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Intraspecific variation shapes community-level behavioural responses to urbanisation in spiders: from traits to function

Maxime Dahirel[a,b]*, Jasper Dierick[a], Maarten De Cock[a] and Dries Bonte[a]

[a] Ghent University, Department of Biology, Terrestrial Ecology unit, Ghent, Belgium

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

* corresponding author: maxime.dahirel@yahoo.fr

Running headline: urbanisation and behaviour in spiders

Summary

1. Approaches based on functional traits have proven especially valuable to understand how communities respond to environmental gradients. Until recently, they have, however, often ignored the potential consequences of intraspecific trait variation (ITV). This position becomes potentially more problematic when studying animals and behavioural traits, as behaviours can be altered very flexibly at the individual level to track environmental changes.

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20 **2.** Urban areas are an extreme example of human-changed environments, exposing
21 organisms to multiple, strong, yet relatively standardized, selection pressures.
22 Adaptive behavioural responses are thought to play a major role in animals' success or
23 failure in these new environments. The consequences of such behavioural changes for
24 ecosystem processes remain understudied.
25 **3.** Using 62 sites of varying urbanisation level, we investigated how species turnover and
26 ITV influenced community-level behavioural responses to urbanisation, using orb web
27 spiders and their webs as models of foraging behaviour.
28 **4.** ITV explained around 30% of the total trait variation observed among communities.
29 Spiders altered their web-building behaviour in cities in ways that increase the capture
30 efficiency of webs. These traits shifts were partly mediated by species turnover, but
31 ITV increased their magnitude. The importance of ITV varied depending on traits and
32 on the spatial scale at which urbanisation was considered. Available prey biomass
33 decreased with urbanisation; the corresponding decrease in prey interception by
34 spiders was less important when ITV in web traits was accounted for.
35 **5.** By facilitating trait-environment matching despite urbanisation, ITV thus helps
36 communities to buffer the effects of environmental changes on ecosystem functioning.
37 Despite being often neglected from community-level analyses, our results highlight
38 the importance of accounting for intraspecific trait variation to fully understand trait
39 responses to (human-induced) environmental changes and their impact on ecosystem
40 functioning.
41

42 **Key-words** ecosystem functioning; foraging; human-induced rapid environmental changes
43 (HIREC); plasticity; spider web; variation partitioning

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Introduction

Trait-based approaches to community ecology have provided a valuable framework to understand how communities respond to environmental gradients, and the consequences for ecosystem functioning (Lavorel & Garnier 2002; Moretti *et al.* 2009; Cornwell & Ackerly 2009; Lavorel *et al.* 2011; Dray *et al.* 2014; Jung *et al.* 2014; Simons, Weisser & Gossner 2016). 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 commonly-held assumption that ITV is negligible relative to between-species variation (Albert *et al.* 2011; Violle *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).

Compared to morphological traits typically used in trait-based (plant) community ecology, animal behaviours are usually seen as more flexible (Pigliucci 2001; Duckworth 2008; Sih *et al.* 2010), which would allow for a greater importance of ITV to community-level responses. However, and despite the fact that intraspecific variation in behaviour can have wide-ranging impacts on community dynamics and ecosystem functioning (Modlmeier *et al.* 2015), the relative effects of inter- *versus* intraspecific behavioural variation are rarely compared. We expect that intraspecific variation in behaviour will be even more relevant for communities experiencing rapid and strong environmental changes, such as human-induced rapid environmental changes (HIREC *sensu* Sih *et al.* 2010), as behavioural flexibility is the first and fastest line of response of animals in these contexts (Sih *et al.* 2010; Wong & Candolin

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2015). Both adaptive and maladaptive changes in behaviours in response to HIREC have been recorded within numerous taxa, and many questions remain on the determinants of these changes, and their impact on community-level processes and ecosystem functioning (Wong & Candolin 2015).

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, Güneralp & Hutyra 2012; Liu *et al.* 2014; United Nations Population Division 2015). The strong and multiple environmental changes associated with urbanisation all contribute to create evolutionary novel environments in which many species are unable to fit and disappear, yet some manage to exploit these new opportunities and persist or even proliferate (McKinney 2006, 2008; Croci, Butet & Clergeau 2008; Aronson *et al.* 2014; Knop 2016). Species able to pass such a strong and multivariate external filter (*sensu* Violle *et al.* 2012) 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.

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 among and within species (Bonte *et al.* 2008; Sensenig, Agnarsson & Blackledge 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, and are thought to reflect adaptive decisions aiming to maximize the benefits/costs ratio of trap-building in different contexts (Sherman 1994; Blackledge & Eliason 2007; Bonte *et al.* 2008; Blamires 2010; Scharf, Lubin & Ovadia 2011; Eberhard 2013). Orb webs can therefore be seen as high-resolution and easy to access archives of

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93 foraging decisions (Sherman 1994), greatly facilitating the acquisition of *in situ* behavioural
94 data for all species in a community. The prey control function of spider communities often
95 goes beyond mere consumption, as webs may capture more prey than are actually eaten
96 (Riechert & Maupin 1998), and the mere presence of silk can deter herbivorous insects from
97 feeding on a given plant (Hlivko & Rypstra 2003; Rypstra & Buddle 2013). Juvenile orb web
98 spiders can disperse over large distances by ballooning, yet their movement is generally much
99 more limited after settlement (Lubin, Ellner & Kotzman 1993; Foelix 2010); spiders are
100 therefore expected to be strongly affected by local conditions (Sattler *et al.* 2010; but see
101 Lowe, Wilder & Hochuli 2014).

102 Here we used orb-web spiders and urban ecosystems to test the hypothesis that ITV has a
103 significant role in shaping community-level behavioural responses to environmental changes
104 and their consequences for ecosystem functioning, and that this impact varies with the spatial
105 scale of environmental change. We predicted (1) that urbanisation would negatively influence
106 prey biomass availability, (2) that the average spider web-building strategy would shift to
107 track these prey changes, with a predominant contribution of ITV to observed responses; (3)
108 that the contribution of ITV to overall trait variation would be non-negligible, but less
109 important in body size and traits strongly constrained by body size (e.g. web investment) than
110 in "strict" behavioural traits (e.g. web shape and positioning). Spider body size was also
111 expected to vary due to both changes in prey availability and higher temperature in cities (the
112 heat island effect; Pickett *et al.* 2001), the latter favouring larger spiders (Entling *et al.* 2010),
113 with potential constraining effects on the range of available web-building strategies (Gregorič,
114 Kuntner & Blackledge 2015). Finally, we investigated the effect of intraspecific variation in
115 web-building on changes in a measure of ecosystem functioning, namely the prey control
116 potential of orb-web spider communities, across the urbanisation gradient.

