



UNIVERSITÀ DEGLI STUDI DI TORINO

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

Islands in cities: urbanization and fragmentation drive taxonomic and functional variation in ground arthropods

This is the author's manuscript
Original Citation:
Availability:
This version is available http://hdl.handle.net/2318/1723130 since 2023-01-27T10:20:43Z
Published version:
DOI:10.1016/j.baae.2020.02.001
Terms of use:
Open Access
Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

1 Islands in cities: urbanization and fragmentation drive taxonomic and functional variation in ground

- 2 arthropods
- 3 Elena Piano, Davide Giuliano, Marco Isaia*
- 4 Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123
- 5 Turin, Italy
- 6 *Corresponding author. Tel: +390117604544
- 7 E-mail address: marco.isaia@unito.it

8 Abstract

9 The conversion of natural lands in urban areas is exponentially increasing worldwide, causing a major 10 decline in biodiversity. Environmental alterations caused by urbanization, such as land conversion and 11 isolation of natural patches, favour tolerant and generalist species, causing both species loss and replacement. In addition, selective pressure is exerted on particular functional traits, driving a functional 12 13 homogenization or turnover of biotic communities. We sampled ground arthropods within the municipality 14 of Turin (NW-Italy), wherein an isolated and a connected control subplot were repeatedly sampled at 15 15 stations distributed along a gradient of increasing urbanization. Such a nested sampling design allowed us 16 to investigate the taxonomic and the functional responses of carabids and spiders to both the urbanization 17 level and patch isolation. First, we highlighted the dominant role played by species homogenization 18 (nestedness) in explaining both taxonomic and functional variation in both groups of arthropods. Secondly, 19 we showed that urbanization causes simultaneously functional homogenization and replacement in both 20 carabid and spider assemblages, whereas patch isolation influences carabid species composition and 21 homogenizes and shifts spider taxonomic and functional composition. Lastly, by relating community-22 weighted means of body length, dispersal capacity and trophic strategy to the urbanization and isolation 23 gradients, we demonstrated that urbanization alters the trophic structure of both taxonomic groups and 24 increases the average dispersal capacity of spiders. On the other hand, patch isolation affected the functional composition of spiders only, reducing the body size and increasing dispersal capacity and the proportion of web-builder species. Our results demonstrate that both urbanization and patch isolation alter species composition by causing functional and taxonomic homogenization. In addition, they exert a strong filtering effect on community functional traits, increasing the proportion of phytophagous species in carabids, and increasing dispersal capacity and web-builders occurrence in spiders, while reducing spider body size.

31 Keywords: taxonomic homogenization; functional homogenization; carabids; spiders; traits

33 Introduction

34 Throughout recent human history, the conversion of natural lands in urban areas increased exponentially 35 everywhere in the world (Seto et al., 2011), representing today one of the main anthropogenic impacts on 36 natural ecosystems (Grimm et al., 2006). In particular, the process of urbanization induces major 37 detrimental effects on the environment, as a result of the severe and fast changes in landscape structure 38 and physical conditions (Parris, 2016). These alterations are common to all urban settlements, and they are 39 expected to drastically affect biodiversity in all continents (McKinney, 2006). However, although an 40 increasing number of studies investigated the relationship between urbanization and species richness, the 41 underlying mechanisms that drive biodiversity patterns in urban areas are not fully understood (but see 42 Shochat et al., 2006, 2010; Pickett et al., 2011; Turrini & Knop, 2015), with inconsistent results among the 43 studied taxa (see Chace & Walsh, 2006; McKinney, 2008; Niemela & Kotze, 2009; Luck & Smallbone, 2010; Jones & Leather, 2012; Ramirez-Restrepo & MacGregor-Fors, 2017, Piano et al., 2019). 44

45 From an evolutionary point of view, urbanization represents a primary selective pressure on biotic 46 communities, especially when considering the hindrance to the establishment and/or survival of certain 47 species (McKinney, 2002). Such a strong environmental filter is expected to differentially affect species 48 from the regional pool, by either favouring tolerant taxa or disfavouring the most sensitive ones, with 49 subsequent changes in species composition, mostly due to species loss (Sadler et al., 2006; Magura et al., 50 2008; Niemelä & Kotze, 2009; Piano et al., 2017) or to species replacement (Sattler et al., 2010; Vergnes et 51 al., 2014; Knop, 2016) along the urbanization gradients. As a result, both phenomena result in biotic 52 homogenization, due to the loss of rare and specialised species, and the gain of widespread tolerant ones 53 (McKinney, 2006).

In this context, a prerequisite to properly describe the mechanisms that drive variations in taxonomic and functional community composition (β -diversity) is the evaluation of the relative contribution of *turnover* and *nestedness*, whereby *turnover* measures the degree to which species are replaced by others—species replacement—and *nestedness* measures the degree to which communities of species-poor sites are a subset of those in species-rich sites—i.e. species loss (Ulrich, Almeida-Neto & Gotelli, 2009). To our knowledge, this approach has never been applied to investigate ground arthropod communities in urban
areas (but see Brice, Pellerin & Poulin, 2017 and Gianuca et al., 2017 as examples in other contexts).

61 According to the "habitat templet theory" (Southwood, 1977, 1988), the above-mentioned selection 62 process may have major effects on particular functional traits, like morphological or physiological 63 attributes, or it could affect the realized niche of a certain species (Webb et al., 2010). Interestingly, several 64 studies confirmed this hypothesis, providing evidence that, by filtering species according to their life-history 65 traits and ecological needs, urbanization often determines shifts in life-history community traits, i.e. 66 functional replacement (e.g. Vergnes et al., 2014; Concepción et al., 2015; Gianuca et al., 2017; Merckx et 67 al., 2018), or deletions of some functional groups, i.e. functional loss (e.g. La Sorte et al., 2014; Piano et al., 68 2017). As a consequence, urbanization may favour species with common traits conferring positive fitness 69 under local conditions, causing the overall functional homogenization of urban communities (Olden et al., 70 2004).

