



Cross-taxon relationships in Mediterranean urban ecosystem: A case study from the city of Trieste

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ARTICLE INFO

Keywords:

Ants
Beetles
Carabids
Congruence
Mantel Test
Vascular Plants
Urban green areas

ABSTRACT

Urbanization directly and indirectly impacts biodiversity to the extent that it is considered one of the main causes of biotic homogenization and extinction. However, urban green areas can act as reservoir of biodiversity, and knowledge regarding species distribution in such contexts is crucial to define appropriate conservation and management strategies. Since inventories of species are generally time-consuming and costly, a commonly used approach consists in the use of surrogate species. However, studies investigating the effectiveness of surrogate species in urban environments still seem to be under-represented. In this research, we investigated the biodiversity of ants, plants, and carabid beetles in six different green areas within the urban area of the city of Trieste. The role of vascular plants as a potential surrogate for the diversity of ants and carabid beetles has been tested, investigating the influence of the environmental variables (dead wood, litter, anthropic disturbance, bare soil, bedrocks and rocks) on these relationships. Patterns of species richness and complementarity were compared among the sampled sites and their correlations were tested with Mantel tests and Co-Correspondence Analysis (Co-CA). Results pointed out that even disturbed and isolated sites within the urbanised matrix can sustain a high diversity of species of ants, carabids and plants, while in the semi-natural sites intermediate diversity levels were found. Plants were found to correlate directly with the diversity of ants; on the contrary, carabid species composition resulted only indirectly influenced by vascular plants, confirming the key role of abiotic variables in determining carabid diversity. Co-CA showed a clear distinction between forested and semi-natural environments and more open and disturbed environments. Furthermore, the Co-CA highlighted that the considered environmental variables (particularly dead wood, anthropic disturbance, rocks and litter) can significantly influence the distribution of analyzed taxa. Our results highlight the important role of urban green areas within the urban matrix as source of biodiversity and, furthermore, once more, support the role of vascular plants as meaningful surrogate for the diversity of ants and carabids.

1. Introduction

Urbanized areas cover approximately 6% of Earth's surface (Alberti et al., 2003), hosting ca. 55% of the world's human population (United Nations, 2018). The effects of urbanization affect ecosystems from local to global scale (Alberti et al., 2003; Wu, 2008), being generally associated with high levels of pollution, changes in land use and cover, alteration of biogeochemical cycles, habitat fragmentation and loss, introduction and spread of non-indigenous species (Grimm et al., 2000;

Wu, 2008). In such a scenario, human activities strongly affect, both directly and indirectly, biodiversity and ecosystem functioning in cities (Kowarik, 2011).

Urban green areas provide important ecosystem services, such as noise and micro-climate regulation, sequestration of air pollutants, seed dispersal (Bolund and Hunhammar, 1999; Gómez-Baggethun et al., 2013). Additionally, they can be a powerful tool to conserve and restore urban biodiversity, if appropriately managed (Alvey, 2006). One of the main factors affecting species communities in cities is the conversion of

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<https://doi.org/10.1016/j.ecolind.2021.107538>

Received 3 August 2020; Received in revised form 10 February 2021; Accepted 15 February 2021

Available online 4 March 2021

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land cover (Alberti et al., 2003; McKinney, 2006). Indeed, urban areas are often characterized by impervious surfaces, patchiness and by high levels of disturbance, which usually lead towards the loss or fragmentations of suitable areas for plants and animals (McKinney, 2002, 2008). Nonetheless, urbanization may promote the establishment of novel habitats (*sensu* Kowarik, 2011), colonized only by those species able to withstand the above-cited limiting factors (McKinney, 2008).

The effects of urbanization on local biodiversity are still debated in literature since urban green areas are usually strongly influenced by management practices which impact plant diversity and, in turn, may affect diversity of certain groups (e.g., birds; Savard et al., 2000; McKinney, 2002). On the other hand, the high spatial heterogeneity combined with the prompt availability of resources (e.g., water, fertilizers, food; McKinney, 2002) can sustain high levels of biodiversity, where even complex communities can establish (Wania et al., 2006; Shochat et al., 2006; Ortega-Álvarez and MacGregor-Fors, 2009). Vascular plants, for instance, frequently show high levels of species richness in urban areas (Kühn et al., 2004; Alvey, 2006; Kowarik, 2011) and may therefore act as important biodiversity refuges for other taxonomic groups like soil Arthropoda (i.e., ants and spiders; Trigoso-Peral et al., 2020).

In order to address appropriate conservation measures, knowledge concerning urban species and habitat distribution is fundamental (Margules and Pressey, 2000; Kowarik, 2011). Notwithstanding the recent expanding interest in urban ecosystems and diversity, few studies have investigated relationships between urban flora and fauna (Nielsen et al., 2014).

However, assessing diversity of living organisms and how they could respond to management practices is generally time and money consuming (Favreau et al., 2006) and, as a consequence, methods based on surrogates are often applied in ecological research (Margules and Pressey, 2000; Rodrigues and Brooks, 2007). The use of surrogate taxa and the assessment of cross-taxon congruence (i.e., the degree of correlation between individual species or groups of species) proved useful when monitoring biodiversity under limited financial resources (Howard et al., 1998; Santi et al., 2010a; Burrascano et al., 2018; Brunbjerg et al., 2019). If congruence is high, then a single taxon is representative of a broader range of co-occurring taxa; consequently, such taxa can benefit of conservation measures and studies based only on that single taxon (Margules and Pressey, 2000; Westgate et al., 2014). Indeed, high levels of congruence across taxa occur when diversity and/or composition patterns covary spatially (Rooney and Azeria, 2015). Nonetheless, to define which proxies better represent biodiversity in an area is not as intuitive as it can seem (Santi et al., 2010a), since there could be a variation in the degree of surrogacy, especially in complex ecosystems (Gerlach et al., 2013; Duan et al., 2016) and based on the taxa under consideration (Bräuniger et al., 2010). Other factors influencing this pattern are the spatial scale of observation (Burrascano et al., 2018) and the type of variables analyzed (e.g., occurrence or abundance data; Santi et al., 2016).

Several studies investigated the validity of different environmental variables and taxonomic groups as surrogates in different environments, ranging from protected areas (e.g., Santi et al., 2010a), riparian ecosystems (e.g., Bacaro et al., 2019), sand dune systems (Marignani et al., 2020), wetlands (Santi et al., 2010b; Guareschi et al., 2015), modified landscape (e.g., Yong et al., 2016), disturbed forests (e.g., Jokela et al., 2018) and artificial coniferous plantations (Barbato et al., 2019). Concerning urban ecosystems, contrasting results were observed depending on the taxa investigated. For instance, Blair (1999) found a high degree of concordance between birds and butterflies along an urban gradient while there was a taxa-dependent effect reported in Bräuniger et al. (2010). Other studies (e.g., Piano et al., 2020) analyzed the effect of local and landscape urbanization on abundance and species richness of different taxa but, to the best of our knowledge, no studies have examined cross-taxon relationships in urban green areas within the Mediterranean region.

In this study, by using data of vascular plants, ground-dwelling beetles and ants, along with information about collected abiotic variables, we aimed at: 1) quantifying urban diversity of carabid beetles, ants and vascular plants within six urban green areas of the city of Trieste, in terms of both their richness and composition; 2) assessing cross-taxon congruence among the surveyed taxa, particularly focusing on the structural role of vascular plants as habitat for ants and carabids, and investigating whether vascular plants can be used as surrogates of biodiversity of the studied taxa; 3) evaluating the role of environmental variables in affecting biodiversity and cross-taxon relationships in the study area.

We also discussed how urban habitats could help to sustain high levels of biodiversity and, to answer our research questions, we attempt to extrapolate from our results whether urban green areas represent possible sinks to sustain urban biodiversity with relevant implications for urban planners and biodiversity conservation within cities.