117 Material and Methods

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118 Study sites and sampling design

119 We sampled 62 orb-weaving spider communities across an urbanization gradient in Flanders
120 (Belgium) (Supplementary Figure 1). The vast majority of the Belgian population is
121 concentrated in cities (97.8%; United Nations Population Division 2015). In order to study the
122 effect of urbanization at different spatial scales, site selection was carried out following a
123 stratified 2-step design, using geographic information system (GIS). First, 21 non-overlapping
124 plots (3 × 3 km, hereafter "landscape scale") were selected to represent three urbanization
125 levels (7 plots by level): "low-urbanisation" plots had less than 3% of their surfaces occupied
126 by buildings and more than 20% by ecologically valuable areas according to the Flanders-
127 wide "Biological Valuation Map" (Vriens *et al.* 2011); "high-urbanisation" plots were defined
128 by a percentage > 10% of built-up surfaces and intermediate areas between 5 and 10%. In a
129 second step, we selected within each plot 3 subplots (200 × 200 m, hereafter the "local
130 scale"), one per urbanization level, this time based on built-up area only. Vegetated areas in
131 selected subplots were grassland-dominated and unforested, with shrubs and low trees (in e.g.
132 gardens, parks or hedgerows). One of these 63 subplots was not sampled in time due to bad
133 weather. Sites belonging to different urbanization levels based on these criteria also differed
134 significantly in estimated population density (higher in high-urbanisation sites at both spatial
135 scales; Supplementary Figure 2) and average temperature (with significantly higher
136 temperatures in urbanised sites; Kaiser, Merckx & Van Dyck 2016).

137 Collection of spiders and species determination

138 Field work took place between August 27 and October 5, 2014. One plot was sampled per
139 day; sampling was organized so there was no significant link between plot-level urbanization
140 and sampling date (ANOVA; N = 21 plots, $F_{2,18}$ = 0.009, p = 0.991). Each subplot was
141 explored until no new orb web could be found, and every encountered spider was caught and

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142 stored in 70% ethanol. The 2456 adult individuals belonging to 18 species were captured and
143 their cephalothorax width measured as a proxy for body size (species determination under
144 binocular microscope, based on Roberts 1993) (Supplementary Table 1).

145 Web characteristics

146 As collecting web information for all sampled spiders was too time-consuming, 944 webs
147 were randomly analysed across all plots. On average, 5.82 webs (*SD* = 15.86, range: 0 - 72)
148 were sampled per species per combination of local and landscape urbanisation levels
149 (hereafter termed the "urban context"). At the level of the local × landscape urban context, the
150 number of webs analysed per species was proportional to the number of spiders captured (162
151 possible species - urban context combinations; $N_{webs} = -1.80 + 0.50 \times N_{spiders}$, $R^2 = 0.85$).

152 For each selected web, the following web design parameters were measured in the field: the
153 vertical and horizontal web diameters (divided between the central area, i.e. the free zone
154 around the hub without sticky spirals, and the peripheral capture area), the number of sticky
155 silk spirals (*sensu* Zschokke 1999) along the horizontal and vertical axes, and web height
156 (distance from ground to web centre). From these, we calculated the total length of sticky silk
157 spirals (capture thread length, or CTL) following Venner *et al.* (2001)'s formula, the average
158 mesh size in the capture area, as well as the web capture area surface (total web surface minus
159 central area surface), by considering orb webs as ellipses (Herberstein & Tso 2000).

160 Prey availability

161 Prey characteristics as a function of landscape and local urbanization levels were assessed
162 only in 9 plots located in the region of the city of Ghent using sticky paper traps. In each
163 subplot three traps (analysed area: 100 cm^2 per trap; Pherobank, Wijk bij Duurstede,
164 Netherlands) were placed at about one meter high (in the present study, the overall mean web
165 height was 89.6 cm, with *SD* = 39.45 cm). Traps were operational during the spider sampling

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166 period, and were collected on average after 17.8 days (*SD* = 4.41, range: 8 to 26 days).
167 Because some traps went missing or were destroyed before collection, data were only
168 available for 25 out of the 27 sampled subplots. Preys were counted in the lab and their body
169 length measured to the mm. Prey biomass was approximated using the following equation:
170 dry mass (mg) = 0.04 × body length (mm)$^{2.26}$ (Sabo, Bastow & Power 2002); this applies
171 well to Diptera that are the main prey for orb web spiders in the studied landscapes (Ludy
172 2007).

173 Statistical analysis

174 All analyses were carried out using R, version 3.2 (R Core Team 2016).

175 For each spider trait (body size, web height, CTL, capture area surface and mesh size), we
176 investigated shifts in mean values across the urbanization gradient with community-weighted
177 mean values: $CWM = \sum_{i=1}^{S} p_i \, x_i$, where S is the number of species in the community, x_i the
178 relevant trait value of species i and p_i its relative abundance in the sample. We used the
179 definitions and methods of Lepš *et al.* (2011) to distinguish the contributions of inter- and
180 intra-specific variation to changes in these mean trait responses across environmental
181 gradients. For each trait at each site we calculated three *CWM* values. "Fixed" averages were
182 based on species mean trait values calculated by averaging over all samples; changes in fixed
183 averages can therefore only reflect the effect of species turnover (changes in species
184 occurrence or relative abundance). "Specific" averages were based on separate species mean
185 trait values for each urban context and thus reflect both species turnover and intraspecific
186 variation in response to the urbanization gradient. The intraspecific trait variation (ITV) effect
187 was defined as the difference between specific and fixed values. In the small minority of
188 species × urban context combinations where no web was sampled at the urban context level

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189 (*N* = 68 individuals out of 2456 = 2.77 % of all sampled spiders, range per site: 0 – 16.67% of
190 individuals), we used the same mean trait value for the fixed and specific *CWM* calculations.

191 Linear models were then fitted to specific, fixed, and ITV values of all traits, allowing us to
192 test for the effect of environment on overall community response and its separate components.
193 We included effects of local- and landscape-scale urbanization level, with an effect of plot
194 identity to account for spatial/temporal clustering. In models for web traits, because most web
195 traits are at least partly correlated with body size (Heiling & Herberstein 1998; Sensenig *et al.*
196 2010; Gregorič *et al.* 2015), we added the fixed and intraspecific components of body size
197 *CWM* as covariates. Given the "specific" response of a trait results by definition from the
198 addition of the fixed and intraspecific responses, and taking the total variability in "specific"
199 values to be 100%, we used ANOVAs and sum of squares (*SS*) decomposition to partition
200 trait variation into its fixed and intraspecific components (each extracted from their respective
201 model; Lepš *et al.* 2011). This uses the fact that the variance of the sum of two independent
202 variables is equal to the sum of their variances: $SS_{specific} = SS_{fixed} + SS_{ITV}$ (with degrees of
203 freedom held constant across all three models). If fixed and intraspecific components are not
204 independent but covary, the total $SS_{specific}$ will be higher or lower than expected based on
205 SS_{fixed} and SS_{ITV}, depending respectively on whether the covariation is positive or negative.
206 We can therefore determine the proportion of total variation due to covariation between inter-
207 and intraspecific responses: $SS_{cov} = SS_{specific} - SS_{fixed} - SS_{ITV}$. This variation partitioning was
208 done for both the overall variation and the part of the variation explained by each variable
209 introduced in linear models (Lepš *et al.* 2011). Given the high number of tests involving
210 community weighted mean traits, all *p*-values from trait ANOVAs were adjusted using
211 Benjamini & Hochberg (1995)'s method, in order to minimize the false discovery rate.
212 Tukey's Honest Significant Differences tests were carried out when a significant urbanization

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effect was found in ANOVAs to identify and quantify differences between urbanization levels.

