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Intraspecific variation shapes community-level behavioral responses to urbanization in spiders

Running head: Intraspecific variation and urbanization

Maxime Dahirel^{a,b,1}, Jasper Dierick^{a,2}, Maarten De Cock^{a,3} and Dries Bonte^{a,4}

^a Ghent University, Department of Biology, Terrestrial Ecology unit, Ghent, Belgium

^b Université de Rennes 1/ CNRS, UMR 6553 Ecobio, Rennes, France

¹ corresponding author: maxime.dahirel@yahoo.fr

² jasper.dierick@outlook.com

³ maarten_de_cock@hotmail.com

⁴ dries.bonte@ugent.be

Abstract

Urban areas are an extreme example of human-changed environments, exposing organisms to multiple and strong selection pressures. Adaptive behavioral responses are thought to play a major role in animals' success or failure in such new environments. Approaches based on functional traits have proven especially valuable to understand how species communities respond to environmental gradients. Until recently, they have, however, often ignored the potential consequences of intraspecific trait variation (ITV). When ITV is prevalent, it may highly impact ecological processes and resilience against stressors. This may be especially relevant in animals, in which behavioral traits can be altered very flexibly at the individual level to track environmental changes. We investigated how species turnover and ITV influenced community-level behavioral responses in a set of 62 sites of varying levels of urbanization, using orb web spiders and their webs as models of foraging behavior. ITV alone explained around a third of the total trait variation observed among communities. Spider web structure changed according to urbanization, in ways that increase the capture efficiency of webs in a context of smaller urban prey. These trait shifts were partly mediated by species turnover, but ITV increased their magnitude, potentially helping to buffer the effects of environmental changes on communities. The importance of ITV varied depending on traits and on the spatial scale at which urbanization was considered. Despite being neglected from community-level analyses in animals, our results highlight the importance of accounting for intraspecific trait variation to fully understand trait responses to (human-induced) environmental changes and their impact on ecosystem functioning.

Keywords: ecosystem functioning; foraging; Human-Induced Recent Environmental Changes (HIREC); plasticity; spider web; variation partitioning

Introduction

Urban areas now concentrate more than 50% of the world population on less than 3% of the world land surfaces, with these two numbers predicted to increase in the near future (Seto et al. 2012, Liu et al. 2014, United Nations Population Division 2015). The urbanization process is one of the strongest and most dramatic forms of human-induced rapid environmental change (HIREC *sensu* Sih et al. 2010). More precisely, it is the combination of several categories of HIREC occurring over different spatial scales: cities are characterized by the replacement and fragmentation of vegetation by buildings and roads, the disturbance brought by intense and frequent human activity, the introduction of exotic species, higher temperatures than the neighboring habitats, as well as by increased chemical, sound and light pollution (Pickett et al. 2001, McDonnell and Hahs 2015, Parris 2016). These cumulated changes create evolutionary novel environments in which many species are unable to fit and disappear, while some manage to exploit these new opportunities and persist or even proliferate (McKinney 2006, 2008, Croci et al. 2008, Aronson et al. 2014, Knop 2016).

As for other environmental changes (Wellstein et al. 2011, Jung et al. 2014), the ability of organisms to respond to urbanization will likely depend on their functional traits. Trait-based approaches to community ecology have provided a valuable framework to understand how species communities respond to environmental variation, and the consequences for ecosystem functioning (Lavorel and Garnier 2002, Moretti et al. 2009, Cornwell and Ackerly 2009, Lavorel et al. 2011, Dray et al. 2014, Jung et al. 2014, Simons et al. 2016). The novel conditions in cities represent a strong and multivariate external filter (*sensu* Violle et al. 2012), and species able to pass this filter are expected to possess consistently different functional trait values than those that cannot and are excluded (*e.g.* Croci et al. 2008), which should lead to shifts in mean community-level trait values in urbanized environments.

Community-level trait responses have generally been investigated by focusing on species turnover, ignoring the potential effects of intraspecific trait variation (ITV) due to plasticity and/or evolutionary change. This has been done both for practical reasons and under the once commonly-held assumption that ITV is negligible relative to between-species variation at the community level (Albert et al. 2011, Viole et al. 2012). An increasing number of studies shows, however, that ITV may represent a non-negligible part of the total trait variation observed within and among communities (reviewed in Siefert et al. 2015), and that correctly accounting for it may greatly change the strength of estimated community-level trait shifts along environmental gradients (Lepš et al. 2011, Jung et al. 2014). In addition, intraspecific rates of phenotypic changes are stronger in cities relative to natural and other anthropogenic systems (Alberti et al. 2017). This means that correctly accounting for ITV in analyses of community responses should be even more important in the context of urbanization, compared to other environmental changes.

