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Wooded areas promote species richness in urban parks

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Abstract
Urban green spaces can have an important role in biodiversity conservation. However, they are not often a focus of biodiversity studies, although their global area is raising. We investigated the impact of habitat characteristics of urban green spaces on an ecologically important group of insects—ants (Hymenoptera: Formicidae). We tested three questions: 1) does ant species richness positively correlate with park size and the extent of wooded areas? 2) Is ground temperature the best predictor of ant activity? 3) Will communities be dominated by thermophilic, dry-tolerant, generalist species? Using pitfall traps, hand collecting, and baiting we sampled 7595 ants belonging to 30 species, across eight localities in urban protected areas of the city of Zagreb, Croatia. Parks with larger wooded areas had high species richness, but park size was not a good predictor of species richness. Ant activity was largely influenced by temperature. Five out of eight localities had similar ant community composition. The remaining three localities each had unique ant communities with no overlap with any other locality. Overall, in addition to typical urban species, we recorded species of conservation interest. Thus, small urban green spaces have the capacity to support and conserve diverse ant communities, but their habitat characteristics need to be considered in urban planning.

Keywords Ants · Insects · Urban green spaces · Urban biodiversity · Insect conservation

Introduction

Urban protected areas are distinct from natural protected areas because they are warmer, drier, smaller, and often contain impervious surfaces. They also receive a higher number of visitors, a higher level of light, noise, and chemical pollution, and they are usually more heavily managed compared to the natural protected areas (Trzyna 2014). Consequently, urban protected areas, and other urban green spaces, are characterized by reduced biodiversity (McKinney 2008; Fattorini 2011a). However, urban green spaces can have an important role in the conservation of threatened species (Carpintero and Reyes-López 2014; Soanes et al. 2019), including key functional groups such as pollinators (Hall et al. 2017) or saproxylic beetles (Fattorini and Galassi 2016), and they provide environmental benefits such as extreme climate mitigation and flood resilience (IPBES 2019). Additionally, biodiversity of areas where people live is important for their ability to connect with nature, which makes them more likely to support or take conservation actions (Miller and Hobbs 2002; Dunn et al. 2006; Dearborn and Kark 2010). Because the global extent of urban area is estimated to triple by 2030 (Seto et al. 2012; Güneralp et al. 2013) our understanding of the urban ecology, and the management of urban green spaces, is becoming more important. Understanding how the variation of habitat characteristics contributes to the capacity of urban green spaces to support wildlife is crucial for their successful conservation management (Uno et al. 2010; Trzyna 2014).

With estimated 5.5 million species, insects are the most diverse group of animals on our planet (Stork 2018). They play a significant role in the functioning of most terrestrial ecosystems as decomposers, consumers, plant dispersers, pollinators, and as food resources. Despite their diversity and importance, research and conservation efforts focusing on insects are still less frequent than those focused on larger, charismatic vertebrates or on plants (Clark and May 2002; Dunn 2005; Seddon et al. 2005; Donaldson et al. 2016; Leandro et al. 2017; Troudet et al. 2017). Consequential lack of knowledge about insects is especially worrisome in the light of recent research that shows that many insect taxa experience significant regional population declines (Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys

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2019; Forister et al. 2019; van Klink et al. 2020), because it reduces our ability to protect them.

To explore how characteristics of protected urban areas affect insect biodiversity we chose ants (family Formicidae) as our study target taxon. Ants are ubiquitous and diverse family of insects (>13,000 species globally), dominant in abundance and biomass in most terrestrial habitats (Holldobler and Wilson 1990; Bolton 2019). Generally, many ant species adapt well to environmental changes associated with urbanization, including habitat disturbance and changes in temperature and humidity (Menke et al. 2011; Jenkins et al. 2011; Del Toro et al. 2015). They are abundant in most urban green spaces and easy to collect using standard methods (Agosti et al. 2000). Previous research shows ants perform many ecosystem services (Del Toro et al. 2012), including those of highly efficient urban scavengers (Youngsteadt et al. 2015). Ants are often used as ecological indicators in conservation and land management practices (Ottonetti et al. 2006; Angulo et al. 2016; Verdinelli et al. 2017), including in urban ecosystems (Sanford et al. 2009), because they quickly respond to habitat changes.

Previous investigations of urban biodiversity recognized the size of urban green spaces as one of the most important predictors of ant species richness (Fattorini et al. 2018). In general, larger urban green spaces are found to be more species-rich and diverse than smaller areas (Yamaguchi 2005; Pacheco and Vasconcelos 2007; Carpintero and Reyes-López 2014; Fattorini et al. 2018), as they enable the establishment of larger, more stable populations. In addition to the size of urban green spaces, the presence and the extent of diverse vegetation cover, especially trees, is often positively correlated with species richness (Vepsäläinen et al. 2008; Slipinski et al. 2012). Tree cover in urban parks contributes to habitat heterogeneity, and provides important nesting sites for ants. Another important factor in structuring ant communities through influencing ant activity is temperature (Cerdá et al. 1998; Jenkins et al. 2011). Thermophilic, dry-adapted, generalist, and invasive species are overrepresented in urban environments (Menke et al. 2011; Carpintero and Reyes-López 2014; Savage et al. 2015). However, some urban green spaces can support rare ant species, indicators of mature habitats, and species of conservation interest (Pacheco and Vasconcelos 2007; Carpintero and Reyes-López 2014; Liu et al. 2019).