In addition, we used data on average web characteristics, spider abundance and prey characteristics to quantify the effect of urbanisation on overall prey interception potential of communities, with or without ITV being taken into account. We evaluated the effect of urbanization level on overall subplot-level spider abundance, mean prey size, mean number of prey and *B*, the mean prey biomass caught per day per cm² of sticky trap using generalized linear mixed models with a Poisson family for the former (N = 62) and linear mixed models for the latter three (N = 25), including a random effect of plot identity to account for site clustering (using the R package lme4, Bates *et al.* 2015). Then, for the 25 communities in which prey were sampled, we evaluated the proportion *P* of the prey biomass *B* expected to actually contact the web and be intercepted: for each web and prey item caught in sticky traps, we assumed the latter would touch the former with a probability = 1 if prey body length > mesh size, with a probability = body length / mesh size otherwise (Evans 2013). The overall daily prey interception potential of a spider community was thus equal to $B \times P \times$ spider abundance × web capture surface *CWM*. As above, we calculated specific, fixed and intra-specific values of prey interception potential, and analysed the effects of local and landscape-level urbanisation, controlling for mean spider size and plot identity, on these different components following Lepš *et al.* (2011).

Results

Effect of urbanization on spider abundance

The total number of spider per sample was significantly affected by urbanization at the local scale (Wald tests, $\chi^2 = 20.49$, df = 2, $p = 3.55 \times 10^{-5}$) 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

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intermediate levels of urbanization, compared to low-urbanization communities (Tukey tests, $p < 7.08 \times 10^{-4}$ for significant differences; means ± SD = 36.8 ± 8.1, 37.4 ± 6.3 and 44.7 ± 9.6 spiders per 4 ha site, respectively; overall average: 39.6 ± 8.8).

Trait variation partitioning (Fig. 1, Table 1)

Species turnover alone explained 30.93 (web height) to 78.18% (body size) of the total variance in specific mean values, depending on traits (average: 59.32%), with intraspecific trait variation and covariation between inter- and intra-specific responses making up for the difference. 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 %). The proportion of web trait variation explained by intraspecific variation in body size was much lower (max. 3.0 % for mesh width, average for the four web traits: 1.22 %). Urbanisation (landscape and local scales combined) accounted for between 10.31 (body size) and 75.74 % (web height) of total variation, depending on traits (average: 34.94 %). Based on Lajoie and Vellend (2015), we calculated the relative contribution of ITV to responses to urbanisation: $SS_{ITV(urbanisation)}$ / ($SS_{ITV\ (urbanisation)}$ + $SS_{fixed\ (urbanisation)}$), excluding the covariation between the two components $SS_{cov\ (urbanisation)}$. It ranged from 44.69% (mesh width) to 90.31% (web surface) (average across the five tested traits: 67.26 %).

Effect of urbanization on community-weighted mean trait values (Fig. 2, Table 1)

No significant effect of local or landscape-level urbanisation was detected on either specific mean body size or its separate turnover and intraspecific variation components after *p*-value correction.

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261 Spiders built their webs significantly higher as the local level of urbanisation increased,
262 whether one considered specific values or their separated turnover and ITV components
263 (Tukey HSD tests, *p*-values for all pairwise comparisons < 0.03). At the landscape scale, webs
264 were also built significantly higher in highly urbanised communities when compared to more
265 natural sites; this effect was observed with specific values (Tukey HSD tests, $p = 0.008$) and
266 turnover components ($p = 0.011$), but not with ITV values.

267 Regarding web investment, specific and ITV-only, but not turnover-only, values of CTL
268 were, at the landscape scale, significantly higher in highly and moderately urbanised sites
269 when compared to low-urbanisation communities (Tukey HSD tests, $p < 4.38 \times 10^{-7}$). At the
270 local scale, the same differences were found, but only on the turnover component (Tukey
271 HSD tests, $p = 0.027$).

272 All measures of mesh width variation (specific, turnover-only and ITV-only) were
273 significantly affected by urbanisation at both spatial scales. In all cases, mesh width values
274 were significantly lower in highly urbanised sites when compared to low-urbanisation
275 communities (Tukey HSD tests, $p < 0.021$), moderately urbanised sites exhibiting
276 intermediate values.

277 Mean web surface values were also significantly affected by urbanisation but, contrary to
278 other web traits, here the effects of local and landscape-level urbanisation went in opposite
279 directions in some cases. At the local 200 × 200 m scale, specific and ITV-only values of web
280 surface were significantly lower in highly urbanised sites when compared to low-urbanisation
281 communities (Tukey HSD tests, $p < 0.010$), moderately urbanised sites exhibiting
282 intermediate values. For the turnover-only component, the only significant difference was
283 between highly and moderately urbanised sites, the former having here again the lowest
284 values (Tukey HSD tests, $p = 1.70 \times 10^{-4}$, the *p*-value for the high-/ low-urbanisation pairwise

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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 urbanised sites when compared to low-urbanisation communities (Tukey HSD tests, $p < 1.55 \times 10^{-4}$). The turnover component, on the other hand, presented significantly lower values in highly urbanised sites (Tukey HSD test, p = 0.037).

Effect of urbanisation on prey characteristics and availability

The number of prey caught daily per cm² of trap did not differ significantly between urbanisation levels (Wald tests, p > 0.05; overall mean ± SD: 0.06 ± 0.02). The body length of the average prey and the estimated biomass caught daily per cm² in traps were significantly different between urbanisation levels both at the local (Wald tests, $\chi^2 = 9.62$, df = 2, $p = 8.15 \times 10^{-3}$ and $\chi^2 = 12.00$, df = 2, $p = 2.48 \times 10^{-3}$, respectively) and landscape scale ($\chi^2 = 8.17$, df = 2, $p = 0.02$ and $\chi^2 = 8.07$, df = 2, $p = 0.02$, respectively). For both variables and both spatial scales, highly urbanised sites presented lower values than natural habitats (Fig. 3).

Effect of urbanization on the prey interception potential of spider communities

The ITV component explained only a small part (SS_{ITV} =7.0%) of the between-community variance in estimated daily intercepted prey biomass, but there was a substantial negative covariation with the species turnover component (SS_{cov} = -31.9%, Pearson's r = -0.54, p = 0.005) (Fig. 4, top). For both specific (turnover + ITV) and fixed (turnover-only) estimates, and at both spatial scales, there was a significant decline in prey interception potential with increased urbanisation (Fig. 4, bottom; ANOVAs, Supplementary Table 2; Tukey HSD tests, p < 0.01 for comparisons between high and low-urbanisation sites). However, there was a significant increase in ITV values with increased landscape-level urbanisation (ANOVA, $F_{2,12} = 20.61$, $p = 1.31 \times 10^{-4}$; Fig. 5). This effect means the decrease in community prey

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309 interception when going from low to high urbanisation landscapes is on average 110.12
310 mg/day (95% CI: 52.56 - 167.68) less important when taking ITV into account, compared to
311 estimates ignoring it (Tukey HSD test on the ITV component, $p = 7.02 \times 10^{-4}$, Fig. 5). There
312 was no significant effect of the local level of urbanisation on the ITV component of prey
313 interception (ANOVA, $F_{2,12} = 0.06$, $p = 0.94$).