Compared to morphological traits typically used in trait-based (plant) community ecology, animal behaviors are usually seen as more flexible (Pigliucci 2001, Duckworth 2008, Sih et al. 2010), which should allow for a greater contribution of ITV to community-level responses. Despite the fact that intraspecific variation in behavior can have wide-ranging impacts on community dynamics and ecosystem functioning (Modlmeier et al. 2015), the relative effects of inter- *versus* intraspecific behavioral variation are rarely compared. We expect that intraspecific variation in behavior will be even more relevant for communities experiencing human-induced rapid environmental changes such as urbanization, as behavioral flexibility is the first and fastest line of response of animals in these contexts (Sih et al. 2010, Wong and Candolin 2015). Both adaptive and maladaptive changes in behaviors in response to HIREC have been recorded within numerous taxa, but many questions remain

on the determinants of these changes, and their impact on community-level processes and ecosystem functioning (Wong and Candolin 2015).

Orb-web weaving spiders (Arachnida; Araneae; main families: Araneidae and Tetragnathidae) are ubiquitous generalist predators present in many natural and human-altered terrestrial ecosystems (Roberts 1993, Sattler et al. 2010, Foelix 2010). Orb-web design and size are highly variable both at the inter- and intraspecific levels (Bonte et al. 2008, Sensenig et al. 2010). Differences between species, populations and individuals in e.g. silk investment, web positioning, capture area, or mesh width have been linked to prey availability, nutritional quality and body size, and are thought to reflect adaptive decisions aiming to maximize the benefits/costs ratio of trap-building in different contexts (Sherman 1994, Blackledge and Eliason 2007, Bonte et al. 2008, Blamires 2010, Scharf et al. 2011, Eberhard 2013). Web-building behavior is also strongly influenced by nutritional status (Mayntz et al. 2009). Orb webs can therefore be seen as high-resolution and easy to access archives of foraging decisions (Sherman 1994), greatly facilitating the acquisition of *in situ* behavioral data for all species in a community. Juvenile orb web spiders can disperse over large distances by ballooning, yet their movement is generally much more limited after settlement (Lubin et al. 1993, Foelix 2010, Thomas et al. 2003); adult spiders in cities are therefore expected to be strongly affected by local rather than landscape/regional conditions (Sattler et al. 2010, but see Lowe et al. 2014).

Here we used orb-web spiders to test the hypothesis that ITV has a significant role in shaping community-level behavioral responses to urbanization, and that this impact varies with the spatial scale of urbanization. We also studied the effects of urbanization on spider body size. Indeed, spider size may respond to both changes in prey availability and higher temperature in cities (the urban heat island effect; Pickett et al. 2001), the latter favoring larger spiders (Entling et al. 2010); this may have potential constraining effects on the range of available

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web-building strategies (Gregorić et al. 2015). We made several predictions on the effects of urbanization. First, we predicted that urbanization would negatively influence prey availability; human-induced land use changes associated with urbanization may reduce prey density (e.g. Teglhøj 2017), and the urban heat island effect is expected to reduce insect prey size, following the temperature-size rule (Horne et al. 2017). Second, we predicted that the average spider web-building strategy would shift to track these prey changes, with a predominant contribution of ITV to observed responses. Finally, in line with the common expectation that behaviors are more flexible than morphological traits, we predicted the contribution of ITV to overall trait variation would be non-negligible, but less important in body size and traits constrained by body size (e.g. web investment) than in “strict” behavioral traits (e.g. web shape and positioning).

Material and Methods

Study sites and sampling design

We sampled 62 orb-weaving spider communities across northern Belgium, a region where urbanization levels and human population density are among the highest in Europe (Appendix S1: Fig. S1; 97.8% of the population in cities; United Nations Population Division 2015). We used the same site selection procedure, and many of the same sites, as previous studies realized in this region (Kaiser et al. 2016, Piano et al. 2017, Brans et al. 2017). We used available data on land use (the Large-scale Reference Database, an object-oriented reference map of Flanders; <https://www.agiv.be/international/en/products/grb-en>) to select sites using the percentage of built-up surfaces as a proxy of urbanization. This metric only accounts for buildings and excludes e.g. roads, parking spaces or pavements, meaning that percentages higher than 10% already correspond to highly urbanized contexts. This procedure was chosen because cities are often defined as areas where built infrastructure covers a large proportion of land areas (Pickett et al. 2001, Parris 2016); increases in surface occupied by

buildings are thus one of the only land use changes that can unambiguously be attributed to urbanization, as opposed to other human-induced environmental changes. To ensure human disturbance was minimal in chosen low-urbanization plots, we also accounted for the proportion of ecologically valuable areas according to the Flanders-wide “Biological Valuation Map”, i.e. areas with particularly rare, vulnerable and/or biodiverse vegetation (Vriens et al. 2011). In order to study the effects of urbanization at different spatial scales, 63 sites were selected in two steps following a hierarchically nested design. First, 21 non-overlapping plots (3×3 km, hereafter “landscape scale”) were selected to represent three urbanization levels (7 plots by level): “low-urbanization” plots had less than 3% of built-up surfaces and more than 20% of ecologically valuable areas; “high-urbanization” plots were defined by a percentage $> 10\%$ of built-up surfaces and intermediate areas between 5 and 10%. In a second step, we selected within each of the 21 plots 3 subplots (200×200 m, hereafter the “local scale”), one per urbanization level, this time based on built-up area only. This design enabled us to independently evaluate the effects of urbanization at both scales. Vegetated areas in selected subplots were grassland-dominated and unforested, with shrubs and low trees (in e.g. gardens, parks or hedgerows). One of these 63 initial subplots was not sampled due to bad weather. Sites belonging to different urbanization levels based on these criteria also differed significantly in estimated human population density (higher in high- relative to moderate and low-urbanization sites at both spatial scales; Appendix S1: Fig. S2) and average temperature (predominantly at the local scale, average temperature increased as urbanization increased; Kaiser et al. 2016).