71 The study of urban-rural gradients has been successfully used to highlight the effects of urbanization on 72 biotic communities (McDonnell & Hahs, 2008). However, urbanization gradients are indirect and complex, 73 since they include different types of disturbance acting at different spatial scales (Pickett et al., 2011; Parris, 74 2016), and changes in community may depend on several factors associated with urbanization (Rebele, 75 1994; Seto et al., 2011). For instance, urbanization correlates with a higher presence of impervious 76 surfaces, which are known to have an effect on temperature, soil nutrient cycling and gas exchange and 77 other physical or chemical parameters (Parris, 2016). In addition, the growth of urban areas is responsible 78 for natural and semi-natural habitat fragmentation, which creates small and isolated residual patches, 79 which are typically highly dynamic and impermanent ecosystems (Parris, 2016). Accordingly, since physical 80 and landscape alterations are strongly correlated, even acting synergistically along urbanization gradients 81 with similar demographic consequences, it is often difficult to distinguish their effects on biotic 82 communities. Therefore, in order to isolate and describe their effects on biodiversity, a hierarchical 83 approach is required, taking into consideration the nested nature of ecological systems (McDonnell & Hahs, 84 2008).

85 In this research, we aimed to assess which mechanisms are involved in shaping ground arthropod 86 assemblage composition in urban areas, focusing on the role of taxonomic/functional turnover and/or 87 nestedness, and how functional traits respond to urbanization. Spiders (Araneae) and carabids (Coleoptera, 88 Carabidae) were selected as model groups, because of their well-defined ecology and taxonomy, together 89 with their well-known response to urbanization, both in terms of taxonomic and functional diversity (e.g. 90 Niemelä & Kotze, 2009; Sattler et al., 2010; Vergnes, Le Viol & Clergeau, 2012; Vergnes et al., 2014; Piano et 91 al., 2017; Buchholz et al., 2018). The assemblages of the two selected groups were investigated by means 92 of a hierarchical sampling design, combining data from isolated and connected control environmental patches along an urbanization gradient. The inner areas of traffic roundabouts were selected as isolated 93 94 plots, while control patches were established on green areas connected with the surrounding 95 environmental matrix. Specifically, we investigated whether: i) nestedness and turnover components 96 differentially explain total variation (β -diversity) in taxonomic and functional diversity; ii) the urbanization 97 level and patch isolation affect taxonomic and functional composition of carabid and spider communities, 98 both in terms of homogenization (nestedness) and shift (turnover); and iii) functional traits show differential 99 responses to the urbanization level and patch isolation.

100

101 Materials and methods

102 Sampling design

103 The study was carried out in 15 sampling plots (Fig. S1), randomly selected along an urbanization gradient 104 in the municipality of Torino (about 880,000 inhabitants, NW-Italy). The average distance between the 105 centre of sampling plots was 8,878 m (sd = $\pm 1,705.6$), ranging from 1,408 to 18,512 m. In order to test the 106 effects of patch isolation on spiders and carabids, in each plot two sampling subplots were identified: i) one 107 in an isolated patch, within a traffic roundabout; and ii) the other in the nearest green area, connected with 108 the surrounding environmental matrix (connected control patch) (Fig. 1). Sampling plots consisted in 109 circular areas of 150 m diameter (approximately 18,000 m²), centred on the roundabout. Roundabouts 110 ranged from 6 to 30 m radius (i.e. approximately from 150 to 2,500 m² of surface area), and we evaluated

111 their age using historical aerial maps on Google Earth (https://www.google.com/earth/download/ge/). Based on the year of construction, we equally distributed them among three age classes (1 = less than 10 112 113 years; 2 = 10 years (built in 2007); 3 = more than 10 years) (see Appendix A: Table S1). Given that both 114 taxonomic groups were not affected by these factors, namely the area and the age of the roundabouts, we 115 did not include this information in our subsequent analyses. Connected control subplots were placed in the 116 closest green area within the sampling plot, being represented by small green urban patches (1,000 m²), 117 urban parks or seminatural areas at the city borders (up to a few hundreds of hectares). The isolated patch 118 (roundabout) within a certain sampling plot was always smaller than the green area encompassing the connected control subplot. In all sampling plots, subplots were located in comparable semi-natural 119 120 grassland habitats, maintained by regular mechanical mowing (see Fig. S2 for real examples). Roundabouts 121 were assumed to represent a good approximation of isolated patches, since they are completely 122 surrounded by roads, which likely constitute a selective barrier for our targeted arthropod groups.

123 The urbanization level was assessed in each sampling plot by extrapolating the impervious surface coverage 124 (ISA, Elvidge et al., 2007) from aerial images of the study area. We used the proportion (%) of impervious 125 surfaces as a proxy for the urbanization level, which was calculated from updated digital maps (year 2017) 126 by means of the QGIS software (QGIS Development Team, 2018) in a buffer of 1,600 m radius (see Fig. S1). 127 We tried as much as possible to avoid overlapping buffer areas. However, due to logistic constraints related 128 to permissions issued by the local authorities to access the areas of the roundabouts, our final design 129 implied an overlap of 9.6 km² between buffer areas, corresponding to about 8% of the total area covered 130 by the buffers (approximately 120 km²). Given that carabid beetles and spiders often respond to factors at 131 different scales (Braaker et al., 2014; 2017), we checked whether this spatial scale represents the best 132 option to evaluate the response of ground arthropods to urbanization in the investigated area (see 133 Supplementary Materials).

134 Data collection

Ground-active arthropods were captured in each sampling subplot within a sampling section 30 m long
using three pitfall traps (5-10 m apart), placed at least 20 cm from the patch border, and at least 5 m apart

137 to increase catch efficiency (Ward, New & Yen, 2001). Plastic jars (diameter 90 mm, length 110 mm) were 138 dug into the ground so that the upper edge of the glass was flush with the soil surface, and filled with 20 ml 139 of 50% propylene glycol solution. All traps were emptied every three weeks, in three sampling sessions 140 between the 16th of May and the 18th of July 2017. The collected material was preserved in a 70% ethanol 141 solution. Spiders and carabids were sorted, identified and counted in the laboratory according to the keys 142 provided by Pesarini & Monzini (2010) and Boeken et al. (2002) for carabids, and by Nentwig et al. (2018) 143 for spiders. Data from pitfall traps collected in the same subplot were pooled together for subsequent 144 analyses.

145 It should be pointed out that pitfall traps provide data on activity density rather than real abundances of 146 species, thus overestimating extremely active species. Although the pitfall trap-based sampling method 147 introduces some bias in relative species abundances, the extent of the bias should be similar for each 148 sampling site.

149 Functional traits

Body length, dispersal capacity and trophic requirements – hunting mode for spiders and trophic level for
carabids – were considered as key functional traits, based on Buchholz et al. (2018).