314 **Discussion**

315 Intraspecific trait variation (ITV) contributed substantially to observed between-communities
316 variation in mean trait values (on average around a third, in line with values found in plants;
317 Siefert *et al.* 2015). Urbanisation had negative impacts on both prey biomass availability and
318 spider abundance. ITV generally increased the magnitude of trait changes in response to
319 urbanisation, though the strength of this effect depended on the trait and spatial scale
320 considered. By contrast, it dampened changes in a metric of ecosystem functioning, the
321 potential biomass of prey caught daily.

322 Based on the common assumption that behaviours are more flexible than morphological traits
323 (Pigliucci 2001; Duckworth 2008), we hypothesized that ITV would be quantitatively more
324 important in "purely" behavioural traits than in web traits more constrained by body size, or
325 body size itself. This is only partly validated by our results. On the one hand, web height, the
326 behavioural trait that was the least constrained by body size (Fig. 1), had the strongest
327 contribution of ITV to among-communities differences, compared to other web traits or body
328 size (Fig. 1). However, the relative contribution of ITV to changes along the urbanisation
329 gradients is more important for CTL and capture surface, which are more constrained by body
330 size (Fig. 1). The fact that the two main components of foraging strategy, namely web-
331 building behaviour and web energetic investment (*sensu* Sherman 1994), appear to be flexible

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in orb-web spiders means that intraspecific variation should be an important element to understand how spider traits respond to urbanisation.

Responses to urbanisation varied among traits (Fig. 2). No clear effect of urbanisation on community-averaged body size was detected. Population- and community-level changes in orb web spider body size have been observed in response to several of the individual environmental changes associated with urbanisation (Miyashita, Shinkai & Chida 1998; Mayntz, Toft & Vollrath 2003; Opell, Berger & Shaffer 2007; Entling *et al.* 2010), and body size changes with urbanisation have been reported in zooplankton communities, using the same plots as the present study (Kristien Brans et al., unpublished data). While the decrease in prey biomass availability (Fig. 3) may limit growth (Mayntz *et al.* 2003), the heat island effect is expected to favour 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.

By contrast, all studied web traits responded to urbanisation. Spiders built on average their webs higher as the urbanisation level increased. 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, Thompson & Hochuli 2007; Foelix 2010). The presence of high human-built structures, e.g. street lights, might also provide new anchoring points and favour spiders building their webs higher in cities, both at inter- and intra-specific levels.

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355 Available prey biomass decreased as urbanisation increased at both spatial scales, due to a
356 decrease in prey body size, but not prey abundance (Fig. 3). This may be driven by the loss of
357 potential habitat and food resources due to habitat degradation, loss or fragmentation during
358 urbanisation (Smith *et al.*; Oliveira *et al.* 2016; Renauld *et al.* 2016). Contrary to e.g.
359 vertebrates (Fischer *et al.* 2012), orb web spiders cannot switch partly or completely to
360 anthropogenic food sources; urban spider communities thus face strong pressures to build
361 webs adapted to the new prey spectrum. Spiders built webs with smaller mesh widths as
362 urbanisation increased (Fig. 2). This effect was present and quantitatively similar at both
363 spatial scales (Fig. 2) and was both driven by species turnover and intraspecific variability.
364 Mesh width is highly variable between species (Sensenig *et al.* 2010), but also very plastic;
365 individual spiders are able to change this parameter from one web to the next, based on
366 current prey availability and characteristics (Schneider & Vollrath 1998; Blamires 2010).
367 Webs with smaller mesh widths may help maximize prey capture in urban contexts both by
368 facilitating the interception of smaller insects that would pass through looser webs (Sandoval
369 1994), and/or by increasing the number of contact points between webs and prey, particularly
370 large preys, making them less likely to escape (Blackledge & Zevenbergen 2006). Assuming
371 spiders only have a finite amount of silk to allocate to webs, a small mesh width must be
372 traded off against a smaller web capture surface (Eberhard 2013). Larger webs can intercept
373 more prey, and are better at stopping prey (e.g. Prokop & Grygláková 2005; Harmer *et al.*
374 2015). However, web investment was not constant across urbanisation gradients: at the
375 landscape scale, community-averaged Capture Thread Length values increased with
376 urbanisation, an effect driven by ITV (Figs 1, 2). There was no such effect at the local scale
377 when ITV was accounted for (Figs 1, 2). The ITV-driven increase in web surface with
378 landscape-level urbanisation, despite a decrease in mesh width, is likely linked to the ITV-
379 driven increase in CTL along the same gradient. Similarly, the absence of overall changes in

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CTL with local urbanisation, in combination with the decrease in mesh width, likely explains the decrease of web surface with urbanisation at this spatial scale.

Overall, observed shifts in community web traits in response to urbanisation appear to be adaptive responses to prey spectrum, particularly prey size, changes. In particular, the ITV-driven increase in silk investment with landscape-level urbanisation allowed for simultaneous adaptive shifts in mesh width and web surface at this spatial scale, despite an existing trade-off between these two traits. Effects of species replacement and ITV mostly went in the same direction, but ITV generally accentuated responses (Fig. 2). The fact that spiders were less abundant in locally urbanised communities may indicate that these changes, however, do not fully compensate the strong decrease in prey availability, at least at this spatial scale.

Intraspecific variation in web characteristics has important consequences for prey control by spider communities in cities. Prey biomass intercepted daily decreased with increased urbanisation at both spatial scales and whether ITV in webs was considered in estimates or not. However, this decrease was less important at the landscape scale when ITV was accounted for (Figs 4, 5). By contrast, intraspecific variation had no significant effect on local scale responses. These results also hold for *per capita* measures of prey interception (Supplementary Figure 3), meaning they are not only caused by variation in spider abundance (or the lack thereof). Intraspecific trait variation may therefore buffer ecosystem functioning against the effects of urbanisation. This effect is likely mediated by CTL, as it is only observed at the landscape scale. These results are in line with predictions that high intraspecific trait variation should contribute to ecosystem function stability in changing environments when the relationship between trait and function depends on environmental conditions (Wright, Ames & Mitchell 2016), as is the case with orb-webs.

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403 Consequences of urbanisation were scale-dependent: spider communities were less able to
404 compensate for the negative effects of urbanisation on abundance, traits or function at the
405 more local scale. Local scale conservation actions (in e.g. urban parks or gardens) may
406 therefore provide opportunities to maintain biodiversity and ecosystem functioning in larger
407 urban ecosystems (Philpott *et al.* 2013). This study highlights the importance of intraspecific
408 variation in community responses to urbanisation and other forms of anthropogenic changes.
409 Although trait shifts mediated by species turnover are observed, ignoring ITV can potentially
410 lead to underestimates of community trait responses to environmental changes. In addition,
411 the proportion of among-communities variation explained by ITV is not always a good
412 indication of its ecological importance, as ITV can contribute disproportionately to responses
413 to environmental gradients. By facilitating trait-environment matching, intraspecific trait
414 variation is also an important component of ecosystem function resilience in the face of
415 urbanisation. While we do acknowledge this may in some cases be too costly or time-
416 consuming (but see Lepš *et al.* 2011), we therefore plead for a more systematic assessment of
417 ITV contributions during trait-based analyses, especially in the case of behavioural traits or
418 responses to human-induced environmental changes.