Collection of spiders and species identification

Field work took place between August 27 and October 5, 2014. One plot was sampled per day; sampling was organized so sites were visited during calm weather only (no rain), and there was no significant link between plot-level urbanization and sampling date (ANOVA; N

= 21 plots, $F_{2,18} = 0.009$, $p = 0.991$). Each subplot was explored for about 4.5 person-hours, and every encountered spider was caught and stored in 70% ethanol. In most cases, no new orb web could be found even before the end of the sampling period. The 2456 adult individuals belonging to 18 species were captured and their cephalothorax width measured as a proxy for body size (species identification under binocular microscope, based on Roberts 1993) (Appendix S1: Table S1).

Web characteristics

As collecting web information for all sampled spiders was too time-consuming, 944 webs were randomly analyzed across all plots. On average, 5.82 ± 1.25 webs (mean \pm SE, range: 0 - 72) were sampled per species per combination of local and landscape urbanization levels (hereafter termed the “urban context”). At the level of the local \times landscape urban context, the number of webs analyzed per species was proportional to the number of spiders captured (162 possible species - urban context combinations; $N_{webs} = -1.80 + 0.50 \times N_{spiders}$, $R^2 = 0.85$). For each selected web, we measured web height (distance from ground to web centre) as well as web inclination (angle between the vertical and the web plane). We additionally calculated several web parameters from field-taken measurements: the total length of sticky silk spirals (capture thread length, or CTL) following Venner *et al.* (2001); the web capture area surface (total web surface minus central area surface), by considering orb webs as ellipses (Herberstein and Tso 2000); and the average mesh size in the web capture area (averaged over the horizontal and vertical axes).

Prey availability

Potential prey characteristics as a function of landscape and local urbanization levels were assessed using sticky paper traps in 9 plots located in the region of the city of Ghent (equally distributed among all urbanization levels). Note that because the actual prey spectrum depends on a complex interplay between prey, spider and (dynamic) web characteristics, this

method can only provide a coarse overview of prey availability (Ludy 2007). In each subplot three traps (analyzed area: 100 cm² per trap; Pherobank, Wijk bij Duurstede, Netherlands) were placed at about one meter high (in the present study, the overall mean web height ± SE was 88.1 ± 1.24 cm, with N = 944). Traps were operational during the spider sampling period, and were collected on average after 17.8 ± 0.9 days (mean ± SE; range: 8 to 26 days; mean number of prey caught per subplot: 278.72 ± 18.28). Because some traps went missing or were destroyed before collection, data were only available for 25 out of the 27 sampled subplots. Prey were counted in the lab and their body length measured to the mm. Diptera accounted for >95% of all prey caught, with aphids and <1% of other Hemiptera accounting for the remaining fraction.

Statistical analysis

All analyses were carried out using R, version 3.3 (R Core Team 2016). We first quantified the effect of urbanization on prey characteristics as well as spider abundance, species richness and diversity. We evaluated the effect of urbanization level on overall subplot-level spider abundance, species richness, Shannon evenness index, mean prey size and mean number of prey. We used generalized linear mixed models with a Poisson family for the former two and linear mixed models for the latter three, including a random effect of plot identity to account for site spatial and temporal clustering (using the R package lme4, Bates et al. 2015).

For each spider trait (body size, web height, web inclination, CTL, capture area surface and mesh size), we investigated shifts in mean values with urbanization using community-weighted mean values: $\bar{x}_{\text{CWM}} = \frac{\sum_{i=1}^S p_i x_i}{\sum_{i=1}^S p_i}$, where S is the number of species in the community, x_i the relevant trait value of species i and p_i its relative abundance in the sample. We used the definitions and methods of Lepš *et al.* (2011) to distinguish the contributions of inter- and intra-specific variation to changes in these mean trait responses across environmental gradients. For each trait at each site we calculated three CWM values. “Fixed”

averages were based on species mean trait values calculated by averaging over all samples; changes in fixed averages can therefore only reflect the effect of species turnover (changes in species occurrence or relative abundance). “Specific” averages were based on separate species mean trait values for each urban context and thus reflect both species turnover and intraspecific variation in response to urbanization. The intraspecific trait variation (ITV) effect was defined as the difference between specific and fixed values. In the small minority of species \times urban context combinations where no web was sampled at the urban context level ($N = 68$ individuals out of 2456 = 2.77 % of all sampled spiders, range per site: 0 – 16.67% of individuals), we used the same mean trait value for the fixed and specific CWM calculations, as advised by Lepš *et al.* (2011).

