species responses to urbanization. This might also indicate that studies on insect herbivores tend to focus on problematic species having outbreaks in cities (Dale and Frank, 2018). Furthermore, in the case of species-level observations on herbivores, several studies examined a single species reared in the laboratory and placed on potted plants along urbanization gradients (Rocha and Fellowes, 2020; Turrini et al., 2016). This may have released them from adverse interactions such as interspecific competition (Kaplan and Denno, 2007; Shochat et al., 2010) and may contribute to the positive effect of urbanization on herbivore species compared to communities. The observed negative effects of urbanization on natural enemy communities suggests potential destabilizing effects at the community scale and higher sensitivity to urbanization at higher trophic levels.

Our result coincides with previous findings showing that urbanization weakens top-down control of insect herbivores by arthropod natural enemies (Korányi et al., 2021; Raupp et al., 2010; Turrini et al., 2016). The functioning of species at higher trophic levels depends not only on the availability and connectivity of urban green areas, but also on their quality and management. Decreasing complexity of habitat patches and vegetation (e.g. plant community structure and diversity) is often associated with the reduced number of alternative prey items and refuges, unfavorable microclimatic variations, and thus altered food web structure and limited biological control services in cities (Burkman and Gardiner, 2014; Dale and Frank, 2018; Raupp et al., 2010). We found a stronger adverse effect of urbanization on predation than parasitism. This is an interesting result, as we expected a greater decrease in the level of biological control provided by this more specialized functional group compared to predators (Table S5). The reason for this may be that parasitism can be driven by the availability of herbivore hosts even in cities (Rocha and Fellowes, 2018; Tooker and Hanks, 2000), and thus, in particular, parasitoids of sap-feeder insects might be less disadvantaged by urbanization. In addition, parasitism is not only negatively affected by urbanization due to the presence of species tolerating high levels of anthropic disturbances and potentially impacting herbivore populations (Egerer et al., 2018c; Fenoglio et al., 2009). Although we were not able to analyze it directly, the decline of poorly dispersing predatory arthropods may be one possible explanation for the lower level of biological control in urban areas. Such predators can remain present even when insect herbivore populations are small, and thus, provide favorable predator/prey ratios. In contrast, highly mobile, non-sedentary predators generally exert maximum pressure when prey populations are large enough to overcome mortality rates due to predation (Pekár et al., 2015; Piñol et al., 2009; Welch and Harwood, 2014). For instance, relatively weak suppression of aphid populations by non-sedentary predators is often reported in agricultural landscapes (Gómez-Marco et al., 2016; Piñol et al., 2009; Welch and Harwood, 2014), which might also explain high aphid numbers in highly urbanized areas.

We have to note that our results rely primarily on studies conducted in America and Europe and observations on the abundance patterns of certain arthropod groups (especially aphids, carabids, and spiders). Furthermore, only a few studies considered other factors that could have a

potential impact on biological control and associated trophic groups (e.g. management and connectivity of green spaces). Therefore, further research, especially in large and rapidly urbanizing regions (e.g. India, China, and Africa), and observations on other groups of herbivores (e.g. defoliators, gall makers, stem borers, and fruit feeders) and natural enemies (e.g. earwigs, rove beetles, flies, and mites) are needed. In addition, more studies considering further aspects of urbanization, including the quality and spatial configuration of green areas within cities (e.g., distribution and connection with semi-natural areas), would help achieve a more holistic global picture.

5. Conclusions

Biological control is one of the most important services with an estimated economic value of more than 400 billion dollars per year worldwide (Rusch et al., 2010) and also relevant to urban forest functions, urban agricultural and horticultural productivity, and public health and wellbeing. Indeed, pest outbreaks in urban environments can lead to massive defoliation events, and it is estimated that natural pest control provides 1.12 billion dollars per year in urban agriculture globally (Clinton et al., 2018). Our meta-analyses demonstrated that factors associated with urbanization reduce this service and lead to outbreaks of sap-feeder insects, which are highly damaging and challenging to control among arthropod pests of urban plants (Dale and Frank, 2018). Weakened biological control can increase the maintenance costs and inputs for urban greenspace management (Dale and Frank, 2018; Vogt et al., 2015) and therefore pose serious risks due to high levels of pesticide use (Lowe et al., 2019). Therefore, the management of urban landscapes and public and private green spaces to strengthen biological pest control is an important concern for sustainable land use policy and urban planners in order to mitigate the negative environmental and health impacts of synthetic chemicals (Aronson et al., 2017; Lowe et al., 2019). Poorly dispersing, sedentary predators may have the potential to control urban herbivorous pest insect populations (Welch and Harwood, 2014). Based on previous evidence (Burkman and Gardiner, 2014; Langelotto and Denno, 2004; Vergnes et al., 2014), their spread can be promoted by providing green infrastructures connecting semi-natural habitats to city centers that incorporate green spaces with diverse and structurally complex vegetation (e.g. mix of tall grasses, shrubs, and trees), and alternative management regimes (e.g. occasional mowing, limited removal of leaf litter and dead woods). In addition to maintaining diverse vegetation during green space planning, selecting plants that are less susceptible to infestations (e.g. *Fagus*, *Aesculus*, *Robinia*, and *Catalpa* species) can dampen the outbreaks of sap-feeding pests in cities (Laćan and McBride, 2008). However, exotic plant species might support fewer local herbivorous insects and receive reduced herbivory (Bezemer et al., 2014; Dale and Frank, 2018; Matter et al., 2012); we recommend planting these species only in small proportion to support diverse and abundant natural enemy communities in urban environments (Ballard et al., 2013; Salisbury et al., 2017).

CRedit authorship contribution statement

Dávid Korányi: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing - Original draft preparation. **Monika Egerer:** Validation, Writing - Reviewing and editing. **Adrien Rusch:** Validation, Writing - Reviewing and editing. **Borbála Szabó:** Validation, Writing - Reviewing and editing. **Péter Batáry:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing - Reviewing and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data used for this study is listed in the Supplementary material (Tables S1, S2, and S3).

Code availability

Model codes support this study are available in the Supplementary material.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.155396>.

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