2. Materials and methods

2.1. Study area

This study was carried out within the urban area of Trieste, a border city and an important seaport located in north-eastern Italy (Lat. 40° 45' N, Long. 13° 46' E; Nimis, 1985) with an urbanized area of about 28 km² (Martini, 2006), where green spaces occupy only ca. 4% (Savi et al., 2015). Transition from coastal to hilly areas occurs quite rapidly, resulting in a variety of different landscapes. Climate is transitional, ranging from Mediterranean to Continental types, showing markedly differences between coastal and inner areas (Nimis, 1985). Indeed, according to the recent climatology, the mean annual air temperature recorded in city was 14.5 °C, while in the Karst it was 12.3 °C. Likewise, mean annual precipitation was 986 mm in the urban zone, while 1,342 mm in the hilly ones (Favretto, 2018). Additionally, Trieste is exposed to *Bora*, an intense and dry wind blowing from East-North-East, occurring especially during winter (Nimis, 1985; Favretto, 2018). Its strength not only increases the soil erosion, but also contributes to its desiccation (Kaligarić et al., 2006). The flora in the coastal areas is mainly Mediterranean, dominated by *Quercus ilex* and *Phillyrea latifolia* (Tretiach, 1992). On the other hand, the Karst Plateau is characterized by mixed deciduous woodlands of *Quercus pubescens*, *Ostrya carpinifolia* and *Fraxinus ornus* enriched by unique elements coming from eastern flora (Tretiach, 1992; Uboni et al., 2019). The administrative territory of Trieste includes 122 vascular plant families: about 13.2% of the urban flora consists of introduced species (Martini, 2009).

In order to capture the largest landscape variability of Trieste, a sampling campaign was carried out within areas characterized by a different degree of urbanization; in particular, we identified semi-natural forests in the first city outskirts (Bosco Bovedo - BB) and in the urban zone (Bosco Farneto - BF), and green spaces located deeply in the interior of the urban fabric (Giardino Pubblico - GP, Orto Lapidario - OL, Museo - MU). The areas selected for sampling are identified in Fig. 1. Inside Bosco Farneto, two sampling areas (BF1 and BF2, respectively) were chosen in order to investigate possible differences in biodiversity due to the proximity of the city as a proxy of anthropic disturbance: indeed, BF1 is located in the vicinity of the Karst, while BF2 is a portion close to the city center as shown in Fig. 1.

2.2. Sampling locations

BB is an urban semi-natural forest, located nearby residential buildings of Trieste and at the foot of the Karst region, representing a potential connection between urban and natural areas. It extends for ca. 94.8 ha and, because of its stony substrate, it has never been cultivated, with the only exception of grapevines. Vegetation in BB is classified as oakwood dominated by *Quercus petraea* with the presence of *Fraxinus ornus*, *Castanea sativa* and pine trees. Bosco Bovedo hosts a unique flora



Fig. 1. Location of the sampling areas (yellow squares), within the city of Trieste. GP, OL and MU coincide with the whole urban green sites containing them, while BB is a sub-area inside of Bosco Bovedo, as well as BF1 and BF2 are sub-areas inside Bosco Farneto. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

characterized by Mediterranean species (i.e., *Cistus salviifolius*) on the northern edge, and by Continental species (i.e., *Erica carnea* and *Calluna vulgaris*) on the southern one.

BF is a Mediterranean suburban forest crossing the eastern part of Trieste. It extends from the proximities of the city center to the Karst plateau, covering an area of 238 ha (Brandmayr et al., 2009) and is a rare example in Europe of urban forest that persisted nearly unchanged since the medieval age. Its vegetation was originally dominated by oaks (particularly *Quercus petraea*) and *Sesleria autumnalis* (Associazione Sportiva, 1994; Poldini, 1989) and, even though Farneto was subjected to an extensive clear-cutting in 1944, most of its surface was re-occupied by native trees forty years later (Brandmayr et al., 2009). Nevertheless, in those years it was recorded also the presence of the allochthonous species *Robinia pseudoacacia*, which reaches, in some areas, 20% of the forest canopy (Brandmayr et al., 2009).

GP is a popular urban garden in the city center of Trieste. It covers an area of about 3 ha and hosts a rich human-planned set of both native and non-native trees and shrubs. Regarding arboreal species, there are 368 individuals belonging to 49 species, among which alien species *Morus kagayamae* and *Aesculus hippocastanum* are the most common ones (Colin, 2019). Shrublands comprehend specimens of native species such as *Buxus sempervirens*, and specimens of introduced species, such as *Aucuba* sp. or *Pittosporum* sp. (Nimis and Tomé, 2014).

OL complex is part of the “J.J. Winckelmann” museum of antiquities, located nearby the San Giusto hill. This urban meadow consists of a managed area mainly characterized by grasses belonging to Poaceae family (e.g., *Festuca* sp. or *Phalaris* sp.); moreover, it presents arboreal species (e.g., *Celtis australis*, *Acer pseudoplatanus*), and patches with *Hedera helix* and the allochthonous *Robinia pseudoacacia*. It extends for about 1.1 ha and, within the garden, vineyards and orchards were also

cultivated in the past. To date, medieval and modern artifacts (epigraphs, headstones and sculptures) are here exposed (Cervi, 2004). This area is delimited by the only portion of city walls from the fourteenth century that are still intact (Bravar, 1992).

Finally, MU sampling area corresponds to a roadside grassland area nearby the Museo Civico di Storia Naturale, where an encroaching vegetation, mainly consisting of the autochthonous *Hedera helix*, *Rubus ulmifolius* and *Clematis vitalba*, as well as the allochthonous *Robinia pseudoacacia* and *Ailanthus altissima*, dominates the surrounding. It extends for ca. 2.4 ha, from the city center to a portion of a railway that originally connected Trieste to Karst and Slovenia. It is an abandoned area where no management activities or vegetation clear-cuttings usually take place.

2.3. Arthropods sampling

Ground-dwelling arthropods were sampled using pitfall traps. This method provides a standard and high replicative method of studying ground-dwelling arthropods (Ribera et al., 2001). In this study, pitfall traps were filled only with a preservative liquid consisting in a mix of antifreeze (propylene glycol, as proposed by Bestelmeyer et al., 2000), detergent (in order to break surface tension) and NaCl, diluted 20%. Each area was sampled three times between April and August 2018, placing randomly 10 pitfall traps but with a minimum distance of ca. 20 m apart from each other. Pitfall traps were left in place for, approximately, two weeks and then removed. Due to the citizens attending the areas, traps were placed in the nearest hide place available with respect to the selected point. Traps were labeled, buried at the surface level, protected and hidden with stones, dead wood or other materials present in their proximities. The exact locations of pitfall traps were recorded in

the field using a Garmin™ Monterra GPS Mapping. A total of 180 traps were placed (10 traps for each of the 6 sampling areas, for three sampling periods). However, since some of the traps were found overturned or tampered, 58 out of the 180 traps were not considered in the analysis. Replicates along the time periods were merged, and a total of 56 traps were considered in this study (up to the expected 60). Arthropods were cleaned from preservative liquid and soil residuals, and conserved in 70% alcohol. Coleoptera and Formicidae were sorted, separately, from the other trapped arthropods. First, beetle and ant taxa were identified at species level on the basis of their morphology (*morphospecies*), and their abundance (in terms of number of individuals) was recorded. Every new morphospecies found was pinned using entomological pins or mounted on cards with glue.

Regarding beetles, only carabids were considered for the following analysis. Carabid nomenclature was verified following the update version of the family Carabidae in the Fauna Europaea by Vigna Taglianti (2013) and de Jong et al. (2014). A complete list of the identified species (with full names and abbreviations) is reported in Supplementary Material S1.