Linear models were then fitted to specific, fixed, and ITV values of all traits, allowing us to test for the effect of environment on overall community response and its separate components. We included effects of local- and landscape-scale urbanization level, with an effect of plot identity to account for spatial/temporal clustering. In models for web traits, because most web traits are at least partly correlated with body size (Heiling and Herberstein 1998, Sensenig *et al.* 2010, Gregorič *et al.* 2015), we added the fixed and intraspecific components of body size CWM as covariates. Given the “specific” response of a trait results by definition from the addition of the fixed and intraspecific responses, and taking the total variation in “specific” values to be 100%, we used ANOVAs and sum of squares (SS) decomposition to partition trait variation into its fixed and intraspecific components (each extracted from their respective model; Lepš *et al.* 2011). This uses the fact that the variance of the sum of two independent variables is equal to the sum of their variances: $SS_{specific} = SS_{fixed} + SS_{ITV}$ (with degrees of freedom held constant across all three models). If fixed and intraspecific components are not independent but covary, the total $SS_{specific}$ will be higher or lower than expected based on SS_{fixed} and SS_{ITV} , depending respectively on whether the

covariation is positive or negative. We can therefore determine the proportion of total variation due to covariation between inter- and intraspecific responses: $SS_{cov} = SS_{specific} - SS_{fixed} - SS_{ITV}$. This variation partitioning was done for both the overall variation and the part of the variation explained by each variable introduced in linear models (Lepš et al. 2011). Given the high number of tests involving community weighted mean traits, all *p*-values from trait ANOVAs were adjusted using Benjamini and Hochberg (1995)'s method, in order to minimize the false discovery rate. Tukey's Honest Significant Differences tests were carried out when a significant urbanization effect was found in ANOVAs to identify and quantify differences between urbanization levels.

Results

Effect of urbanization on spider richness, diversity and abundance

The number of species per sample was not significantly influenced by urbanization at the local (Wald test, $\chi^2 = 2.21$, df = 2, $p = 0.33$) or landscape scale ($\chi^2 = 5.36$, df = 2, $p = 0.07$) (6.19 ± 0.21 species per site). Similarly, Shannon-based evenness values did not vary with urbanization at the local or landscape scale ($\chi^2 = 2.68$, df = 2, $p = 0.26$ and $\chi^2 = 3.43$, df = 2, $p = 0.18$, respectively; mean evenness \pm SE: 0.77 ± 0.01). The total number of spider per sample was significantly affected by urbanization at the local scale ($\chi^2 = 20.49$, df = 2, $p < 0.001$) but not at the landscape scale ($\chi^2 = 1.10$, df = 2, $p = 0.58$). Spiders were less abundant in communities experiencing locally high and intermediate levels of urbanization, compared to low-urbanization communities (Tukey tests, $p < 0.001$ for significant differences; means \pm SE = 36.8 ± 1.8 , 37.4 ± 1.41 and 44.7 ± 2.1 spiders per 4 ha site, respectively; overall average: 39.6 ± 1.1).

Effect of urbanization on prey characteristics and availability

The number of potential prey caught daily per cm² of trap did not differ significantly between urbanization levels ($\chi^2 = 2.32$, df = 2, $p = 0.31$ and $\chi^2 = 5.17$, df = 2, $p = 0.07$, for the local and landscape scale respectively; overall mean \pm SE: 0.06 ± 0.004). The average potential prey was smaller in highly urbanized sites than in natural habitats, both at the local and landscape scale (-18.3% and -18.4% on average, $\chi^2 = 9.62$, df = 2, $p = 0.008$ and $\chi^2 = 12.00$, df = 2, $p = 0.002$, respectively; Fig. 1).

Trait variation partitioning

Species turnover alone explained from 30.93 (web height) to 78.18% (body size) of the total variance in specific mean values, depending on traits (average: 57.74%), with intraspecific trait variation and covariation between inter- and intra-specific responses making up for the difference (Fig. 2). Covariation between inter- and intra-specific values was generally positive (on average $12.4 \pm 5.4\%$ of the total variation and $31.9 \pm 7.2\%$ of the variation explained by urbanization was attributable to this covariation). Plot identity accounted for a great part of the variation in body size (44.54%). The turnover component of body size differences among communities explained a substantial part of the overall variation in average mesh size (30.15 %), CTL (35.96 %) and web surface (57.95 %), but not in average web height (0.98 %) or web inclination (8.09 %). The proportion of web trait variation explained by intraspecific variation in body size was much lower (maximum 6.72 % for web inclination, average for the five web traits: 2.32 %). Urbanization (landscape and local scales combined) accounted for between 10.31 (body size) and 75.74 % (web height) of total variation, depending on traits (average: 35.71 %; Fig. 2). Based on Lajoie and Vellend (2015), we calculated the relative contribution of ITV to responses to urbanization: $SS_{ITV(\text{urbanization})} / (SS_{ITV(\text{urbanization})} + SS_{\text{fixed } (\text{urbanization})})$, excluding the covariation between the two components $SS_{\text{cov } (\text{urbanization})}$. It ranged from 33.75% (web inclination) to 90.31% (web

surface) (average across the six tested traits: 61.67 %). ITV contributed more to the response to urbanization than expected based on its relative contribution to overall trait variation ($N = 6$ traits, 61.67 vs 35.84 %, *t* test for paired data, $t = -2.648$, $p = 0.046$, Fig. 3).