419 ## Authors' Contributions

420 DB and MD conceived the ideas and designed methodology (DB: general and sampling
421 methodology; MD: analysis methodology); DB, JD and MDC collected the data; JD, MDC
422 and MD analysed the data; MD led the writing of the manuscript. All authors contributed
423 critically to the drafts and gave final approval for publication.

424 ## Acknowledgements

425 We are grateful to Pieter Vantieghiem for his assistance during field sampling. Financial
426 support came from the Belspo IAP project P7/04 SPEEDY (SPatial and environmental

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determinants of Eco-Evolutionary DYnamics: anthropogenic environments as a model). MD is a postdoctoral fellow funded by a grant from the Fyssen Foundation.

Data Accessibility

Data will be made available on Dryad upon final acceptance

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Figure legends

Figure 1. 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 covariation. Asterisks denote significant effects on the habitat-specific/turnover/ITV components, in that order (ANOVAs; *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$ after false discovery rate adjustments; full details of statistical tests are presented in Table 1).

Figure 2. Community weighted mean values of the five 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. Relevant statistical tests are presented in Table 1.

Figure 3. Characteristics of prey caught in sticky traps (top: average body length; bottom: biomass.day^{-1}.cm^{-2}) 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 subplot, different letters denote significant differences between urbanization levels ($p < 0.05$, Tukey tests) based on the fixed effects of linear mixed models.

Figure 4. (top) Partitioning of the variation in daily prey interception of spider communities. See Figure 1 for legend details. (bottom) Prey interception potential as a function of local (left) or landscape (right) level of urbanization. Boxes indicate the first and third quartiles, whiskers the range. Horizontal lines inside boxes indicate medians, dots denote means. Relevant statistical tests are presented in Supplementary Table 2.

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655 **Figure 5.** Effect of landscape-scale urbanisation on the intraspecific component of daily prey
656 interception potential. See Fig. 2 for legend details. Levels with different letters are
657 significantly different ($p < 0.05$, Tukey tests)

Tables

Table 1 (continues on next page) Results from ANOVAs linking variation in spider community-weighted mean traits to urbanisation. The overall trait responses (habitat-specific values), the turnover component and the intraspecific variation component are analyzed separately (Lepš *et al.* 2011). Significant effects ($p < 0.05$ after correcting for false discovery rate following Benjamini & Hochberg 1995) are in bold.

			Habitat specific values (species turnover + ITV)			Species turnover component			ITV component		
Trait	Effect	df	*F*	$p_{(uncorrected)}$	$p_{(fdr\text{-}corrected)}$	*F*	$p_{(uncorrected)}$	$p_{(fdr\text{-}corrected)}$	*F*	$p_{(uncorrected)}$	$p_{(fdr\text{-}corrected)}$
Body size	Urbanisation (0.2 × 0.2 km scale)	2	4.281	0.021	0.051	1.150	0.327	0.538	3.472	0.041	0.091
	Urbanisation (3 × 3 km scale)	2	0.117	0.890	0.973	0.119	0.889	0.973	0.213	0.809	0.940
	Plot identity	18	2.083	0.028	0.065	**3.054**	**0.002**	**0.006**	0.140	1.000	1.000
	Residuals	39	--	--	--	--	--	--	--	--	--
Web height	Urbanisation (0.2 × 0.2 km scale)	2	**80.714**	**3.207×10^{-14}**	**8.506×10^{-13}**	**29.501**	**2.185×10^{-8}**	**1.675×10^{-7}**	**33.538**	**4.906×10^{-9}**	**4.232×10^{-8}**
	Urbanisation (3 × 3 km scale)	2	**5.555**	**0.008**	**0.021**	**5.069**	**0.011**	**0.030**	0.727	0.490	0.705
	Body size (turnover)	1	2.229	0.144	0.255	**6.516**	**0.015**	**0.038**	0.136	0.714	0.940
	Body size (ITV)	1	1.326	0.257	0.432	0.060	0.807	0.940	2.256	0.142	0.255
	Plot identity	18	0.817	0.670	0.925	1.447	0.167	0.289	0.223	0.999	1.000
	Residuals	37	--	--	--	--	--	--	--	--	--
CTL	Urbanisation (0.2 × 0.2 km scale)	2	2.514	0.095	0.185	**5.847**	**0.006**	**0.019**	0.909	0.412	0.646
	Urbanisation (3 × 3 km scale)	**2**	**28.606**	**3.095×10^{-8}**	**2.136×10^{-7}**	2.501	0.096	0.185	**58.688**	**3.335×10^{-12}**	**5.752×10^{-11}**
	Body size (turnover)	**1**	**63.66**	**1.469×10^{-9}**	**1.448×10^{-8}**	**87.065**	**2.927×10^{-11}**	**4.039×10^{-10}**	0.047	0.829	0.940
	Body size (ITV)	1	2.357	0.133	0.248	0.577	0.452	0.664	2.909	0.096	0.185
	Plot identity	18	0.654	0.831	0.940	0.755	0.734	0.940	0.686	0.803	0.940
	Residuals	37	--	--	--	--	--	--	--	--	--

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Table 1 (end)

Trait	Effect	df	Habitat specific values (species turnover + ITV)			Species turnover component			ITV component		
			F	$p_{(uncorrected)}$	$p_{(fdr\text{-}corrected)}$	*F*	$p_{(uncorrected)}$	$p_{(fdr\text{-}corrected)}$	*F*	$p_{(uncorrected)}$	$p_{(fdr\text{-}corrected)}$
Mesh width	Urbanisation (0.2 × 0.2 km scale)	2	**12.298**	**8.030×10^{-5}**	**3.695×10^{-4}**	**7.231**	**0.002**	**0.008**	**7.926**	**0.001**	**0.005**
	Urbanisation (3 × 3 km scale)	2	**9.66**	**4.213×10^{-4}**	**0.002**	**5.842**	**0.006**	**0.019**	**5.779**	**0.007**	**0.019**
	Body size (turnover)	1	**41.883**	**1.450×10^{-7}**	**9.080×10^{-7}**	**72.127**	**3.230×10^{-10}**	**3.710×10^{-9}**	0.054	0.817	0.940
	Body size (ITV)	1	4.137	0.049	0.103	0.645	0.427	0.655	4.836	0.034	0.079
	Plot identity	18	0.665	0.821	0.940	0.938	0.543	0.765	0.543	0.917	0.973
	Residuals	37	--	--	--	--	--	--	--	--	--
Web surface	Urbanisation (0.2 × 0.2 km scale)	2	**12.954**	**5.440×10^{-5}**	**2.681×10^{-4}**	**10.297**	**2.784×10^{-4}**	**0.001**	**6.214**	**0.005**	**0.015**
	Urbanisation (3 × 3 km scale)	2	**13.533**	**3.884×10^{-5}**	**2.061×10^{-4}**	3.386	0.045	0.096	**21.804**	**5.542×10^{-7}**	**3.187×10^{-6}**
	Body size (turnover)	1	**140.42**	**3.698×10^{-14}**	**8.506×10^{-13}**	**734.554**	**5.254×10^{-26}**	**3.625×10^{-24}**	0.000	0.986	1.000
	Body size (ITV)	1	0.015	0.903	0.973	0.579	0.451	0.664	0.051	0.823	0.940
	Plot identity	18	0.661	0.826	0.940	1.077	0.410	0.646	0.369	0.987	1.000
	Residuals	37	--	--	--	--	--	--	--	--	--