2.4. Vegetation sampling

A 10x10 m squared plot was materialized in the field, centered on the exact location of each pitfall trap always using the same N-S and E-W orientation. In each plot, vascular plants presence and abundance (expressed as cover percentage, visual estimation) were recorded. Species not identified in the field were collected for laboratory identification (nomenclature followed Pignatti, 1982; Martellos and Nimis, 2018; Nimis et al., 2013; Nimis and Tomé, 2014). Alien species were determined following Galasso et al. (2018). A complete list of the identified plant species (with full names and abbreviations) is reported in Supplementary Material S1. Hereafter Her Hereafter, the term sampling site will be used to indicate both a trap and its corresponding plot.

2.5. Environmental variables

The following abiotic variables were recorded at the 10x10 m plot scale and expressed as percentage cover (visual estimation): litter cover, bedrocks (rocky and stony substrata), rocks, bare soil, dead wood (evaluated considering both dead standing trees and dead wood lying on the ground) and anthropic disturbance including each sign of human activities (e.g., waste or mowing and gardening activity) and human-related constructions such as walls, fences, and artificial substrates. Mean and standard deviation of the percentage cover of the sampled environmental variables, within each area, are reported in the Supplementary Material S1.

2.6. Statistical analysis

2.6.1. Diversity patterns at different spatial scales

For each taxonomic group, α diversity (i.e., species richness) was calculated for each sampling site in each area. A Kruskal-Wallis rank sum test was performed, for each taxon, to test differences among areas. When significant, post-hoc pairwise comparisons using Nemenyi-test with Chi-squared approximation for independent observations were applied. We used *kruskal.test* and *kruskalmc* functions within R package *pgirmess* (Siegel and Castellan, 1988; Giraudoux, 2018).

β diversity, measured as the mean of the site-to-site dissimilarities within a group (Whittaker, 1972; Legendre et al., 2005) was calculated for each taxonomic group using the Jaccard dissimilarity (for presence-absence data). On these dissimilarity matrices, differences for β diversity among areas, for each taxon, were tested using the procedure described in Bacaro et al. (2012, 2013). The procedure is based on any pairwise plot-to-plot dissimilarities, and checks deviation from randomness by computing the F-statistic and randomly permuting n times within-group dissimilarities, among groups, without considering between-group

dissimilarities (Anderson et al., 2006; Bacaro et al., 2013). Differences in β diversity among site, for each taxon, were tested by means of the *betadispersion2* R function (available in Bacaro et al., 2013 and using the R package *vegan*), setting 999 permutations. Finally, to quantify the contribution of diversity components at different spatial scales for the analyzed taxa, α , β and the total γ diversity were calculated performing an additive diversity partitioning analysis. This analysis, by partitioning diversity into additive components at hierarchical spatial scales, allows to compare the different components of diversity (α , β and γ) within and among communities (Lande, 1996). Here, three hierarchical spatial levels, $i = 1, 2, 3$, were considered where level 1 represents the sampling site scale (trap for arthropods, plot for vegetation), level 2 the sampling area scale and level 3 the whole study area (i.e., the whole set of sampling areas). For each taxonomic group, α_i represents the mean species richness found within spatial level i with respect to the whole study area; $\gamma (= \alpha_3)$ is the total species richness of the study area, while β_1 and β_2 are the variation in species composition found among sampling sites and areas, respectively. Following Crist et al. (2003):

$$\beta_1 = \alpha_2 - \alpha_1 \quad (1)$$

and, at the highest hierarchical level:

$$\beta_2 = \gamma - \alpha_2 \quad (2)$$

To verify whether the observed diversity values are determined by random sampling effects rather than by consistent ecological patterns, a null model test was also performed using R package *vegan* (Crist et al., 2003; Oksanen et al., 2019). The significance level of deviation from chance in the observed diversity values was estimated performing 999 permutations of the observed matrices.

2.6.2. Cross-taxon congruence in species richness

Congruence in species richness among plants, ants and carabids was evaluated via Mantel Tests. First, site-to-site Euclidean distance matrices (one for each taxon) were calculated, considering species richness values. Mantel test computes correlations between two distance matrices, testing for significant deviation from randomness in the observed correlations by permuting n times rows and columns of one of the two matrices (Mantel, 1967; Mantel and Valand, 1970; Legendre, 2000). Mantel tests, based on Pearson product-moment correlation coefficient, were performed among all the taxa pairs. Statistical significance was assessed by running 4999 permutations for each test. Correlations in species richness among taxa were also tested controlling for the influence of the environmental variables by performing a partial Mantel test (Legendre, 2000). Specifically, the association between pairs of distance matrices was assessed while controlling for the effect of the Euclidean distance matrix calculated on the environmental variables described above. The *mantel* and *mantel.partial* functions within the R package *vegan* (Oksanen et al., 2019) were used.

2.6.3. Congruence in species composition

Congruence in species composition was evaluated by 1) Mantel test and 2) Co-Correspondence Analysis (hereafter Co-CA). Correlations in terms of species composition between each pair of taxa were evaluated computing Jaccard distance matrices among sampling sites. Then, Mantel and partial Mantel tests were performed as specified in the previous section for species richness. At last, to evaluate congruence among taxa and to quantify the predictive power of plants species composition on ant and carabid species composition, Co-CAs were performed (ter Braak and Schaffers, 2004). Co-CA enables to directly correlate two different communities, surveyed at the same sites, and to identify common patterns between them (ter Braak and Schaffers, 2004). It finds the species scores that maximize the weighted co covariance between the site scores of the two communities of interest (ter Braak and Schaffers, 2004). Site scores (traps for arthropods, plots for plants) are defined for each community as weighted averaging of species scores, where the weights are the entries of the presence/absence

matrices. Here, the predictive form of Co-CA was used where a community (vascular plants in our study) is used to predict the other one (ant and carabid species composition, respectively), by combining the weighted averaging with a partial least squares model (ter Braak and Schaffers, 2004).

To assess the variance explained by each Co-CA ordination axis and the strength of relationships, two different tests were performed: cross-validation and permutation test. On one hand, leave-one-out cross validation computes the model n times, where n is the number of sampling site, each time leaving out one of them (Schaffers et al., 2008). Then, the obtained model is used to predict response species composition of the omitted site, from its predictor species (ter Braak and Schaffers, 2004). Prediction accuracy is defined in terms of cross-validated fit (%) for each axis; generally, fit values of axes above zero express that prediction obtained is better than that obtained by chance, validating the model (Schaffers et al., 2008). On the other hand, the permutation test verifies deviation of the observed explained variance from randomness by permuting n times the response matrix and calculating the F -ratio (ter Braak and Schaffers, 2004). Here, *coca* function from the *cocorresp* R package (Simpson, 2009) was used, setting 999 permutations. Once predictive Co-CAs were fitted, the set of environmental variables were overlaid to the ordination plot by means of the *envfit.coca* function available in the *cocorresp* R package (Simpson, 2009). The squared Pearson correlation coefficient, along with its statistical significance (based on 999 permutations), was calculated among environmental variables and the Co-CA axes. Co-CAs were performed with presence/absence and abundance species data. All statistical analyses were performed using R 3.2.6 (R Core Team, 2019).

3. Results

3.1. Diversity patterns at different spatial scales

The cumulative number of species recorded during the sampling campaign, the number of sampling sites for each sampling area, and the number of species for each taxonomic group are summarized in Table 1. The following number of individuals were collected: 106 individuals of carabid beetles belonging to 13 species and 15,387 individuals of ants belonging to 36 species. Concerning vascular plants, 216 species were identified, 45 of which were alien species.

Detailed information regarding the mean abundance of carabid and ant species for each area, along with the mean percentage cover of plant species and their alien status, are reported in Supplementary Material S1.

Kruskal-Wallis test performed on species richness revealed significant differences between areas for plants ($\chi^2(5) = 17.55$, p -value < 0.01) and ants (ants $\chi^2(5) = 26.08$, p -value < 0.001) but not for carabid beetles ($\chi^2(5) = 11.03$, p -value = 0.05). Pairwise comparisons among species richness recorded at each area were not significant for carabids, while significant differences in plant and ant species richness were found between GP and OL, where the lowest and the highest levels of ant and plant species richness were found, respectively. Moreover, ant species richness recorded in GP significantly differs also from that recorded in MU and BB, i.e., the other two areas where high ant species richness was

found (Fig. 2).