152 Carabid species were assigned to two trophic groups (1 = zoophagous; 2 = phytophagous) according to 153 Vanbergen et al. (2010), and to three dispersal groups based on wing development (1 = brachypterous; 2 =154 dimorphic; 3 = macropterous) according to Desender et al. (2008). The average body size was assigned to 155 each species according to Desender et al. (2008). Spider species were assigned to functional groups 156 reflecting their strategy of food provision, according to Cardoso et al. (2011). In order to obtain a 157 comparable number of species among categories, we referred to a broader classification (1 = hunters; 2 = hu158 web-builders), without considering in detail the specific hunting strategies. Spiders were assigned to three 159 dispersal groups (1 = non- or sporadic ballooners; 2 = ballooners at juvenile stages only; 3 = ballooners at 160 juvenile and adult stages), based on Blandenier (2009), Bell et al. (2005) and Simonneau, Courtial and 161 Pétillon (2016). Each species' male and female average body sizes were extrapolated from Nentwig et al. (2018). We retained only female's data due to the high correlation between the two measures (Pearson's
correlation test: r = 0.97; P < 0.001).

164 Data analysis

165 All statistical analyses were performed using the *R* software (R Core Team, 2017).

Preliminary Analyses. In order to identify the best scale of response to the urbanization level for carabids 166 167 and spiders, we calculated the degree of urbanization for each station in three progressive larger buffers, 168 defined as circles with a 100 m (small scale), 400 m (medium scale) and 1600 m (large scale) radius - with 169 the roundabout as the centre. For each taxonomic group, we proceeded with fitting three separated 170 models, one for each scale of the urbanization level, after eliminating outliers in our dependent variables 171 following the standard protocol for data exploration proposed by Zuur et al. (2009). We tested the response 172 of the total abundance of carabids and spiders against the urbanization level, patch isolation and their 173 interaction by means of Generalized Linear Mixed Models (GLMMs) (Zuur et al. 2009), performed with the 174 function "glmer.nb" in the Ime4 package (Bates et al., 2015). We assumed a negative binomial distribution 175 after checking for the overdispersion of our dependent variables. To account for the spatial and temporal 176 dependency, a station (PlotID) and a session identifier (Session) were incorporated as random factors in the 177 models. We selected the one with the lowest AICc and, given that the best response was observed at the 178 large scale (see Appendix B: Table S2), our subsequent analyses were performed using the urbanization 179 level measured in the buffer of 1,600 m of radius. We then tested whether the total abundance of carabids 180 and spiders in the isolated patch is influenced by the area and the age of the roundabout and by the 181 distance of the roundabout from the control patch with the same model structure. No corrections to the 182 data from the isolated patches were introduced to keep into account the effects of the area and the age of 183 the roundabout and the distance between the roundabout and the control patch, since both groups were 184 not affected by these factors (see Appendix B: Table S3).

185 <u>Multivariate statistics.</u> Firstly, we investigated the variation in taxonomic and functional composition in 186 spider and carabid assemblages by calculating taxonomic and functional β -diversity across the study area. β -187 diversity was here intended as dissimilarity among samples and it was calculated by means of the complement of the Sørensen index, which ranges from 0 (samples are composed exactly by the same species or functional groups) to 1 (samples do not share any species or functional groups). We used the function "beta" in the *BAT* package (Cardoso, Rigal & Carvalho, 2015), which returns the overall β-diversity and the contribution of its components, namely *turnover* and *nestedness*.

192 Secondly, we investigated the effects of the urbanization level and patch isolation on taxonomic and 193 functional composition of both groups with multivariate statistics, performed with the vegan package 194 (Oksanen et al., 2018). We first converted the urbanization level into a categorical variable by assigning 195 sampling plots to one of three categories of urbanization: low (ISA < 50%), intermediate (ISA = 50-70%) and high (ISA > 70%). We then created a functional matrix, measuring the community-weighted means (CWM) 196 197 of trait values with the function "functcomp" of the FD package (Laliberté & Legendre 2010; Laliberté, 198 Legendre & Shipley, 2014). We built a site-by-trait matrix by multiplying the site-by-species matrix with a 199 species-by-trait matrix resulting in the CWM trait values, which represent the mean trait value of all species 200 in the community, weighted by their relative abundances, for body length (CWM-BL), dispersal (CWM-Disp) 201 and trophic composition (CWM-Trophic). Increasing values in CWM-Trophic indicates a shift towards 202 phytophagous species in carabids, and towards web-builders in spiders.

203 Taxonomic and functional composition among the three urbanization levels, and between control and 204 isolated patches, were visualized by means of a Principal Coordinate Analysis (PCoA). We then tested 205 whether the urbanization level and patch isolation were responsible for either taxonomic or functional 206 homogenization by means of the Test of Homogeneity for Multivariate Dispersion (Anderson, Ellingsen & 207 McArdle, 2006). This test measures the distance of each site to its associated group median calculated on a 208 site-by-site distance matrix and subjects these values to an ANOVA (9,999 permutations) to assess if the 209 variance differed among groups. For taxonomic diversity, the site-by-site distance matrix was computed on 210 the matrix of relative abundance of species using the Bray-Curtis distance, whereas the Gower distance was 211 applied to the CWM matrix to obtain the site-by-site distance matrix for functional diversity. To detect 212 possible shifts in taxonomic and functional composition among urbanization and isolation levels, we 213 performed a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001), specifying urbanization, isolation and their interaction as factors. Statistical significance was tested via 9,999 random
 permutations with the sampling session (*Session*) and the ID of each sampling plot (*PlotID*) as strata.

To identify which taxa are specifically linked to the urbanization level and patch isolation categories, an Indicator Species Analysis was performed through the calculation of the *IndVal* (Indicator Value) index (Dufrêne & Legendre, 1997), using the function "multipatt" in the *indicspecies* package (De Caceres & Legendre, 2009).

220 Statistical models. The effects of the urbanization level, patch isolation and their interaction on community-221 averaged functional traits were tested with Generalized Linear Mixed Models (GLMMs) (Zuur et al., 2009), performed with the function "glmer" in the Ime4 package (Bates et al., 2015) assuming a normal error 222 223 distribution. To account for the spatial and temporal dependency, a plot (PlotID) and a session identifier 224 (Session) were incorporated as random factors in the models. The set of functional metrics employed in this 225 analysis as dependent variables were extracted from the previously calculated functional matrices. In 226 addition, in order to check for spatial autocorrelation, we calculated the observed Moran's I for each 227 model, comparing it with the expected values.