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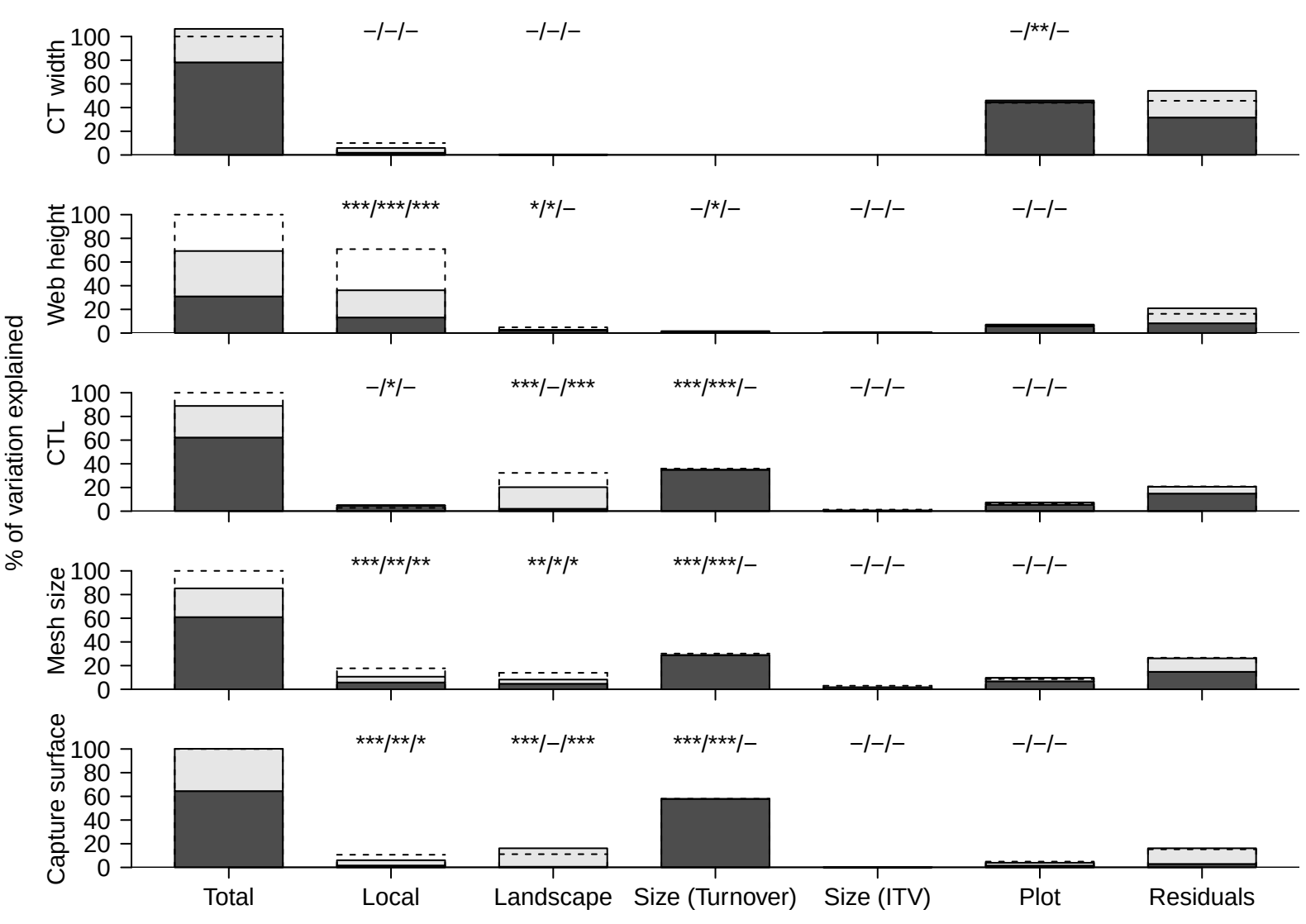
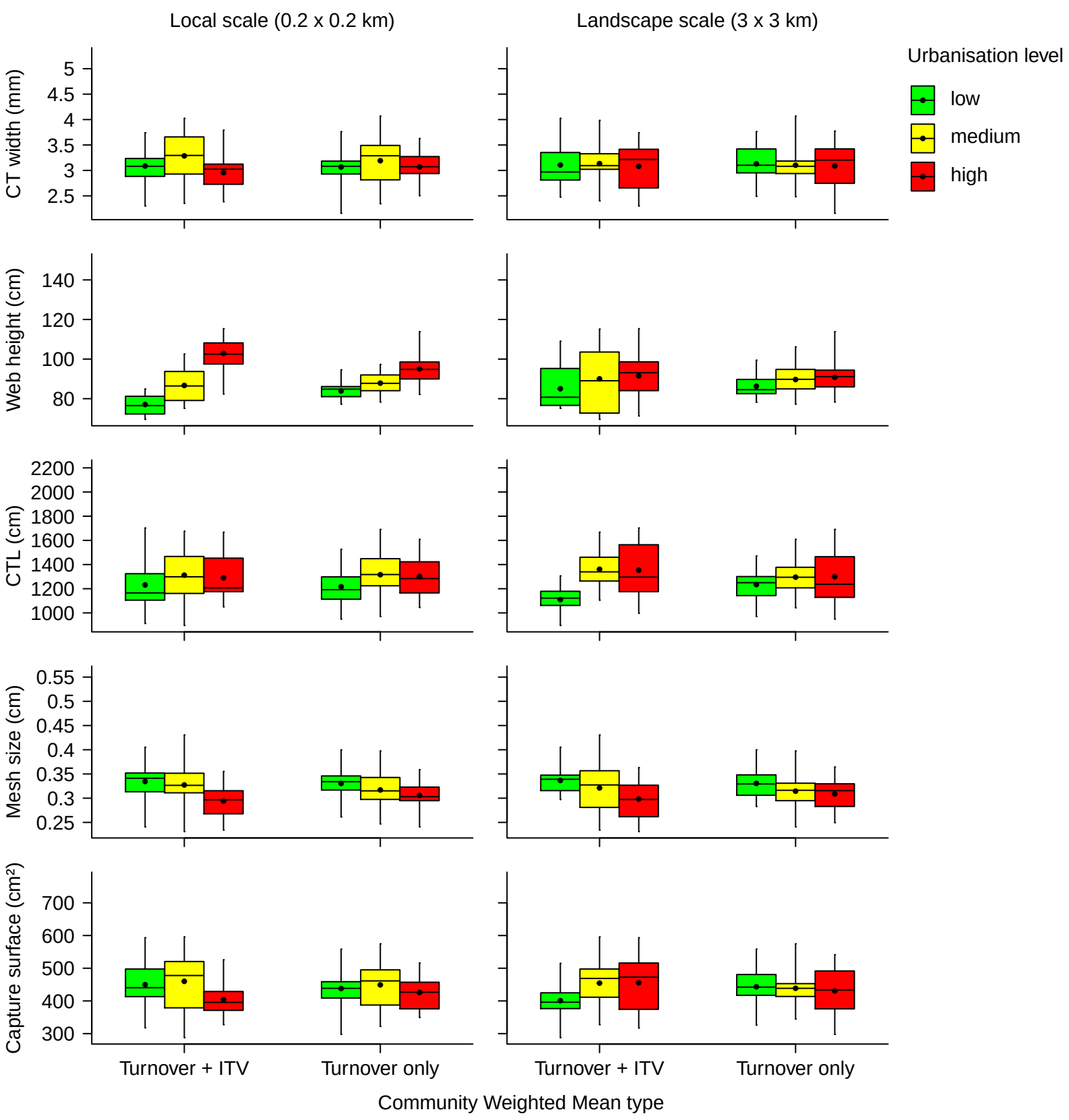