Effect of urbanization on community-weighted mean trait values

No significant effect of local or landscape-level urbanization was detected on either specific mean body size or its separate turnover and intraspecific variation components after *p*-value correction (Fig. 4, Appendix 1: Table S2).

Spiders built their webs significantly higher as the local level of urbanization increased, disregarding whether one considered specific values or the turnover-only and ITV-only components (Fig. 4, Appendix 1: Table S2, Tukey HSD tests, *p*-values for all pairwise comparisons < 0.03). At the landscape scale, webs were also built significantly higher in highly urbanized communities when compared to more natural sites; this effect was observed with specific values (Fig. 4, $p = 0.008$) and turnover-only components (Fig. 4, $p = 0.011$), but not with ITV-only values.

Web inclination was significantly affected by urbanization at the local scale. Spiders from highly and moderately urbanized communities built significantly less inclined webs than spiders from low-urbanization sites; this effect was observed with specific values (Fig. 4, Appendix 1: Table S2, Tukey HSD tests, $p < 0.001$), turnover-only (Fig. 4, $p < 0.001$) and ITV-only values ($p < 0.003$). No significant effect of landscape-level urbanization on web inclination was detected.

At the landscape scale, web investment, as measured by CTL, was significantly higher in highly and moderately urbanized sites compared to low-urbanization communities (Fig. 4, Appendix 1: Table S2, Tukey HSD tests, $p < 0.001$). This effect was however only observed

in specific and ITV-only values. At the local scale, the same differences were found, but only on the turnover component (Fig. 4, Tukey HSD tests, $p = 0.027$).

All measures of mesh width variation (specific, turnover-only and ITV-only) were significantly affected by urbanization at both spatial scales (Fig. 4, Appendix 1: Table S2). In all cases, mesh width values were significantly lower in highly urbanized sites when compared to low-urbanization communities (Tukey HSD tests, $p < 0.021$), moderately urbanized sites exhibiting intermediate values.

Mean web surface values were also significantly affected by urbanization but, contrary to other web traits, here the effects of local and landscape-level urbanization went in opposite directions in some cases (Fig. 4, Appendix 1: Table S2). At the local 200×200 m scale, specific and ITV-only values of web surface were significantly lower in highly urbanized sites when compared to low-urbanization communities (Tukey HSD tests, $p < 0.010$), moderately urbanized sites exhibiting intermediate values. For the turnover-only component, the only significant difference was between highly and moderately urbanized sites, the former having here again the lowest values (Tukey HSD tests, $p < 0.001$, the p -value for the high-/low-urbanization pairwise comparison being equal to 0.061). At the landscape scale on the other hand, specific and ITV values of web surface were significantly higher in highly urbanized sites when compared to low-urbanization communities (Tukey HSD tests, $p < 0.001$).

Discussion

Intraspecific trait variation (ITV) contributed substantially to observed variation between communities in mean trait values. Observed values of ITV were on average around a third, in line with values found in plants and animals using the same or similar methods (Siefert et al. 2015, Griffiths et al. 2016, Brans et al. 2017). Urbanization had negative impacts on both

prey size and spider abundance (although only at the local scale for the latter), but did not influence mean prey numbers. ITV generally increased the magnitude of trait changes in response to urbanization, though the strength of this effect depended on the trait and spatial scale considered.

Based on the common assumption that behaviors are more flexible than morphological traits (Pigliucci 2001, Duckworth 2008), we hypothesized that ITV would be quantitatively more important in “purely” behavioral traits than in web traits more constrained by body size, or body size itself. This is only partly validated by our results. On the one hand, web height, the behavioral trait that was the least constrained by body size (Fig. 2), had the strongest contribution of ITV to overall among-communities differences, compared to other web traits or body size (Fig. 2). However, the relative contribution of ITV to changes along the urbanization gradients was more important for CTL and capture surface, which were more constrained by body size (Fig. 2). This accords with existing data showing that although web design and area may be broadly constrained by body size (Sensenig et al. 2010, Gregorić et al. 2015), they can be highly variable in response to currently experienced environmental conditions (Blamires 2010, Scharf et al. 2011). The fact that the two main components of foraging strategy, namely web-building behavior and web energetic investment (*sensu* Sherman 1994), appear to be flexible in orb-web spiders means that intraspecific variation should be an important element to understand how spider traits respond to urbanization and other human-induced rapid environmental changes (HIREC).