228

229 Results

A total of 215 out of 270 pitfall traps were retrieved during the whole sampling season. Overall, we collected a total of 1,722 carabids, belonging to 52 species, and 4,811 spiders, belonging to 66 species, with a mean of $5.28 \pm sd = 3.49$ (min = 4 and max = 13 species per subplot) and $6.86 \pm sd = 3.57$ (min = 1 and max = 19 species per subplot) species and 21.8 ± sd = 22.4 (min = 1; max = 126) and 34.9 ± sd = 32.6 (min = 3; max = 162) individuals per subplot respectively (see Appendix C: Tables S4-S5 for details on the recorded species of carabids; and Appendix D: Tables S6-S7 for details on the recorded species of spiders).

The pairwise dissimilarity (Fig. 2) among carabid communities (total β -diversity) within the sampling area, was on average higher for taxonomic (0.84 ± sd = 0.15) than for functional diversity (0.62 ± sd = 0.12). The contribution of the *nestedness* component to total β -diversity was higher than the *turnover* component in both taxonomic diversity (*turnover* = 0.34 ± sd = 0.26; *nestedness* = 0.51 ± sd = 0.28) and functional diversity (*turnover* = 0.12 ± sd = 0.21; *nestedness* = 0.51 ± sd = 0.28). Similarly, total β -diversity was on average higher for taxonomic diversity (0.77 ± sd = 0.17) than for functional diversity (0.55 ± sd = 0.21) among spider communities within the sampling area and again the *nestedness* component showed a higher contribution than the *turnover* one for both taxonomic diversity (*turnover* = 0.32 ± sd = 0.24; *nestedness* = 0.44 ± sd = 0.27) and functional diversity (*turnover* = 0.10 ± sd = 0.10; *nestedness* = 0.44 ± sd = 0.27).

The test of homogeneity for multivariate dispersion showed significant functional homogenization of both groups along the urbanization gradient (Table 1 and Fig. 3), whereas significant taxonomic homogenization was observed in isolated patches and urbanized plots for spiders (Table 1 and Fig. 4). The PERMANOVA revealed significant shifts in taxonomic and functional composition along the urbanization gradient for both groups. Spider taxonomic and functional composition was affected also by patch isolation and the interaction between urbanization and isolation, whereas carabid taxonomic composition showed a shift from connected to isolated patches (Table 2).

The indicator species analysis highlighted no indicator species for urbanization categories in both groups. Some indicator species were identified for connected control subplots, namely *Harpalus serripes* (*IndVal* = 0.562; P = 0.001) and *Harpalus tardus* (*IndVal* = 0.385; P = 0.043) for carabids; *Trochosa ruricola* (*IndVal* = 0.549; P = 0.008), *Thanatus arenarius* (*IndVal* = 0.461; P = 0.036) and *Pardosa tenuipes* (*IndVal* = 0.366; P = 0.049) for spiders. No indicator species were identified for isolated subplots.

257 The response of carabid community-averaged functional traits revealed a significant increase of the 258 proportion of phytophagous species with increasing urbanization level (range: 0.01-0.50), whereas no 259 significant results were recorded for CWM-BL (body size) and CWM-Disp (Dispersal) (Table 3 and Fig. 5). 260 Regarding spiders, body size was negatively affected by patch isolation, whereas the interaction term 261 showed a significant positive effect, underlying that CWM-body size of spiders in isolated patches increases 262 with increasing urbanization (Table 3). Both dispersal and trophic groups were significantly affected by all 263 terms (Table 3). CWM-Disp (dispersal) showed an increasing trend along the urbanization gradient, ranging 264 from 2.06 to 2.64, and higher values in the isolated $(2.26 \pm sd = 0.25)$ than in the control $(2.16 \pm sd = 0.34)$ 265 subplots (Fig. 5), while the interaction factor displayed a negative effect. Regarding CWM-Trophic, the relative proportion of web-builders significantly increased along the urbanization gradient (range = 0.27-0.82) and it was significantly higher in isolated ($0.68 \pm sd = 0.27$) than in control ($0.69 \pm sd = 0.30$) subplots, while a negative effect was observed for the interaction factor (Fig. 5).

Lastly, Moran's *I* revealed that CWM-Disp and CWM-Trophic, but not CWM-BL, of both carabids and spiders
show significant spatial autocorrelation (Table 4).

271

272 Discussion

In this work, we analyzed how urbanization and fragmentation drive the *turnover* and *nestedness* patterns of taxonomic and functional diversity within two taxonomic groups of ground arthropods, namely carabids and spiders. Since we consistently sampled the same habitat type (i.e. semi-natural grasslands) exposed to the same management practices, we could clearly depict the effect of site location within the conurbation, without confounding factors due to local habitat characteristics.

278 Our results showed that taxonomic variation was higher than functional variation within both carabid and 279 spider communities along the urbanization and isolation gradients. This is in accordance with the functional 280 redundancy concept (Lawton & Brown, 1993) stating that multiple species perform similar roles in 281 communities and ecosystems (e.g. Petchey et al., 2007). This would guarantee high ecological resilience to 282 disturbance, which is particularly crucial for the maintenance of ecosystem functions in extremely altered 283 habitats, like urban areas. Decomposing β -diversity into its components revealed that the same 284 mechanisms drive variation in taxonomic and functional composition in the two taxa studied. Since 285 nestedness was the dominant component, some sampling plots host a subset of species of other sites. We 286 can hypothesize that both carabid and spider communities are composed of both specialized species, 287 surviving only in few localities, and generalist species, which can exploit a broad range of ecological 288 conditions. In the same way, some functional traits are removed from some sites without being replaced, 289 with possible repercussions on ecosystem functionality.

290 Results of the test of homogeneity for multivariate dispersion showed that spiders were more affected by 291 the urbanization level and patch isolation than carabids. Taxonomic homogenization (i.e. *nestedness*) was

292 observed only in spiders and it was explained by both the urbanization level and patch isolation. In 293 addition, the role of isolation as a driver of taxonomic homogenization was further confirmed by the 294 indicator species analysis that revealed indicator species for connected control subplots only. According to 295 these results, we may hypothesize that connected control subplots could provide source populations for 296 the isolated ones, guaranteeing their survival in disturbed habitats, likely recalling the island biogeographic 297 model in fragmented landscapes (MacArthur & Wilson, 1967; Leibold & Chase, 2017). However, no 298 indicator species were identified for the urbanization categories. Indicator species may not have been 299 detected because they are too scarce and irregularly distributed among the subplots within each category. 300 This result may however suggest that the observed *nestedness* pattern along the urbanization gradient may 301 be due to varying relative abundances, instead of an effective substitution of species.