In terms of β diversity, average dissimilarity values for each taxonomic group, both for each considered area and for the whole dataset, indicate, on average, high dissimilarity in plants, followed by ants and carabids (Table 2). Indeed, GP sampled traps and plots were the most heterogeneous in terms of both plant and ant species composition, followed by MU. On the contrary, GP traps resulted quite homogeneous in terms of carabid species composition, and the most diverse carabid community was found in OL. In forest sampling areas (BB, BF1 and BF2) the most homogeneous plant community was recorded, as well as the most homogeneous ant community.

β dispersion among areas (the average dissimilarity from individual observation units to their group centroid in multivariate space), within the same taxon, showed significant difference for all the taxa investigated, with greater variation for plants ($F_{(5, 229)} = 30.544$, p -value < 0.001), followed by carabids ($F_{(5, 229)} = 15.562$, p -value < 0.001) and ants ($F_{(5, 229)} = 20.646$, p -value < 0.001). The same test repeated comparing β -dispersion among taxa across the whole study area, also resulted statistically significant ($F_{(2, 4617)} = 1203.5$, p -value < 0.001), indicating different pattern of beta diversity distribution among these taxa. Percent contribution of diversity components (α_1 , β_1 and β_2) to total γ diversity increased with the spatial scale in each taxonomic group (see Fig. 3). At the lowest spatial level, i.e., the sampling site one, ants revealed the highest levels of both α_1 and β_1 diversity, followed by carabids. α_1 and β_1 diversity values were significant at this spatial level for all the surveyed taxa. Conversely, plants revealed lower levels of α_1 and β_1 diversity at plot level but, at the sampling area scale, levels of species complementarity, β_2 , were higher than those of the other groups. All diversity components were statistically significant.

3.2. Patterns of cross-taxon congruence

Concerning correlations between species richness of the different taxa, Mantel tests revealed slightly positive (and significant) correlations between plants-carabids and plants-ants, and relatively higher (and significant) correlation between carabids and ants (Fig. 4a). These relationships remained consistent also when accounting for environmental variables (Table 3). With respect to species composition, Mantel tests revealed positive (and significant) correlations between plant-carabid and plant-ant species composition, this latter was higher than the one considering species richness. This relationship did not change for plants and ants when the correlation was controlled for the effect of the environmental variables while, for the same analysis, congruence between plant and carabid composition resulted not significant (Table 3). Conversely, correlation between ant and carabid species composition resulted negative but not significant (Fig. 4b).

Regarding Co-CA performed on presence/absence data between plants and carabids, only the first axis resulted significant with increasing and above zero cross-validated fit value, explaining a variance of 12.7% (Table 4). Conversely, Co-CA performed on abundance data did not produce significant axes (Table 4). Co-CA and cross-validation performed on presence/absence data between plants and ants showed 3 axes with increasing values of cross-validated fit above zero, but only the first one resulted significant, explaining a variance of

Table 1

Total number of species recorded at each area for the three taxa, species richness (mean \pm standard deviation), number of sampling site within each area and total number of species recorded at each area.

Areas	Vascular Plants	Carabids	Ants	# Sampling sites	Mean # plants \pm SD	Mean # carabids \pm SD	Mean # ants \pm SD
BB	49	4	18	9	17.00 \pm 3.12	1.00 \pm 0.87	9.33 \pm 2.29
BF1	45	5	14	8	19.00 \pm 3.29	1.00 \pm 0.75	6.87 \pm 2.64
BF2	38	3	14	10	15.90 \pm 4.60	0.80 \pm 0.63	6.80 \pm 2.10
GP	55	1	11	9	12.55 \pm 5.13	0.22 \pm 0.44	4.55 \pm 2.65
MU	76	5	22	10	22.30 \pm 8.21	1.40 \pm 1.17	9.10 \pm 2.23
OL	75	7	25	10	25.40 \pm 8.15	2.20 \pm 2.04	12.30 \pm 3.83
Total sampled species	216	13	36				

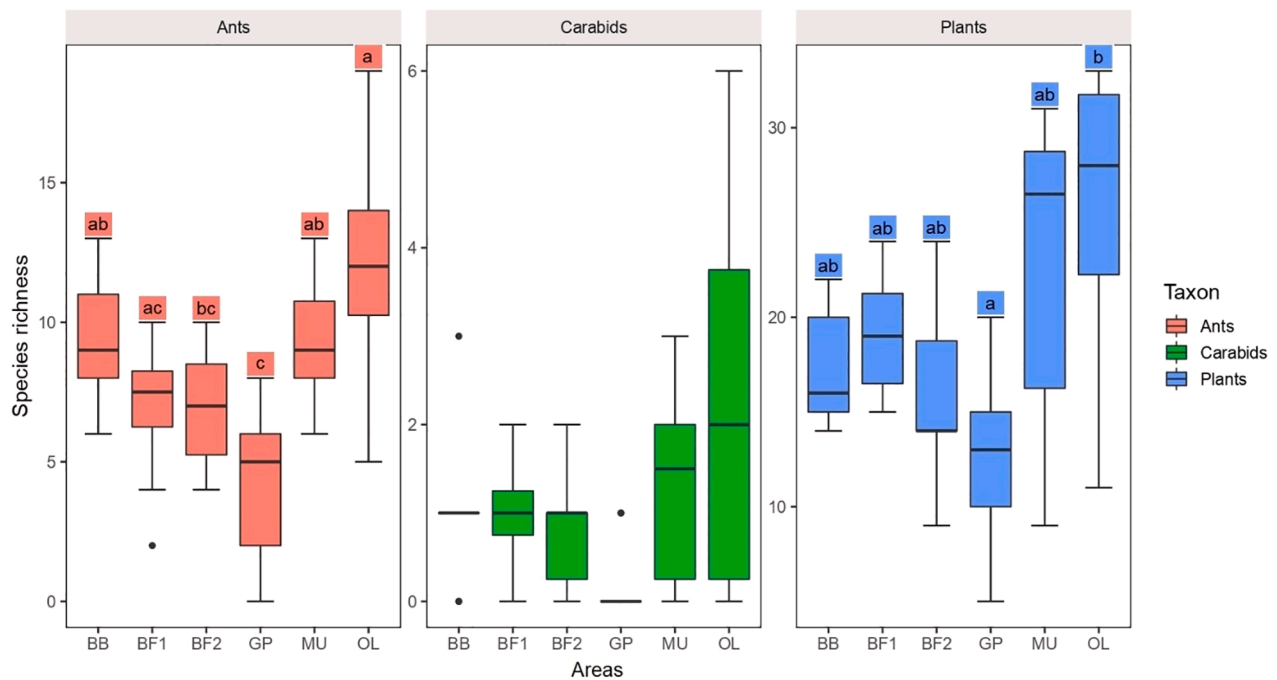


Fig. 2. Patterns of species richness in the six sampling areas. Horizontal black lines indicate, starting from the bottom, the minimum, the first quartile, the median (in bold), the third quartile and the maximum. Letters indicate significant differences based on Nemenyi's pairwise multiple comparisons, while black dots represent outliers.

Table 2

Average differences for each taxonomic group in terms of species composition, for each area and for the whole dataset (derived from Jaccard matrices; 0 = no dissimilarity, 1 = maximum dissimilarity).