Responses to urbanization varied in strength and direction among traits (Fig. 4). No clear effect of urbanization on community-averaged body size was detected. This is despite population- and community-level changes in orb web spider body size having been observed in response to several of the individual environmental changes associated with urbanization (Miyashita et al. 1998, Mayntz et al. 2003, Opell et al. 2007, Entling et al. 2010). This is also

surprising as body size changes with urbanization have been reported in other animal (zooplankton) communities in the same region as the present study (Brans et al. 2017). Additionally, the mean size of potential insect prey did decrease with urbanization in the present study (Fig. 1). Decreases in prey biomass availability due to on average smaller prey, prey number being constant, should indeed limit growth in spiders (Mayntz et al. 2003). However, the urban heat island effect is expected to favor larger spiders, due to higher temperatures leading to increased metabolism and longer periods available for development (Entling et al. 2010, Lowe et al. 2014). The absence of overall shift in body size may therefore result from opposite effects of different environmental gradients (possibly on different species) compensating each other, rather than from the absence of actual response to urbanization.

By contrast, all studied web traits responded to urbanization. Spiders built on average their webs higher as the urbanization level increased (Fig. 4). This effect was present at both spatial scales, and driven by both species turnover and ITV (although only at the local scale for the latter). Although the precise drivers are not well understood, web height is often dependent on surrounding habitat characteristics such as prey flying height or cover from predators (Herberstein 1997, Blamires et al. 2007, Foelix 2010). The presence of high human-built structures might also provide new anchoring points and favour spiders building their webs higher in cities, both at inter- and intra-specific levels. Urbanization at the local scale also influenced web inclination, with more vertical webs being built in cities (Fig. 4). Changes in habitat structure, such as the replacement of complex natural vegetation (Parris 2016), which may have previously favored vertically flying insects (Bishop and Connolly 1992), by vertical buildings, may make urban environments less favorable to the building of horizontal webs. Moreover, although they may be more vulnerable to wind, vertical webs tend to be better at retaining intercepted prey (Prokop 2005, Zschokke et al. 2006). Changes

in prey characteristics in cities (Fig. 1), associated with on average lower wind speeds (Britter and Hanna 2003), may favour spiders that prioritise higher web pay-off over lower web destruction risk.

Potential prey (insects) became smaller as urbanization increased at both spatial scales (Fig. 1). This may be driven in part by the loss of potential habitat and food resources due to habitat degradation during urbanization (Oliveira et al. 2016, Renauld et al. 2016, Smith et al. 2016). Alternatively, increases in temperature, such as those observed within urban heat islands, are expected to lead to size reduction in insects (Horne et al. 2017). Contrary to other arthropods (e.g. ants; Penick et al. 2015), orb web spiders cannot switch partly or completely to anthropogenic food sources; urban spider communities thus face strong pressures to build webs adapted to the new prey spectrum, while adjusting to changes in the habitat structure and in thermal conditions. Spiders built webs with smaller mesh widths as urbanization increased (Fig. 4). This effect was present and quantitatively similar at both spatial scales (Fig. 4) and was both driven by species turnover and intraspecific variation. Mesh width is highly variable between species (Sensenig et al. 2010), but also very plastic; individual spiders are able to change this parameter from one web to the next, based on current prey availability and characteristics (Schneider and Vollrath 1998, Blamires 2010). Webs with smaller mesh widths may help maximize prey capture in urban contexts both by facilitating the interception of smaller insects that would pass through looser webs (Sandoval 1994), and/or by increasing the number of contact points between webs and prey, particularly large prey, making them less likely to escape (Blackledge and Zevenbergen 2006). The urban heat island effect might also affect orb-web design: *Araneus diadematus* spiders build webs with a smaller mesh width when maintained at higher temperatures or lower levels of relative humidity (Vollrath et al. 1997). However, based on Vollrath *et al.* (1997), the changes in temperature/humidity needed to observe changes in mesh width of the same magnitude as in

our study are much greater than the average climate differences observed between urban and non-urban sites in our study region (12°C against 1-2°C; Kaiser et al. 2016). This indicates that climate alone is unlikely to explain observed mesh width differences across urbanization gradients. Assuming spiders only have a finite amount of silk to allocate to webs, a small mesh width must be traded off against a smaller web capture surface (Eberhard 2013). Larger webs can intercept more prey, and are better at stopping prey (e.g. Prokop and Grygláková 2005, Harmer et al. 2015). However, web investment was not constant across urbanization gradients: at the landscape scale, community-averaged Capture Thread Length values increased with urbanization, an effect driven by ITV (Figs 2, 4). As for mesh width, climate differences between urban and natural sites may explain a part, but not the total, of this increase in CTL (Vollrath et al. 1997, Kaiser et al. 2016). There was no such effect at the local scale when ITV was accounted for (Figs 2, 4). The ITV-driven increase in web surface with landscape-level urbanization, despite a decrease in mesh width, is likely linked to the ITV-driven increase in CTL along the same gradient. Conversely, the decrease of web surface with urbanization observed at the local scale is likely due to the combination of no overall changes in CTL with a decrease in mesh width.