302 Regarding functional composition, the urbanization level causes functional homogenization in both 303 communities. This may be due mainly to a filtering process, supporting the hypothesis that urbanization 304 alters the functional community composition by shifting species composition towards more functionally 305 homogeneous assemblages. Conversely, patch isolation did not significantly affect the functional 306 composition of both carabid and spider communities, underpinning how the urbanization level alone may 307 explain functional variation among samples. This corroborates the hypothesis that stochastic events, like 308 dispersal-related processes or ecological drift, determine species richness in isolated patches for both 309 carabids and spiders (Chase & Myers, 2011; Leibold & Chase, 2017). These outcomes parallel Concepción et 310 al. (2017) who found functional homogenization with increasing urbanization in vascular plants and birds. 311 On the contrary, our results are in contrast with those reported by Brice, Pellerin and Poulin (2017), who 312 observed both taxonomic and functional differentiation with increasing urbanization in plant communities. 313 These contrasting results are likely due to the fact that plant diversity often increases in urban habitats 314 because of the unique abiotic conditions and disturbance regimes, favoring exotic species (McKinney, 2008). In our case, we did not record any exotic species in the examined communities, thus, at least from 315 316 this point of view, our results seem to reflect the filtering effect of urbanization without confounding 317 factors. However, increasing differentiation might also emerge from differential human activities in urban 318 green spaces, facilitating certain species in some places or eliminating others elsewhere. This could have 319 also happened in our case with spiders and carabid beetles, which could be easily transported in the soil or 320 in plant pots as eggs, juvenile stages or even as adults.

The results of the PERMANOVA performed on taxonomic composition pointed out a combined effect of the urbanization level and patch isolation on the taxonomic shift—i.e. *turnover* component in both taxonomic groups. The role of urbanization as a driver of this process has already been pointed out by Knop (2016) for canopy insects, who observed true species replacement in terms of relative abundances in three insect groups, including ground beetles, when comparing rural against urban areas. Regarding functional composition, urbanization caused a shift in both examined groups, whereas patch isolation affected only spiders, and these trends are confirmed by the analysis of the response of functional traits.

328 Dispersal capacity significantly increased along the urbanization gradient for spiders. In particular, this 329 increasing trend was clear in connected control subplots, while isolated subplots hosted highly dispersive 330 species, regardless of the urbanization level. High dispersal capacity is essential in disturbed habitats in 331 order to escape adverse environmental conditions and to enhance population survival in the area; vice-332 versa in stable, late-successional habitats more energy can be invested in reproduction, favoring the 333 establishment of less dispersive species (Roff, 1975). Hence, the observed decline in low-dispersive species 334 appears in accordance with the dynamic nature of urban environments, where human activities result in 335 high turnover rates of suitable habitat patches (Parris, 2016). The observed high dispersal capacity of 336 spiders in isolated subplots can be explained in the framework of the theory of island biogeography 337 (MacArthur & Wilson, 1967), which predicts that isolation of suitable patches increases extinction rates. 338 Therefore, only highly dispersive species can support viable populations in isolated patches, due to the 339 continuous immigration of new individuals, increasing the average dispersal capacity of the community.

Surprisingly, we did not record any effect of the urbanization level or patch isolation on carabid dispersal capacity, in contrast with the available literature (Piano et al., 2017). The differential response obtained for the two examined arthropod groups might be due to their different dispersal mode, i.e. active dispersal in carabids and passive dispersal in spiders. The peculiar dispersal mode of spiders, i.e. ballooning, requires particular physical conditions to occur (Weyman, 1993; Simonneau, Courtial & Pétillon, 2016) and dispersing individuals have no control over the flight direction (Compton, 2002). In heavily fragmented landscapes, the probability to reach isolated patches is therefore strictly related to the ballooning performance, which is maximized in highly dispersive species (Bonte et al., 2003). Conversely, carabid dispersal, either cursorial or by flight, is active and not constrained by the physical environment, therefore all species likely have the same probability to reach isolated patches.

350 The analysis of the trophic structure revealed how urbanization strongly acts on both examined taxa. 351 Regarding carabids, we observed a significant replacement of zoophagous with phytophagous species. Phytophagous carabids are specialized on seeds from ruderal plants (Thiele, 1977; Honek et al. 2007; 352 353 Honek, Martinkova & Saska, 2011), which typically occur in highly impermanent sites (Ribera et al., 2001). 354 Phytophagous species can therefore be considered adapted to ruderal habitats (Vanbergen et al., 2010), 355 likely supporting viable populations within urban sites in our study. Concerning spiders, the proportion of 356 web-builders significantly increases with increasing the urbanization level in connected control subplots. 357 Conversely, in isolated subplots, web-builder proportion is higher than connected control subplots 358 regardless of the urbanization level, suggesting how the effect of patch isolation overrides urbanization in 359 determining the trophic structure of spiders. This may be due to the fact that patch isolation may 360 negatively affect preys of cursorial spiders (Hawn et al., 2018) with consequent negative effects on hunters 361 (Gravel et al., 2011; Zalewski et al., 2018). However, it should be pointed out that this shift from hunters to 362 web-builders in isolated patches might also be a consequence of the dispersal-based selection, since, in our 363 study, web-builders include most of the highly dispersive species (i.e. linyphilds).

Contrary to our expectations, body size did not respond to the urbanization gradient in our study for both taxonomic groups, in accordance with Buchholtz et al. (2018). However, we observed a significant decrease of spider body size along the urbanization gradient in connected control patches, but not in isolated ones. It has been demonstrated that community-wide body-size shifts occur in urban communities as a consequence of increased temperatures due to the urban heat-island effect, but these shifts are mediated by the dispersal capacity of each taxon (Merckx et al., 2018). Thus, this lack of response may result from the

dispersal-mediated effect, since higher dispersal capacity of spider species recorded in roundabouts maydampen the urban heat-island effect on body size.

Results of the Moran's *I* test revealed that there is high spatial autocorrelation among sampling plots in terms of dispersal capacity and trophic composition, but not of body size, for both groups. These patterns underlie the role of the spatial arrangement of individuals in a landscape, which is rarely random (McGlinn et al., 2019). Instead, most individuals are spatially clustered or aggregated in some way, with repercussions also on the functional traits, as demonstrated by our results.

377

378 Conclusions

Overall, we here highlighted differential mechanisms underlying the selective pressure exerted by urbanization and fragmentation on ground arthropods, showing a more evident response in spiders than carabids. This is in accordance with literature, which highlighted how top predators are usually more sensitive to urbanization than lower trophic levels (Egerer et al., 2017; El-Sabawii, 2018).