Areas	Plants	Carabids	Ants
BB	0.651	0.504	0.375
BF1	0.556	0.530	0.474
BF2	0.562	0.372	0.371
GP	0.781	0.194	0.619
MU	0.752	0.542	0.548
OL	0.708	0.598	0.481
Whole study area	0.860	0.531	0.626

ca. 14% of the ant species variance. On abundance data, the Co-CA between plants and ants resulted in the first two axes significant and with cross-validated fit above zero, explaining a cumulative variance of ca. 31.5% (Table 4). Litter, rocks, anthropic disturbance and dead wood were significantly related to both carabid and plant distributions (presence/absence data). In Co-CA performed on abundance data, only anthropic disturbance and dead wood were both significantly correlated to carabid and plant species ordination axes (see Table 5). Conversely, all the environmental variables significantly correlated to ant and plant distribution in Co-CA performed on occurrence data (except for bare soil and plants), while when projected into the Co-CA performed on abundance data, only bare soil and anthropic disturbance resulted significant, with the exception of anthropic disturbance which did not correlate with plant composition (Table 6). Biplots derived from Co-CA between plant-carabid and plant-ant occurrence data (Fig. 5a and 5b, respectively) showed that compositional patterns, as well as sampling areas, are distributed along the first axes, following a gradient based on the amount of dead wood (on the left in Fig. 5a, on the right in Fig. 5b) and anthropic disturbance (on the right in Fig. 5a, on the left in Fig. 5b). This gradient, in turn, may reflect also a gradient of habitat openness. The biplots allow to identify two main distinct groups of carabid and ant species quite clearly. On one hand, on the left of the first axis in Fig. 5a carabid species commonly associated with woodlands and mature

stands (e.g., *Calosoma sycophanta*, *Calosoma inquisitor*, *Carabus catenulatus*) were found, as well as woodland ant species (e.g., *Dolichoderus quadripunctatus*, *Stenamma striatum*, *Temnothorax parvulus*) on the right of the first axis in Fig. 5b. These two groups are connected to plant species such as *Sesleria autumnalis*, *Dioscorea communis*, *Festuca heterophylla*. On the other, carabid (e.g., *Amara anthobia*, *Amara aenea*, *Harpalus tardus*) and ant species (e.g., *Formica cunicularia*, *Pheidole pallidula*) associated with rural and disturbed environments were found, respectively, on the right and on the left of the first axis for the two ordination biplots (Fig. 5a, 5b). Examples of plant species associated to these groups were *Diplotaxis tenuifolia*, *Cerastium glomeratum*, *Saponaria officinalis* and *Crepis neglecta*. This gradient along the first axis is maintained also in the Co-CA performed on ant-plant abundance data (Fig. 5d), where also a dryness-moisture gradient defined by the bare soil environmental variable can be identified along the second axis.

4. Discussion

4.1. Urban diversity at different spatial scale

Our findings showed that urban green areas within the Trieste Municipality sustain a relatively high level of plant, ant and carabid diversity. In urban areas, high values of plant species richness (such as those observed in OL and MU) have been often observed in other studies on urban flora and vegetation (e.g., Kühn et al., 2004; Wania et al., 2006; Tordoni et al., 2017; Fornal-Pieniak et al., 2019). Different factors such as the presence of non-native species, landscape connectivity with nearby natural areas, and habitat heterogeneity have been advocated as possible factors providing sources of species diversity in urban areas (Zerbe et al., 2003; Matthies et al., 2017; Fornal-Pieniak et al., 2019). In the following part, we discuss separately how the above mentioned factors are expected to influence species richness of the considered taxa in urban parks and urban forests.

The effect of habitat heterogeneity is particularly evident in OL, where the presence of a variety of micro-habitats typical of archaeological sites (e.g., open meadow, walls, ruins, epigraphs and stones, slopes, shaded corners), coupled with moderate disturbances linked to

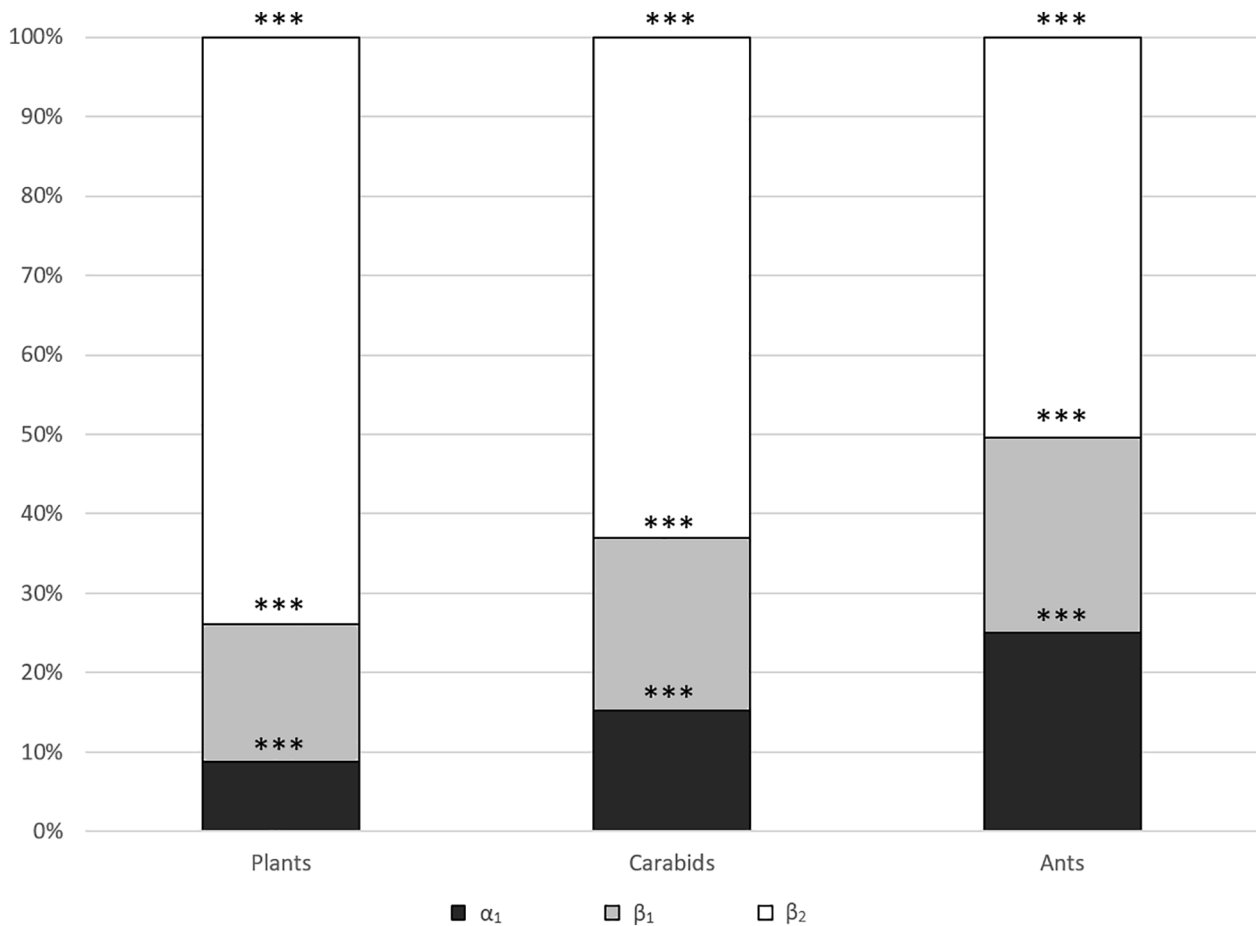


Fig. 3. Additive diversity partitioning among taxa at three hierarchical spatial levels: sampling site level, sampling area level, study area level. Both α_1 and β_1 indicate, respectively, α and β at sampling site, while β_2 denotes β at the area level. *** = p-value < 0.001, ** = p-value < 0.01, * = p-value < 0.05.