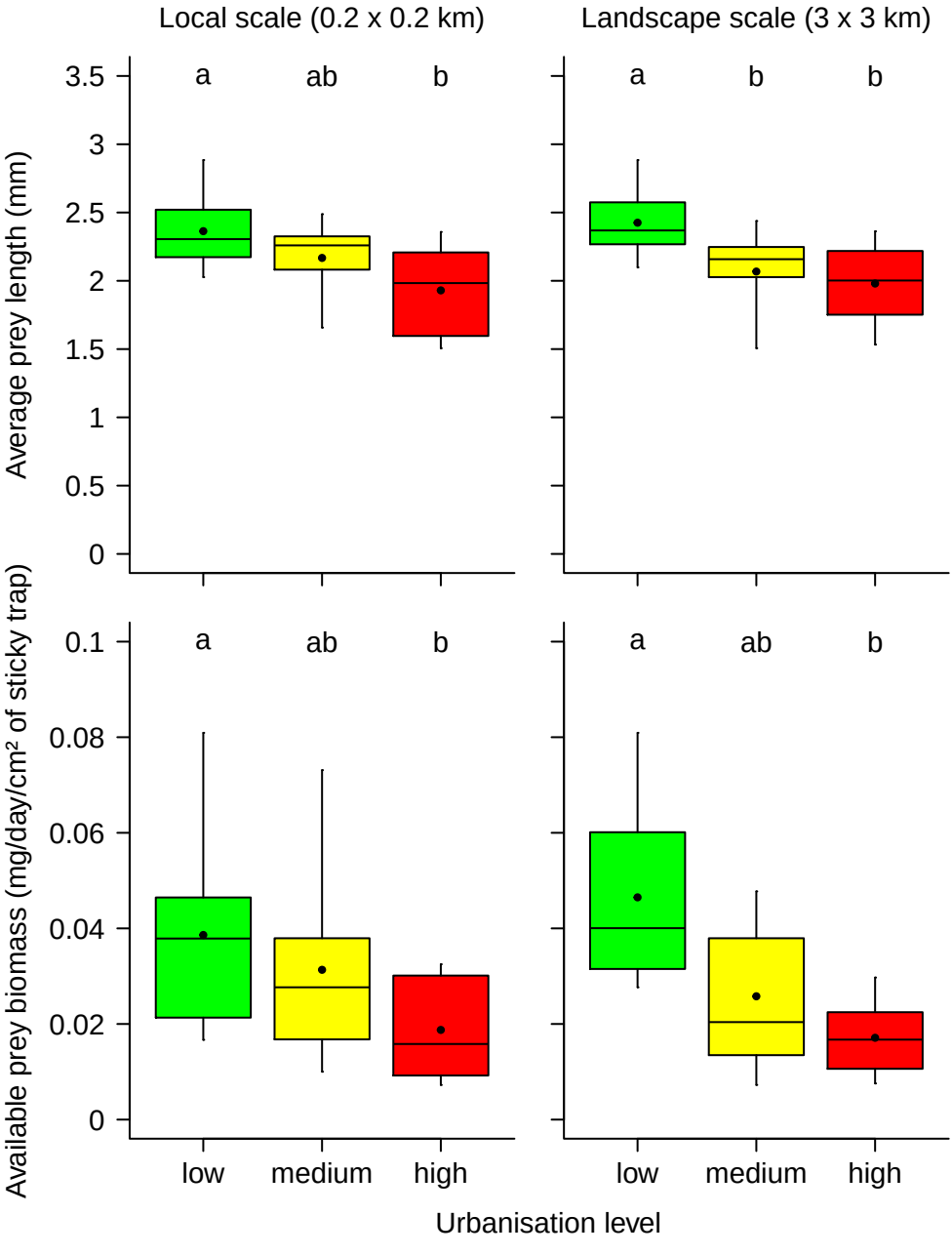
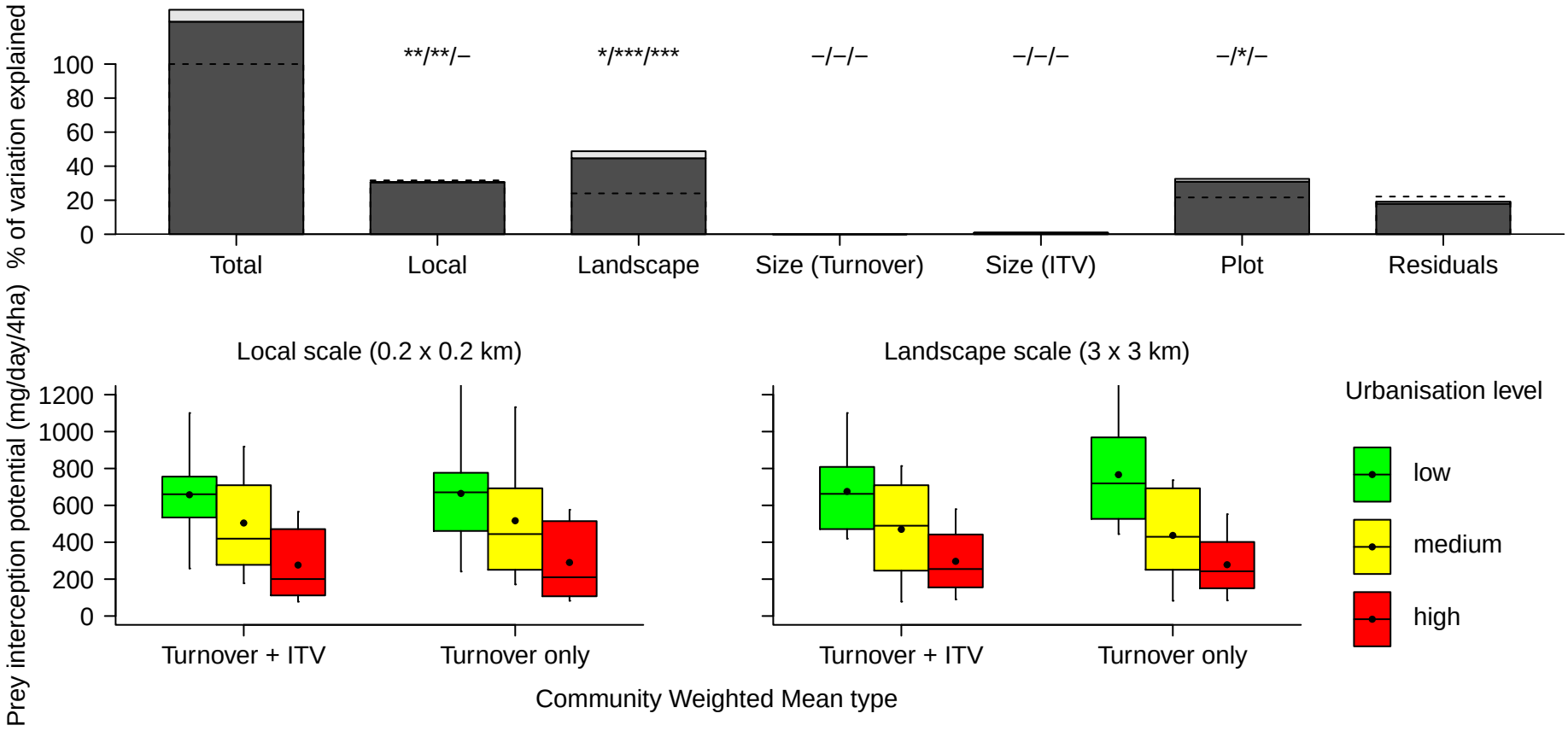
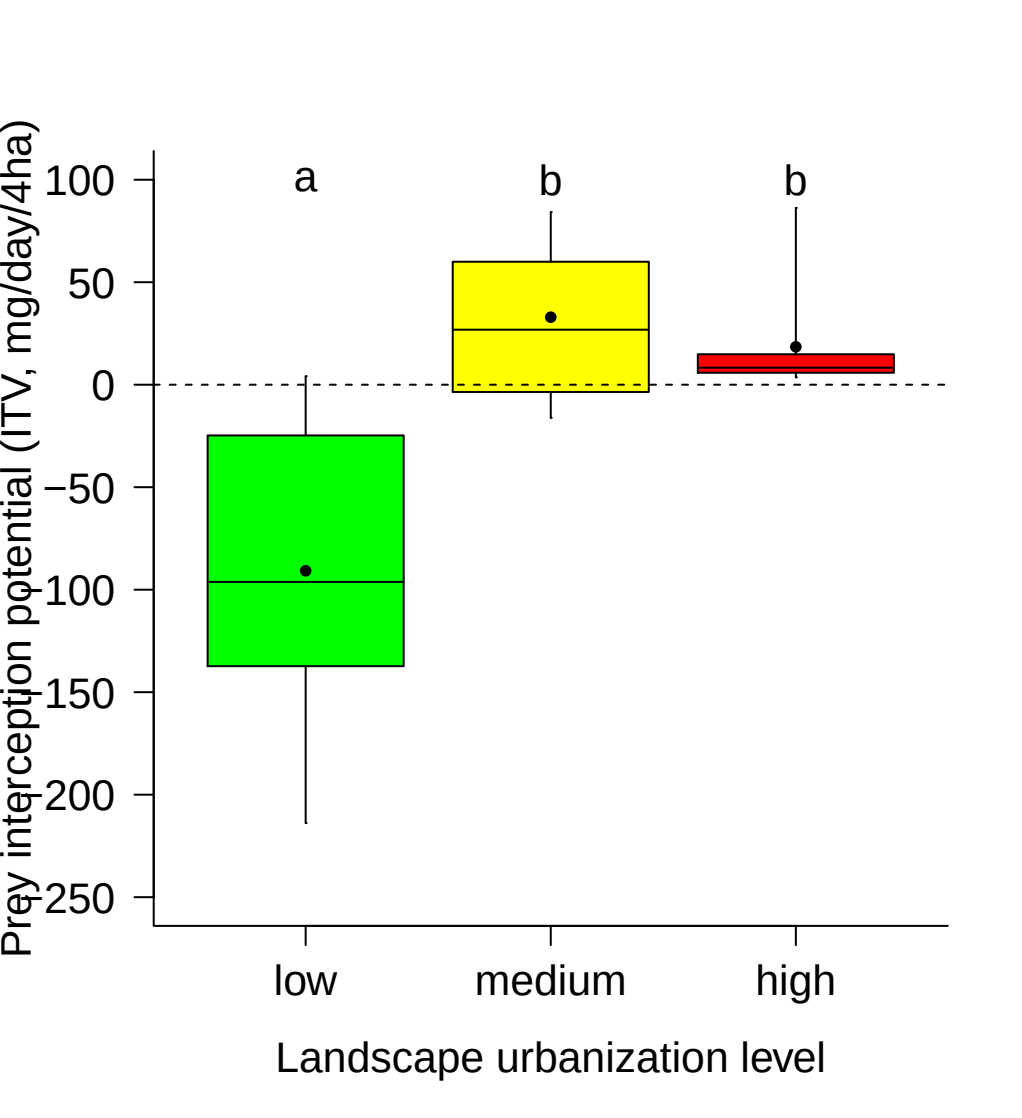