We have demonstrated that *nestedness* more than *turnover* explains taxonomic and functional variation in the examined communities, indicating a loss of species and functionality among sampling plots. This homogenization process is mainly due to urbanization, which filters species based on their functional traits in both the examined groups.

In addition, the high spatial autocorrelation among sampling plots identified for dispersal capacity and trophic composition underlies that stochastic factors, e.g. source-sink dynamics, also play a role in driving the functional composition of examined communities. Stochastic events, like those caused by human activities, may cause the extinction of some species in the examined sampling plots, potentially compromising the species survival in the whole sampling area. This may have repercussions on ecosystem functionality if key stone species are removed from the landscape.

393 Our approach, thus, proved to be particularly useful to understand how different facets of urbanization 394 affect biodiversity, providing a valuable framework to predict how biotic communities will respond to 395 increasing anthropogenic pressures associated with urbanization. In the next future, further investigations

396	should be performed to highlight alterations at the ecosystem level in order to provide management
397	suggestions aiming at reducing negative effects caused by urbanization.

398

399 Acknowledgement

400 We thank Giulia Chiampo and Simone Savio for their help in the field work and in sample sorting, and

401 Giovanni Allegro for checking identifications of carabid species. Alexandra Jones is greatly acknowledged

402 for her linguistic revision. The authors declare no conflicts of interest.

403

404 Funding

- 405 This work is part of the research fellowship "Bando dei Talenti della Società Civile 2016" funded by the
- 406 Fondazione Goria, the University of Turin and the Royal Belgian Institute of Natural Sciences.

- 408 Appendix A. Supplementary data
- 409 Appendix B. Supplementary data
- 410 Appendix C. Supplementary data
- 411 Appendix D. Supplementary data
- 412 Supplementary data associated with this article can be found, in the online version, at XXXXX

413 References

- Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. Austral Ecology,
 26, 32-46.
- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta
 diversity. Ecology Letters, 9(6), 683-693.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using Ime4.
 Journal of Statistical Software, 67(1), 1-48.
- 420 Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005). Ballooning dispersal using silk: world fauna,
- 421 phylogenies, genetics and models. Bulletin of Entomological Research, 95(2), 69-114.
- Blandenier, G. (2009). Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-year
 survey. Arachnology, 14(7), 308-316.
- 424 Boeken, M., Desender, K., Drost, B., van Gijzen, T., Koese, B., Muilvijk, J., Turin, H., & Vermeulen, R. (2002).
- 425 De Loopkevers van Nederland en Vlaanderen (Coleoptera: Carabidae). Stichting Jeugdbondsuitgeverij,
 426 Utrecht.
- 427 Bonte, D., Vandenbroecke, N., Lens, L., & Maelfait, J. P. (2003). Low propensity for aerial dispersal in
- 428 specialist spiders from fragmented landscapes. Proceedings of the Royal Society of London. Series B:
 429 Biological Sciences, 270(1524), 1601-1607.
- Braaker, S., Ghazoul, J., Obrist, M. K., & Moretti, M. (2014). Habitat connectivity shapes urban arthropod
 communities: the key role of green roofs. Ecology, 95(4), 1010-1021.
- 432 Braaker, S., Obrist, M. K., Ghazoul, J., & Moretti, M. (2017). Habitat connectivity and local conditions shape
- taxonomic and functional diversity of arthropods on green roofs. Journal of Animal Ecology, 86(3), 521-531.
- Brice, M. H., Pellerin, S., & Poulin, M. (2017). Does urbanization lead to taxonomic and functional
 homogenization in riparian forests?. Diversity and Distributions, 23(7), 828-840.

- Buchholz, S., Hannig, K., Möller, M., & Schirmel, J. (2018). Reducing management intensity and isolation as
 promising tools to enhance ground-dwelling arthropod diversity in urban grasslands. Urban ecosystems,
 21(6), 1139-1149.
- 439 Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global patterns of guild composition and
 440 functional diversity of spiders. PloS one, 6(6), e21710.
- Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT–Biodiversity Assessment Tools, an R package for the
 measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. Methods in
 Ecology and Evolution, 6(2), 232-236.
- Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: a review. Landscape and Urban
 Planning, 74(1), 46-69.
- Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic
 processes across scales. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1576),
 2351-2363.
- Compton, S. G. (2002). Sailing with the wind: dispersal by small flying insects. In Dispersal ecology (ed. J. M.
 Bullock, R. E. Kenward & R. S. Hails), pp. 113–133. Oxford: British Ecological Society, Blackwell Scientific.
- 451 Concepción, E. D., Moretti, M., Altermatt, F., Nobis, M. P., & Obrist, M. K. (2015). Impacts of urbanization
 452 on biodiversity: the role of species mobility, degree of specialisation and spatial scale. Oikos, 124, 1571453 1582.
- 454 Concepción, E. D., Götzenberger, L., Nobis, M. P., de Bello, F., Obrist, M. K., & Moretti, M. (2017).
 455 Contrasting trait assembly patterns in plant and bird communities along environmental and human-induced
 456 land-use gradients. Ecography, 40(6), 753-763.
- 457 De Caceres, M., Legendre, P. (2009). Associations between species and groups of sites: indices and 458 statistical inference. Ecology, URL <u>http://sites.google.com/site/miqueldecaceres/</u>

- Desender, K., Dekoninck, W., Maes, D. M. M. V., Crevecoeur, L., Dufrêne, M., Jacobs, M., Lambrechts, J.,
 Pollet, M., Stassen, E., & Thys, N. (2008). Een nieuwe verspreidingsatlas van de loopkevers en
 zandloopkevers (Carabidae) in België. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2008
 (INBO.R.2008.13). Instituut voor Natuur- enBosonderzoek, Brussel.
- 463 Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible
 464 asymmetrical approach. Ecological Monographs, 67(3), 345-366.
- 465 Egerer, M. H., Arel, C., Otoshi, M. D., Quistberg, R. D., Bichier, P., & Philpott, S. M. (2017). Urban arthropods

respond variably to changes in landscape context and spatial scale. Journal of Urban Ecology, 3.

- 467 El-Sabaawi, R. (2018). Trophic structure in a rapidly urbanizing planet. Functional Ecology, 32, 1718–1728.
- 468 Elvidge, C.D., Tuttle, B.T., Sutton, P.C., Baugh, K.E., Howard, A.T., Milesi, C., Bhadura, B.L., & Nemani, R.,

469 (2007). Global distribution and density of constructed impervious surfaces. Sensors, 7, 1962e1979.