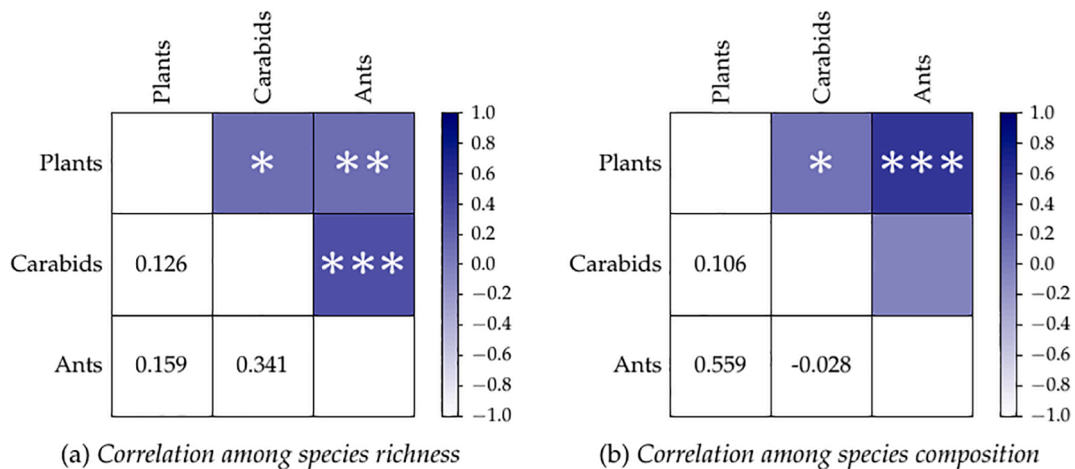


Fig. 4. Plot matrix summarizing Mantel test output considering a) species richness distance matrices (Euclidean distances) and b) dissimilarity (Jaccard dissimilarity). Lower part of the matrix: Pearson correlation coefficient values (r); upper part: p-values, significant correlations are marked with white asterisks; square colours reflect Pearson correlation coefficient values. *** = p-value < 0.001, ** = p-value < 0.01, * = p-value < 0.05.

occasional mowing activities, provide different ecological conditions able to enhance plant diversity (as reported for the urban flora of Rome; Celesti-Grapow et al., 2006) as well as arthropod diversity (Nielsen et al., 2014; Kowarik et al., 2016). Similarly, although MU is surrounded by urban streets, which can contribute to increase habitat fragmentation, it is connected to the Karst via an abandoned railway that may act as corridor for plant species dispersal (Tikka et al., 2001; Kowarik and

von der Lippe, 2011). Although the railway is not vegetated, the vegetation on its surroundings appears as a green line through the urban matrix and could contribute to connect the urban area to nearby green sub-urban zones, positively affecting plant and arthropod richness (Niemi, 2001; Matthies et al., 2017). It is worth noting, however, that high values of plant species richness may be partially explained by the presence of alien plant species, which, as shown by Tordoni et al. (2017)

Table 3

Pearson correlation coefficient (r) and its statistical significance once controlled for environmental dissimilarities (partial Mantel tests, 4999 permutations) among all pairs of taxa and controlling for the effect of environmental variables (the symbol | represents the conditional distance matrix). *** = p -value < 0.001, ** = p -value < 0.01, * = p -value < 0.05, n.s. = not significant.

	Groups Considered	r	p -value
Species Richness	Plants vs Carabids environmental variables	0.124	*
	Plants vs Ants environmental variables	0.157	**
	Carabids vs Ants environmental variables	0.339	***
Species Composition	Plants vs Carabids environmental variables	0.073	n.s.
	Plants vs Ants environmental variables	0.546	***
	Carabids vs Ants environmental variables	-0.048	n.s.

Table 4

Prediction accuracy (cross-validated fit) and cumulative explained variance of the predictive Co-CA axes for carabids and ants (plants are used as predictor variable in both Co-CA analyses), reported both for presence/absence and abundance data. Significant p -values resulted from permutation tests are marked in bold.

	Taxa	Axes	Cross-val. fit (%)	Cumulative expl. variance (%)	p -value
P/A data	Carabids	1	12.009	12.698	0.001
		2	13.956	19.844	0.757
	Ants	1	11.054	13.758	0.001
		2	15.369	20.351	0.176
		3	16.637	24.987	0.573
		1	6.310	9.151	0.172
Abundance data	Carabids	2	9.800	17.944	0.175
		3	12.719	26.944	0.116
	Ants	1	4.686	17.065	0.001
		2	3.014	31.462	0.001

for the city of Trieste, exploit urban connectivity to spread onto urban ecosystems.

The lowest levels of species richness found in GP lead us to suppose that different co-occurring factors influence biodiversity in this area. Indeed, although urban management in parks could increase plant diversity (Blair, 1996), too intense and too frequent mowing as well as gardening activities (including the cultivation of alien ornamental plants), along with the daily presence of many people attending the area and the manual removal of litter from the ground, provide a permanent disturbance that can simplify vegetation structure and negatively affect plant and arthropod species richness (McKinney, 2002; LaPaix and Freedman, 2010; Trigos-Peral et al., 2020). The removal of leaf litter not only affects ants' foraging activities but can also reduce soil microbial activities leading to soil compaction, which can hamper ant nesting (Melliger et al., 2018; Santos et al., 2019). In such a context, the lack of rocks that characterize GP grounds, may have been crucial in limiting ant establishment in this area. Similarly, leaf litter removal may also affect carabid species richness, since it provides prey resources and shelter for this taxon (Magura et al., 2008; Philpott et al., 2019). Noteworthy, in 2016 there were evidences in this area for concentration above-the-threshold level of Polycyclic Aromatic Hydrocarbons (PAHs)

Table 5

Environmental variables projections onto Co-CA ordination performed on carabid-plant presence-absence and abundance data; squared Pearson correlation coefficient (r^2) and p -values are reported. *** = p -value < 0.001, ** = p -value < 0.01, * = p -value < 0.05, n.s. = not significant.

	P/A data		Plants		Abundance data		Plants	
	Carabids r^2	p -value	r^2	p -value	Carabids r^2	p -value	r^2	p -value
Litter	0.178	*	0.259	**	0.227	n.s. (0.059, tendential)	0.222	n.s.
Bedrocks	0.011	n.s.	0.014	n.s.	0.019	n.s.	0.013	n.s.
Rocks	0.361	**	0.331	**	0.310	*	0.255	n.s. (0.060, tendential)
Bare soil	0.036	n.s.	0.047	n.s.	0.001	n.s.	0.006	n.s.
Anthr. dist.	0.412	***	0.533	***	0.389	**	0.328	*
Dead wood	0.258	**	0.299	**	0.438	**	0.377	*

in top soil layers that have probably negatively impacted the arthropod community richness: indeed some studies (e.g., Read et al., 1998; Blakely et al., 2002; Santorufo et al., 2012) found that the degree of contamination by heavy metals and PAHs is an important factor affecting soil invertebrate communities. Notwithstanding the low values of species richness for all the taxa recorded in GP, this site showed the highest variation in plant species (β diversity), mainly represented by ornamental trees and shrubs, due to the area management plan determined by the local administration.

Concisely, for the green areas completely surrounded by the urban matrix, the amount of anthropic disturbance recorded in our study plays a significant role in structuring plant distribution. On one hand, the presence of roads, walls and artificial substrates is related to the presence of ruderal plant species that are able to colonize such surfaces, which act as analogous for natural rocky habitats (e.g., Lundholm and Marlin, 2006). These factors may contribute also to select certain types of carabid or ant species that show anthropophilic tendencies (Trigos-Peral et al., 2020) and benefit from the warmer and drier conditions of these habitats (Lupi et al., 2007; Cordonnier et al., 2019). On the other hand, however, intensive management strategies in urban green spaces have a negative impact on species richness of many taxa: it is well recognized that the management applied in urban areas affects indigenous arthropod assemblages (Davis, 1978; Helden and Leather, 2004; Hartley et al., 2007), especially low mobile species as found by Sattler et al. (2010). Similar conclusions have been also described in other studies for different groups (see, for instance, Aguilera et al., 2019).