% of variation explained
CT width
Web height
CTL
Mesh size
Capture surface
0
20
40
60
80
100
–/–/–
–/–/–
–/**/–
//***
//–
–/*/–
–/–/–
–/–/–
–/*/–
/–/
//–
–/–/–
–/–/–
***/**/**
**/*/*
//–
–/–/–
–/–/–
***/**/*
/–/
//–
–/–/–
–/–/–
Total
Local
Landscape
Size (Turnover)
Size (ITV)
Plot
Residuals


Local scale (0.2 x 0.2 km)
Landscape scale (3 x 3 km)
Urbanisation level
low
medium
high
CT width (mm)
Web height (cm)
CTL (cm)
Mesh size (cm)
Capture surface (cm²)
Turnover + ITV
Turnover only
Community Weighted Mean type


Local scale (0.2 x 0.2 km)
Landscape scale (3 x 3 km)
Average prey length (mm)
Available prey biomass (mg/day/cm² of sticky trap)
a
ab
b
a
b
b
a
ab
b
a
ab
b
3.5
3
2.5
2
1.5
1
0.5
0
0.1
0.08
0.06
0.04
0.02
0
low
medium
high
low
medium
high
Urbanisation level


% of variation explained
100
80
60
40
20
0
//–
*/***/***
–/–/–
–/–/–
–/*/–
Total
Local
Landscape
Size (Turnover)
Size (ITV)
Plot
Residuals
Local scale (0.2 x 0.2 km)
Landscape scale (3 x 3 km)
Prey interception potential (mg/day/4ha)
1200
1000
800
600
400
200
0
Turnover + ITV
Turnover only
Turnover + ITV
Turnover only
Community Weighted Mean type
Urbanisation level
low
medium
high


a
b
b
100
50
0
−50
−100
−150
−200
−250
Prey interception potential (ITV, mg/day/4ha)
low
medium
high
Landscape urbanization level