470 Gianuca, A. T., Engelen, J., Brans, K. I., Hanashiro, F. T., Vanhamel, M., Van den Berg, E. M., Souffreau, C., &

471 De Meester, L. (2018). Taxonomic, functional and phylogenetic metacommunity ecology of cladoceran

- 472 zooplankton along urbanization gradients. Ecography, 41(1), 183-194.
- Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011). Trophic theory of island biogeography.
 Ecology Letters 14, 1010–1016.
- Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2006). Global
 change and the ecology of cities. Science, 319, 756-760.
- Hawn, C. L., Herrmann, J. D., Griffin, S. R., & Haddad, N. M. (2018). Connectivity increases trophic subsidies
 in fragmented landscapes. Ecology Letters, 21(11), 1620-1628.
- Honek, A., Martinkova, Z., Saska, P., & Pekar, S. (2007). Size and taxonomic constraints determine the seed
 preferences of Carabidae (Coleoptera). Basic and Applied Ecology, 8(4), 343-353.

- Honek, A., Martinkova, Z., & Saska, P. (2011). Effect of size, taxonomic affiliation and geographic origin of
 dandelion (Taraxacum agg.) seeds on predation by ground beetles (Carabidae, Coleoptera). Basic and
 Applied Ecology, 12(1), 89-96.
- 484 Jones, E. L., & Leather, S. R. (2013). Invertebrates in urban areas: a review. European Journal of 485 Entomology, 109(4), 463-478.
- 486 Knop, E. (2016). Biotic homogenization of three insect groups due to urbanization. Global Change Biology,
 487 22, 228-236.
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from
 multiple traits. Ecology, 91, 299-305.
- 490 Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: measuring functional diversity from multiple traits, and
 491 other tools for functional ecology. R package version 1.0-12.
- 492 La Sorte, F. A., Aronson, M. F., Williams, N. S., Celesti-Grapow, L., Cilliers, S., Clarkson, B. D., Dolan, R. W.,
- 493 Hipp, A., Klotz, S., Kühn, I., Pyšek, P., Siebert, S., & Winter, M. (2014). Beta diversity of urban floras among
- 494 European and non-European cities. Global Ecology and Biogeography, 23(7), 769-779.
- 495 Lawton, J. H., & Brown, V. K. (1993). Redundancy in ecosystems. In: Schulze, E.-D., & Mooney, H. A. (eds),
- 496 Biodiversity and ecosystem function. Springer, pp. 255–270.
- 497 Legendre, P., & Legendre, L. (1998). Numerical Ecology, Volume 24. Developments in Environmental
 498 Modelling.
- Leibold, M.A., Chase, J.M., (2017). Metacommunity Ecology Monographs in Population Biology, Volume
 500 59. Princeton University Press, 504 pp.
- Luck, G. W., & Smallbone, L. T. (2010). Species diversity and urbanization: patterns, drivers and
 implications. Urban Ecology, 88-119.

- MacArthur, R. H., & Wilson, E. O. (1967). The Theory of Island Biogeography. Princeton University Press,
 Princeton.
- 505 McDonnell, M. J., & Hahs, A. K. (2008). The use of gradient analysis studies in advancing our understanding
- of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology, 23, 11431155.
- McGlinn, D. J., Xiao, X., May, F., Gotelli, N. J., Engel, T., Blowes, S. A., Knight, T., Purschke, O., Chase, J.,
 McGill, B. J. (2019). MoB (Measurement of Biodiversity): a method to separate the scale-dependent effects
 of species abundance distribution, density, and aggregation on diversity change. Methods in Ecology and
 Evolution, 10(2), 258-269.
- 512 McKinney, M. L. (2002). Urbanization, Biodiversity and Conservation. BioScience, 52(10), 883-890.
- 513 McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. Biological Conservation,
 514 127, 247-260.
- 515 McKinney, M. L. (2008). Effects of urbanization of species richness: a review of plants and animals. Urban 516 Ecosystems, 11, 161-176.
- Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel,
 M., Debortoli, N., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hendrickx, F.,
 Higuti, J., Lens, L., Martens, K., Matheve, H., Matthysen, E., Piano, E., Sablon, R., Schön, I., Van Donink, K.,
 De Meester, L., & Van Dyck, H. (2018a). Body-size shifts in aquatic and terrestrial urban communities.
 Nature, 558(7708), 113.
- Nentwig, W., Blick, T., Gloor, D., Hänggi, A., & Kropf, C. (2018). Version December.2018. Online at
 https://www.araneae.nmbe.ch, accessed on December 2018. doi: 10.24436/1
- 524 Niemelä, J., & Kotze, D. J. (2009). Carabid beetle assemblages along urban to rural gradients: A review.
- 525 Landscape and Urban Planning, 92, 65-71.

- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H.
 H., & Wagner, H. (2018). vegan: Community Ecology Package. R package version 2.2-1. <u>http://CRAN.R-</u>
 project.org/package=vegan.
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary
 consequences of biotic homogenization. Trends in Ecology & Evolution, 19(1), 18-24.
- 531 Parris, K. M. (2016). Ecology of Urban Environments. Wiley-Blackwell, Chichester, West Sussex, UK.
- Pesarini, C., & Monzini, V. (2010). Insetti della fauna italiana Coleotteri Carabidi vol. I e II. Museo di Storia
 Naturale di Milano, 296 pp.
- Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity and no
 redundancy in British avian assemblages. Journal of Animal Ecology, 76(5), 977-985.
- Pickett, S. T., Cadenasso, M. L., Grove, J. M., Boone, C. G., Groffman, P. M., Irwin, E., Kaushal, S. S., Marshall,
 V., McGrath, B. P., Nilon, C. H., Pouyat, R. V., Szlavecz, K., Troy, A., & Warren, P. (2011). Urban ecological
 systems: Scientific foundations and a decade of progress. Journal of Environmental Management, 92(3),
 331-362.
- Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., Lens, L., Merckx, T., Mertens, D., van
 Kerckvoorde, M., De Meester, L., & Hendrickx F. (2017). Urbanization drives community shifts towards
 thermophilic and dispersive species at local and landscape scales. Global Change Biology, 23(7), 2554-2564.
- Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel,
 M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L.,
 Hanashiro, F. T. T., Higuti, J., Lens, L., Martens, K., Matheve, H., Matthysen, E., Pinseel, E., Sablon, R., Schon,
 I., Stocks, R., Van Doninck, K., Van Dyck, H., Vanormelingen, P., Van Wichelen, J., Vyverman, W., De
 Meester, L., Hendrickx, F. (2019). Urbanization drives cross-taxon declines in abundance and diversity at
 multiple spatial scales. Global Change Biology, https://doi.org/10.1111/gcb.14934.