Overall, observed shifts in community web traits in response to urbanization appear to be adaptive and linked to changes in prey characteristics, climate and morphological characteristics of the new urban habitats. In particular, the ITV-driven increase in silk investment with landscape-level urbanization allowed for simultaneous adaptive shifts in mesh width and web surface at this spatial scale, despite an existing trade-off between these two traits. Although trait changes due to species turnover alone were observed, accounting for ITV generally accentuated responses (Fig. 4). Generally positive covariations were observed between the effects of species turnover and ITV (Fig. 2). This indicates that urbanization-induced selection on traits goes in the same directions both at the inter-and

intraspécific levels (Lepš et al. 2011). The fact that spiders were less abundant in locally urbanized communities may indicate that these changes, at least at this spatial scale, do not fully compensate the strong decrease in prey availability. Intraspecific variation in web characteristics may have important consequences for ecosystem functioning, namely for prey control by spider communities in cities. When the relationship between trait (web characteristics) and function (biomass captured) depends on environmental conditions (prey availability), a recent conceptual model by Wright et al. (2016) predicts that high intraspécific trait variation should increase ecosystem function stability in changing environments, as it increases trait-environment matching.

Consequences of urbanization were scale-dependent. All web traits, as well as spider abundance, responded to local levels of urbanization, in line with expectations that spiders should be more sensitive to local environmental pressures due to their sedentary lifestyle as adults (Foelix 2010, Sattler et al. 2010). However, some traits also responded at the landscape scale. Landscape-level trait changes may reflect the effects of environmental correlates of urbanization that are only prominent at larger spatial scales (Lowe et al. 2014, McDonnell and Hahs 2015). However, all environmental characteristics observed in this study either varied similarly at both scales (prey size, built-up surfaces) or more prominently at the local scale (urban heat island effect, Kaiser et al. 2016). While other environmental effects cannot be ruled out, trait differences between landscapes also reflect dispersal effects. Juveniles of many spider species may be able to easily disperse by wind within, but much less between 3 × 3 km landscapes (Thomas et al. 2003). This would lead to (partial) trait homogenization between sites in a same landscape, and trait divergence between landscapes. Overall, spider communities appeared less able to compensate for the negative effects of urbanization on abundance and functional traits at the more local scale. Local scale conservation actions (in e.g. urban parks or gardens) may therefore provide opportunities to maintain biodiversity and

ecosystem functioning in larger urban ecosystems (McDonnell and Hahs 2015). This study highlights the importance of intraspecific variation in community responses to urbanization and other HIREC. Although trait shifts mediated by species turnover are observed, ignoring ITV can potentially underestimate community trait responses to environmental changes. In addition, the proportion of overall among-communities variation explained by ITV is not always a good indication of its ecological importance, as ITV can contribute disproportionately to responses to environmental gradients (Fig. 3). By facilitating trait-environment matching, intraspecific trait variation is also an important component of ecosystem function resilience in the face of urbanization. While we do acknowledge this may in some cases be too costly or time-consuming (but see Lepš et al. 2011), we therefore plead for a more systematic assessment of ITV contributions during trait-based analyses, especially in the case of behavioral traits or responses to human-induced recent environmental changes.

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Figure legends

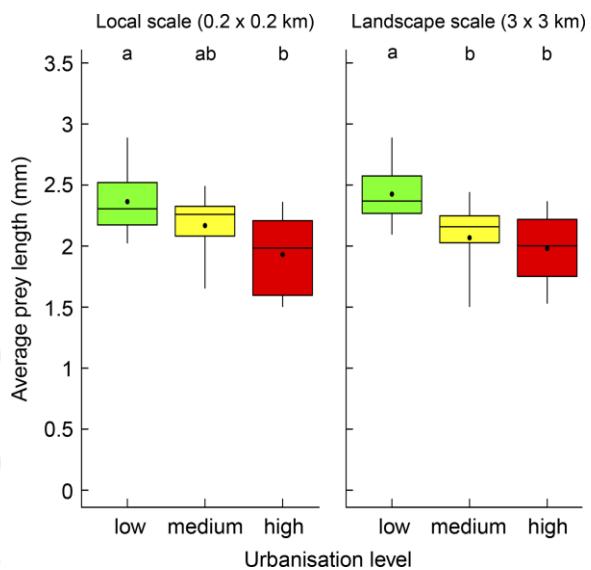
Figure 1. Average body length of potential prey caught in sticky traps as a function of local (left) and landscape-scale (right) level of urbanization. Boxes indicate the first and third quartiles, whiskers the range. Horizontal lines inside boxes indicate medians, dots denote means. Within a panel, different letters indicate significant differences between urbanization levels ($p < 0.05$, Tukey tests) based on the fixed effects of a linear mixed model.