The intermediate levels of plant species richness found in urban woodlands (BB and BF) can be ascribed to a lower presence of alien species compared to more urbanized areas. Indeed, less soil management and disturbances have probably prevented the formation of suitable sites for alien species invasion (Bacaro et al., 2015; Kowarik et al., 2016). A similar trend was recorded also for carabids and ants; the intermediate levels of arthropod species richness in the urban woodlands are probably due to higher soil moisture, higher canopy cover and denser understory, which may be unsuitable for communities requiring more xerothermic conditions (Thompson and McLachlan, 2007; Clarke et al., 2008; Trigos-Peral et al., 2020). Although not statistically different from the other areas, BB showed richer ant communities than the other woodlands. This area is characterized by a stony substrate and a higher amount of rocks, an element positively correlated with the

Table 6

Environmental variables projections onto Co-CA ordination performed on ant-plant presence/absence and abundance data; squared Pearson correlation coefficient (r^2) and p-values are reported. *** = p-value < 0.001, ** = p-value < 0.01, * = p-value < 0.05, n.s. = not significant.

	P/A data		Plants		Abundance data		Plants	
	Ants	p-value	r^2	p-value	Ants	p-value	r^2	p-value
Litter	0.516	***	0.578	***	0.280	n.s.	0.292	n.s.
Bedrocks	0.305	**	0.359	*	0.063	n.s.	0.176	n.s.
Rocks	0.177	*	0.198	*	0.102	n.s.	0.122	n.s.
Bare soil	0.160	*	0.134	n.s. (0.05, tendential)	0.516	*	0.725	**
Anthr. dist.	0.542	***	0.592	***	0.554	*	0.416	n.s.
Dead wood	0.249	**	0.294	**	0.112	n.s.	0.129	n.s.

availability of ant nests (Reyes-López et al., 2003) and thus explicative of the high ant species recorded. Indeed, since ants are thermophilic, stones provide not only protection but also an adequate temperature retaining warmth longer than the ground (Kaspari, 2000).

In general, species composition of plants, ants and carabids showed a relatively high dissimilarity among sampled green areas, although different in relative proportions, and communities resulted well structured considering spatial scales. Comparing diversity components for the three taxa, we observed that most of the diversity of carabids and plants is represented by species composition differences among the six

areas. A different pattern is observed for ants, where at least 50% of total diversity is related to local scale species richness and composition differences among sampling sites within the single area. This important difference is related to taxon-specific dispersal modality, mobility rate and interaction with the local environmental heterogeneity. Spatial heterogeneity, in particular, is considered as the major driver in shaping species composition (Davies et al., 2005); this encompasses several factors such as ecological interactions mainly at the local scale, or geography-based factors such as topography or aspects on a larger scale (Fridley et al., 2004). Since urban development patterns affect spatial

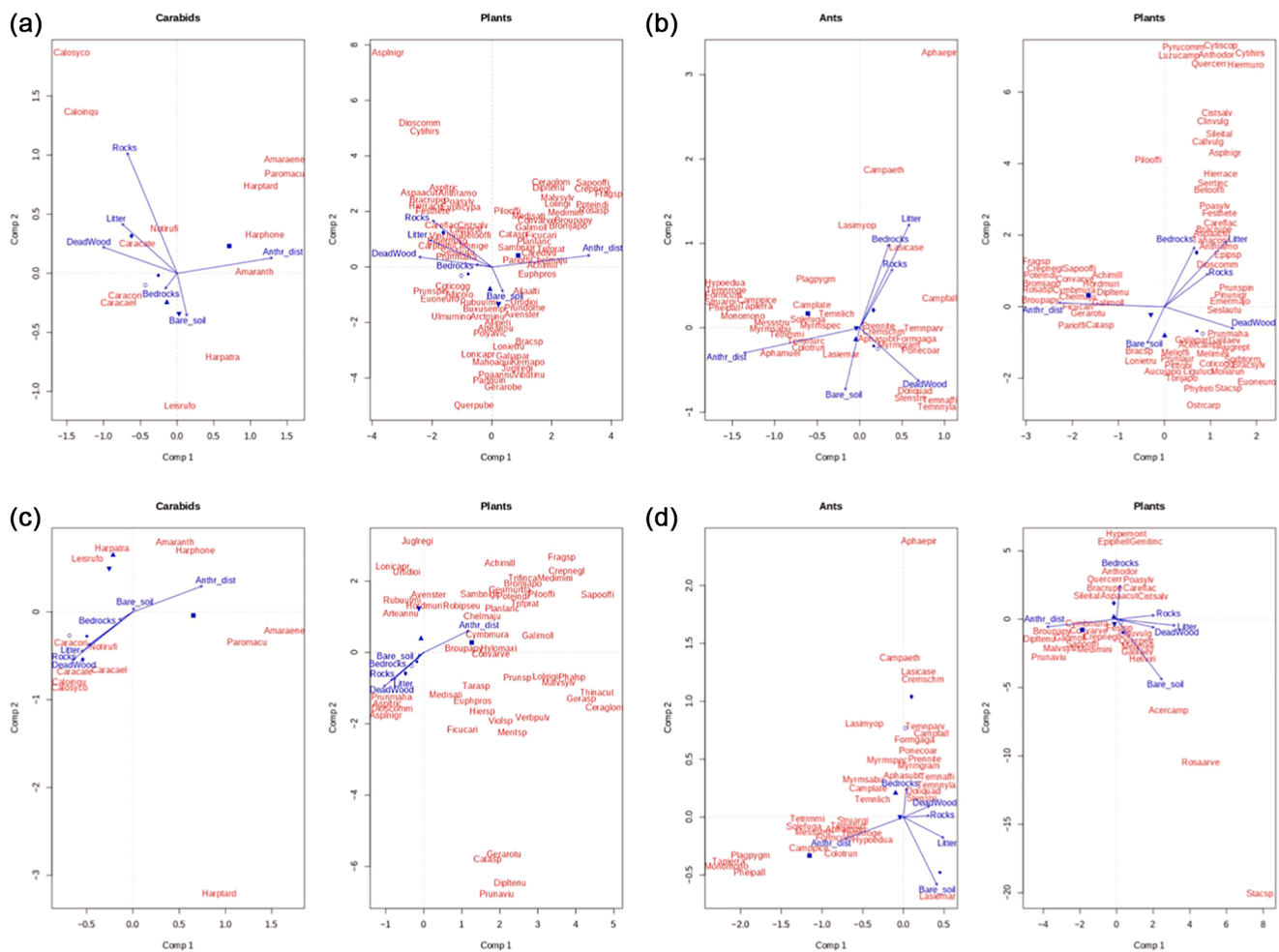


Fig. 5. a) Predictive Co-CA biplots of carabid species composition (left) and plant species composition (right), performed on presence/absence data. b) Predictive Co-CA plots of ant species composition (left) and plant species composition (right), performed on presence/absence data. c) Predictive Co-CA plots of carabid species composition (left) and plant species composition (right), performed on abundance data. d) Predictive Co-CA plots of ant species composition (left) and plant species composition (right) performed on abundance data. Symbols $\blacklozenge, \bullet, \square, \blacktriangle, \blacktriangledown$ and \blacksquare indicate BB, BF1, BF2, GP, MU and OL sampling areas, respectively. For species' abbreviations of all taxa, please refer to Supplementary Materials S1. For the sake of readability, some labels of plant species (in particular, those closest to the origin) were deleted both in the presence/absence and abundances distributions.

heterogeneity of urban ecosystems, we also argue that alternative urban patterns that emerge from human and ecological interactions play an important role in the dynamics and resilience of these peculiar areas (Tordoni et al., 2017). Thus, our study points out how assessing species richness and composition with a multi-scale approach is desirable in order to study the complex relationships among spatial scales, especially in the context of multi-taxa studies, where each group behaves differently to exogenous environmental factors.