- 549 QGIS Development Team (2018). QGIS Geographic Information System. Open Source Geospatial
 550 Foundation Project. http://qgis.osgeo.org
- 551 R Development Core Team (2017). R: A language and environment for statistical computing. R Foundation
- 552 for Statistical Computing, Vienna, Austria. <u>http://www.R-project.org</u>
- Ramírez-Restrepo, L., & MacGregor-Fors, I. (2017). Butterflies in the city: a review of urban diurnal
 Lepidoptera. Urban Ecosystems, 20(1), 171-182.
- Rebele, F. (1994). Ecology and special features of urban ecosystems. Global Ecology and Biogeography
 Letters, 4, 173–187.
- Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on species
 traits of ground beetle assemblages. Ecology, 82(4), 1112-1129.
- Roff, D. A. (1975). Population stability and the evolution of dispersal in a heterogeneous environment.
 Oecologia, 19, 217–237.
- Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M. K., & Moretti, M. (2010). Spider,
 bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology,
 91(11), 3343-3353.
- 564 Seto, K. C., Fragkias, M., Güneralp, B., & Reilly, M. K. (2011). A meta-analysis of global urban land 565 expansion. PLoS ONE, 6(8), e23777.
- 566 Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging 567 processes in mechanistic urban ecology. Trends in Ecology and Evolution, 21(4), 186-191.
- 568 Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H., Nilon, C. H. (2010). Invasion, 569 competition, and biodiversity loss in urban ecosystems. BioScience, 60(3), 199-208.
- 570 Simonneau, M., Courtial, C., & Pétillon, J. (2016). Phenological and meteorological determinants of spider
- ballooning in an agricultural landscape. Comptes Rendus Biologies, 339(9-10), 408-416.

- Small, E., Sadler, J. P., & Telfer, M. (2006). Do landscape factors affect brownfield carabid assemblages?
 Science of the Total Environment, 360, 205–222.
- 574 Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies?. Journal of Animal Ecology, 337-575 365.
- 576 Southwood, T. R. E. (1988). Tactics, strategies and templets. Oikos, 52(1), 3-18.
- 577 Thiele, H. U. (1977). Carabid Beetles in Their Environments: A Study on Habit Selection by Adaptations in
 578 Physiology and Behaviour. Translated by Joy Wieser. Springer-Verlag.
- 579 Turrini, T., & Knop, E. (2015). A landscape ecology approach identifies important drivers of urban 580 biodiversity. Global Change Biology, 21(4), 1652-1667.
- 581 Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. Oikos,
 582 118(1), 3-17.
- 583 Vanbergen, A. J., Woodcock, B. A., Koivula, M., Niemelä, J., Kotze, D. J., Bolger, T., Golden, V., Dubs, F.,
- 584 Boulanger, G., Serrano, J., Lencina, J. L., Serrano, A., Aguiar, C., Grandchamp, A-C., Stofer, S., Szél, G., Ivits,
- 585 E., Adler, P., Markus, J., & Watt, A. D. (2010). Trophic level modulates carabid beetle responses to habitat
- and landscape structure: a pan-European study. Ecological Entomology, 35(2), 226-235.
- Vergnes, A., Le Viol, I., & Clergeau, P. (2012). Green corridors in urban landscapes affect the arthropod
 communities of domestic gardens. Biological Conservation, 145(1), 171-178.
- 589 Vergnes, A., Pellissier, V., Lemperiere, G., Rollard, C., & Clergau, P. (2014). Urban densification causes the
- decline of ground-dwelling arthropods. Biodiversity and Conservation, 23, 1859-1877.
- Ward, D. F., New, T. R., & Yen, A. L. (2001). Effects of pitfall trap spacing on the abundance, richness and
 composition of invertebrate catches. Journal of Insect Conservation, 5(1), 47-53.
- 593 Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & LeRoy Poff, N. (2010). A structured and dynamic
- framework to advance trait-based theory and prediction in ecology. Ecology Letters, 13, 267-283.

- Weyman, G.S. (1993). A review of the possible causative factors and significance of ballooning in spiders.
 Ethology, Ecology and Evolution, 5(3), 279-291.
- 597 Zalewski, M., Hajdamowicz, I., Stańska, M., Dudek-Godeau, D., Tykarski, P., Sienkiewicz, P., Ciurzycki, W., &
- 598 Ulrich, W. (2018). β-diversity decreases with increasing trophic rank in plant–arthropod food chains on lake
- 599 islands. Scientific Reports, 8, 17425.
- 500 Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions
- 601 in ecology with R. Springer Science & Business Media.

602 FIGURE CAPTIONS

Fig. 1. Schematic representation of the nested sampling design adopted in this research. Sampling plots were placed along an urbanization gradient, each one being composed of two subplots (I = isolated; C = connected control). In each sub-plot, three pitfall traps were activated during the sampling period (black dots).

Fig. 2. Barplot representing the contribution of *turnover* (dark grey) and *nestedness* (light grey) to the total
 taxonomic and functional β-diversity for carabids (left panel) and spiders (right panel).

Fig. 3. Ordination of carabid (left) and spider (right) communities, according to the first two PCoA axes performed on taxonomic (upper panel) and functional (lower panel) composition. Ellipses represent standard deviations around the medians of urbanization levels (green = low; orange = intermediate; purple = high). Different symbols represent sampling subplots belonging to different urbanization levels (circles = low; squares = intermediate; triangles = high). The animal silhouettes are from PhyloPic (http://www.phylopic.org).

615 Fig. 4. Ordination of carabid (left) and spider (right) communities, according to the first two PCoA axes 616 performed on taxonomic (upper panel) and functional (lower panel) composition. Ellipses represent 617 standard deviations around the medians of isolation levels (blue = connected control; brown = isolated). Different symbols represent sampling subplots belonging to different isolation categories (circles = 618 PhyloPic 619 connected control; isolated). The animal silhouettes from squares = are 620 (http://www.phylopic.org).

Fig. 5. Predicted CWM values (CWM-Trophic = trophic composition; CWM-BL = body length; CWM-Disp = dispersal) and confidence intervals along the urbanization gradient for carabids and spiders (light blue line = connected control patch data; orange line = isolated patch data). Only significant trends are reported. The animal silhouettes are from PhyloPic (http://www.phylopic.org).