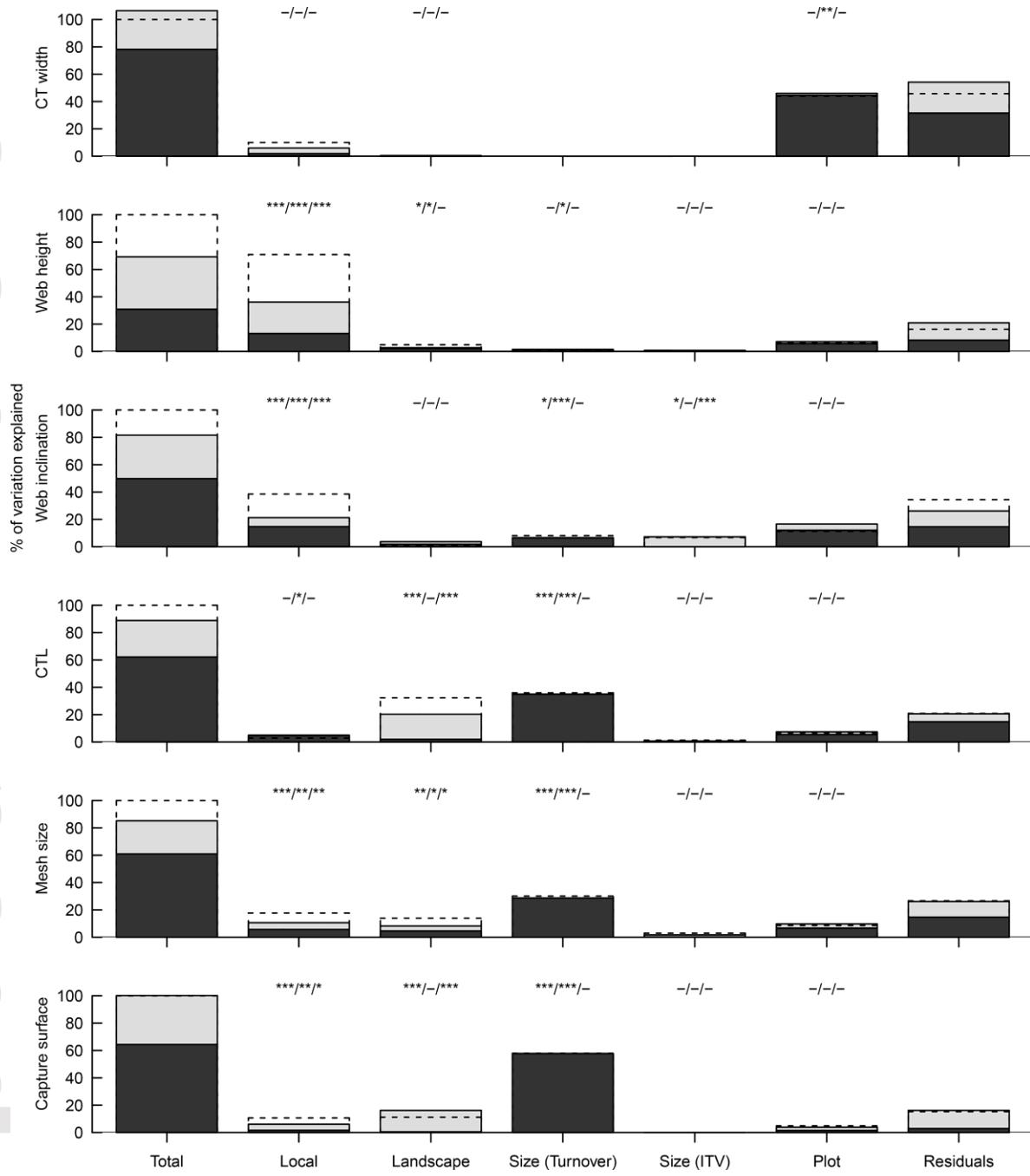
Figure 2. Partitioning of the variation in community-weighted mean trait values, following Lepš *et al.* (2011). Dark grey parts of each bar correspond to species turnover effects, light grey to intraspecific variability (ITV) effects. Dotted lines denote total variation (in “specific” values, i.e. including both turnover and ITV). Differences between the dotted lines and the sum of turnover and ITV effects correspond to the effect of turnover-ITV covariation. Total: overall variation; Local and Landscape: effect of local and landscape-level urbanization; Size: effects of spider body size (turnover or ITV component); Plot: effect of landscape of origin; Residuals: residual variation after the aforementioned effects are accounted for. Asterisks denote significant effects of a variable on the habitat-specific/turnover/ITV components, in that order (ANOVAs; *: <0.05 , **: <0.01 , ***: <0.001 after false discovery rate adjustments; relevant statistical tests are presented in Appendix 1: Table S2).

Figure 3. Relative contribution of intraspecific trait variation to overall variation (left) and to variation in response to urbanization (both spatial scales combined, right), after Lajoie and Vellend (2015) ($N = 6$ traits). Boxes indicate the first and third quartiles, whiskers the range. Horizontal lines inside boxes indicate medians, dots denote means.

Figure 4. Community weighted mean values of the six spider traits under study, as a function of the local (left column) or landscape (right column) level of urbanization. Boxes indicate the first and third quartiles, whiskers the range. Horizontal lines inside boxes indicate

medians, dots denote means. When a significant overall effect of urbanization (corrected $p < 0.05$) is found (relevant statistical tests are presented in Appendix 1: Table S2), different letters are used to indicate significant differences between urbanization levels ($p < 0.05$, Tukey tests).





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