4.2. Carabid beetles congruence pattern and diversity

In accordance with our hypothesis, cross-taxon congruence analysis revealed that plants can be selected as a surrogate to describe carabid diversity in the study area, although with some clarification. Mantel test performed on species richness and composition revealed a covariation pattern between these two taxa, that can be determined for both taxa by the local variation of environmental variables and human influence more than by the effect of the plant community variation on carabids. Our findings seem to agree with those of Sanderson et al. (1995) and Ubani et al. (2019) that indicate the soil characteristics as the most important factor driving carabid distribution. Similarly, plant species abundance and distribution, especially in urban environments, were related to attributes such as natural-passive use park type, wetland presence, hillslope landform, steep slopes, management and irrigation (Taal and Santelmann, 2019).

In general, it is well-known that carabid assemblages are influenced by the indirect effects deriving from vegetation structure, such as the canopy of large trees or dense herb cover, which affect not only microclimate conditions regulating incoming solar radiation, light availability, shading and moisture in soils, but also the presence of preys (Sanderson et al., 1995; Ings and Hartley, 1999; Magura et al., 2008).

From the present study, variation in carabid composition, regarding species occurrence and abundance data, has been mainly observed along a disturbance gradient (in the direction of the first axis of predictive Co-CA ordinations). Soil management and disturbance greatly influence larger species, which require more stable conditions than the smaller ones (Sustek, 1987; Blake et al., 1994). Similarly, we found larger and predator species belonging to genus *Calosoma* and *Carabus* mainly in urban woodlands (BB and BF); however, the predator species *Notiophilus rufipes* was also sampled in OL, suggesting that the high habitat heterogeneity present in this site enhances species co-existence (and thus the availability of prey), as documented for ants and spiders in urban green areas (Trigos-Peral et al., 2020). *Carabus coriaceus* was also recorded in MU and this confirmed that green areas, along the railway, support connections between Karst and the Trieste urban area, enabling the dispersion of flightless species.

The first axis of predictive Co-CA ordinations also reflects the amount of dead wood and litter, indirectly indicating a habitat gradient (from close to open habitats). Species such as *Calosoma inquisitor*, *Calosoma sycophanta* and *Carabus catenulatus*, typically associated with closed and mature stand habitats (Brandmayr et al., 2005; Brandmayr et al., 2009), are clearly separated along this axis from *Amara aenea*, *Amara anthobia*, *Parophonus maculicornis*, *Harpalus tardus*, *Harpalus honestus*, which are species commonly found in open and disturbed habitats (Brandmayr et al., 2005; Magura et al., 2008; Mazzei et al., 2015). The presence of dead wood and litter is also connected with the lack of management (Magura et al., 2008), and may indirectly enhance the abundance and species richness of predatory carabids by increasing the number of preys (Seibold et al., 2016). Indeed, dead wood is usually linked to stable humid microclimate conditions and high amounts of nutrients that favor the colonization of snails, slugs and earthworms, which are preys of large carabids such as *Carabus catenulatus* (Brandmayr et al., 2009; Kotze et al., 2011; Kirchenbauer et al., 2017; Ashwood et al., 2019). Moreover, dead wood and litter provide shelter and favorable microsites for the development of carabid eggs and larvae (Magura et al., 2004).

4.3. Ants congruence patterns and diversity

As expected, ants and plants were highly correlated. In contrast to carabids, partial Mantel test indicated that relation between plant and ant species composition is only slightly controlled by abiotic factors. It is well known that vegetation has a direct effect on ant species composition, mitigating microclimate variations and providing different nesting sites and food resources (Majer, 1983; Alonso, 2000). As a counterpart, ants act as seed dispersers of certain plant species whose seeds contain the elaiosome (Folgarait, 1998), and seed transport mediated by ants can be very important especially in fragmented habitats (Palfi et al., 2017) such as those present in the Trieste urban matrix. By building subterranean tunnels and nests, ants not only contribute to soil aeration and water infiltration, but also redistribute organic and inorganic matter along the soil profile (Folgarait, 1998; Nkem et al., 2000), influencing plant occurrence and enhancing habitat heterogeneity (Streitberger and Fartmann, 2015).

The first axis of Co-CA performed on ant and plant occurrence and abundance data was correlated with the amount of anthropic disturbance, which, in turn, also reflected a gradient of habitat openness. Indeed, our analysis pointed out that ant species such as *Camponotus piceus*, *Strumigenys argiola*, *Formica cunicularia*, *Pheidole pallidula* are mainly associated with xeric and open habitats, and that the last two are also common in disturbed areas, building their nests under stones, in bare ground, wall crevices and railway embankments (Collingwood, 1979; Giacalone and Moretti, 2001; Holecová et al., 2015; AntWeb, 2020). In accordance with the literature (e.g., Giacalone and Moretti, 2001; AntWeb, 2020; Trigos-Peral et al., 2020), we found a correlation between the presence of dead wood and ant species such as *Dolichoderus quadripunctatus*, *Ponera coarctata*, *Stenammina striatulum*, *Temnothorax parvulus* and *T. nylanderii*. Dead wood and rocks can be exploited by ants as nesting site, since they insulate against sudden changes in temperature (Vesnic et al., 2017); moreover, dead trees create canopy gaps with high amount of light, which positively affects not only ants, but also light-demanding vascular plants (Ulanova, 2000; Jokela et al., 2018). However, when abundance data were considered, ant distribution did not significantly correlate with the amount of dead wood and rocks, suggesting that their presence may increase ground complexity, hampering ants' movement during the foraging activity (Lassau and Hochuli, 2004; Uno et al., 2010).

The second axis of Co-CA (which resulted significant only with abundance data) was correlated with the amount of bare soil that defined a dryness-moisture gradient, with two different species at the extremes: on one side, the ubiquitous species *Lasius emarginatus*, which seems to exploit dry ground for foraging activity (Wilson, 1955; Giacalone and Moretti, 2001; Stukalyuk and Radchenko, 2011); on the other side, *Aphaenogaster epirotes*, generally found in humid habitats and woodlands (Borowiec and Salata, 2018). As a general remark, we observed that the high habitat heterogeneity within the study area determined a high variation in ant species composition, allowing the co-existence of both specialist species typically associated with woodlands (e.g., *Dolichoderus quadripunctatus*; Trigos-Peral et al., 2020) and opportunistic species more adapted to urban environments (e.g., *Tetramorium immigrans*; Lassau and Hochuli, 2004; Cordonnier et al., 2019).

5. Conclusion

Although urbanization is considered one of the leading causes of species extinction, some studies revealed that urban green areas can host high species diversity (Kühn et al., 2004; Fornal-Pieniak et al., 2019; Trigos-Peral et al., 2020). Preservation of urban biodiversity is fundamental not only for conservation purposes, but also for human well-being (Kowarik, 2011). Our analysis pointed out that vascular plant diversity is, in combination with the description of the local environment characteristics, a valuable surrogate for the diversity of ants and carabids. We can argue that the observed moderate level of congruence

between plants-carabids and plants-ants could be ascribed to their low rate of dispersion, which increases their dependence on local environmental conditions and disturbances (Alonso, 2000; Duan et al., 2016): the main drivers of biodiversity in urban green areas (Nielsen et al., 2014). Our results can be useful for decision makers and local authorities to develop appropriate conservation strategies and monitoring measures to preserve biodiversity within the urban green areas.

CRedit authorship contribution statement

Laura Zara: Conceptualization, Investigation, Formal analysis, Writing - original draft. **Enrico Tordoni:** Investigation, Formal analysis, Writing - original draft. **Silvia Castro-Delgado:** Writing - original draft. **Andrea Colla:** Supervision, Writing - original draft. **Simona Maccherini:** Writing - original draft. **Michela Marignani:** Writing - original draft. **Francesco Panepinto:** Writing - original draft. **Michele Trittoni:** Writing - original draft. **Giovanni Bacaro:** Conceptualization, Investigation, Supervision, Formal analysis, Writing - original draft.

Declaration of Competing Interest

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

Acknowledgements

This work was supported by Friuli Venezia Giulia Region Operative Program, European Social Fund – 2014/2020 Program, Specific Action n. 53/16: Integrative professional training courses within degree programs.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107538>.

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