To test what shapes community structure of this ecologically important insect group in urban protected areas, we surveyed ants in Zagreb, the capital of Croatia. We tested how different habitat characteristics affect ant species richness and activity. We predicted that urban green spaces of larger size, with larger wooded areas, will support a higher number of ant species than small urban green spaces with smaller wooded areas. We also predicted that ant activity will be most influenced by ground temperature. We predicted that thermophilic, dry-adapted, and generalist species will be overrepresented in Zagreb ant communities and that community composition will be similar across localities.

Methods

Study site We conducted fieldwork in the city of Zagreb, Croatia (45.80°N, 15.99°E, elevation 145 m) that has a human population of about 800,000 (Šiško and Polančec 2019) and temperate continental climate (Zaninović et al. 2008). Based on the last published checklist of Croatian ants (Bračko 2006) and a small-scale study of agricultural habitats (Ješovnik et al. 2019), Zagreb has 31 species of ants.

We sampled ants at eight localities in protected areas of Zagreb (Fig. 1, Table 1): five parks in the city center, and three localities in Maksimir Park—a larger park three kilometers away from the city center. All sampled parks are nationally protected areas, in the category of "monument of park architecture" (Croatian Parliament 2013). Five parks in the city center are small, with relatively small variation in size (0.6–4 ha), and we considered each of those parks a single sampling locality. They differ in the amount of open and wooded areas, urban surfaces, number of visitors, and management intensity (Table 1 and Table S1a). Four of the five parks in the city center (SV, TO, ST, and ZR in Fig. 1) have an intensive management typical for a city-park, characterized by frequent (~bi-weekly) mowing of low vegetation areas. The fifth city park, Botanical garden (BO in Fig. 1), has a mix of frequently mowed areas and areas with low mowing regimes (mowing twice per year). Low mowing regime is a part of Botanical Garden's project "Let It Grow", which promotes the growth of native vegetation and reduced management. In Maksimir Park we surveyed three sampling localities because of its larger total size (356 ha). We chose localities based on habitat structure and management intensity. The first meadow (VI) was a frequently mowed (~bi-weekly) open habitat with low number of trees (similar to most city parks), representing standard management regime for the majority of open habitats in the Maksimir Park. The second meadow (LE) is the only exception to this mowing regime, as this area of ~0.26 ha is mowed only twice a year. The third locality, an oak forest (HR), represents the most common habitat type of Maksimir Park. All sampled localities are within five to six kilometres of Nature Park Medvednica, which is the nearest large natural area (179.2 km^2) and a likely population source for native species inhabiting the green spaces of the city of Zagreb.

Ant sampling We sampled ants once per month from May to August of 2019. Each sampling event consisted of pitfall trap sampling, hand collecting, and baiting across all localities, except in May when we sampled ants using only hand

Table 1 Habitat characteristics and coordinates of sampling localities

	Locality	N	E	Total park area (ha)	Wooded area (ha)	Open area (ha)	Urban area (ha)	Management
City centre	BO - Botanical Garden	45.804780°	15.971705°	4.45	2.23	0.58	0.73	mixed mowing regime
	SV - Petar Svačić Square	45.806950°	15.974420°	0.59	0.16	0.34	0.08	intensive mowing regime
	TO - King Tomislav Square	45.806364°	15.978708°	1.88	0.19	0.92	0.68	intensive mowing regime
	ST - JJ Strossmayer Park	45.808530°	15.978548°	1.55	0.4	0.46	0.7	intensive mowing regime
	ZR - Zrinjevac Park	45.810414°	15.978278°	1.79	0.62	0.73	0.42	intensive mowing regime
Maksimir Park	VI – First meadow	45.824676°	16.022826°	0.69	0.22	0.48	0	intensive mowing regime
	LE - Second meadow	45.831360°	16.023968°	0.26	0	0.27	0	low mowing regime
	HR - Oak forest	45.831282°	16.023288°	0.24	0.24	0	0	no mowing

collecting and baits. We chose not to sample by pitfall traps in May because of the significantly lower daily temperatures (Table S1f, Fig. S1). Lower temperatures can cause a considerable pitfall undersampling due to low ant activity (Engel et al. 2017; Fellers 1989). We sampled ants using baits and hand collecting on rainless, largely sunny days, between 10 am and 5 pm, with average daily temperatures ranging from 19.4 °C to 26.5 °C (Table S1f).

Hand collecting consisted of an active search by an experienced collector across all microhabitats in a given locality. It was designed to maximize the number of species, and we collected 1–10 workers of each species in vials with 95% ethanol (EtOH). To standardize hand sampling we restricted cumulative sampling time to 60 min per locality per sampling event, regardless of the number of collectors (either two people sampled for 30 min, or three people sampled for 20 min).

For pitfall sampling we set up 10 pitfall traps per location, in two linear transects of five, with a 3-m distance between the pitfalls within a transect, and a minimum of 10 m between the two transects. In the Botanical garden, we set up 15 pitfall traps because of its habitat diversity and larger size than other sampling localities (Table 1). We used 50 mL centrifuge tubes with 3 cm diameter as pitfall traps and set them up with an improvised soil core (a metal tube and a hammer). We filled pitfall traps with ~15 mL of 60% EtOH and a few drops of glycerol and left them open for 48 h. Upon collecting all samples were stored in 95% EtOH.

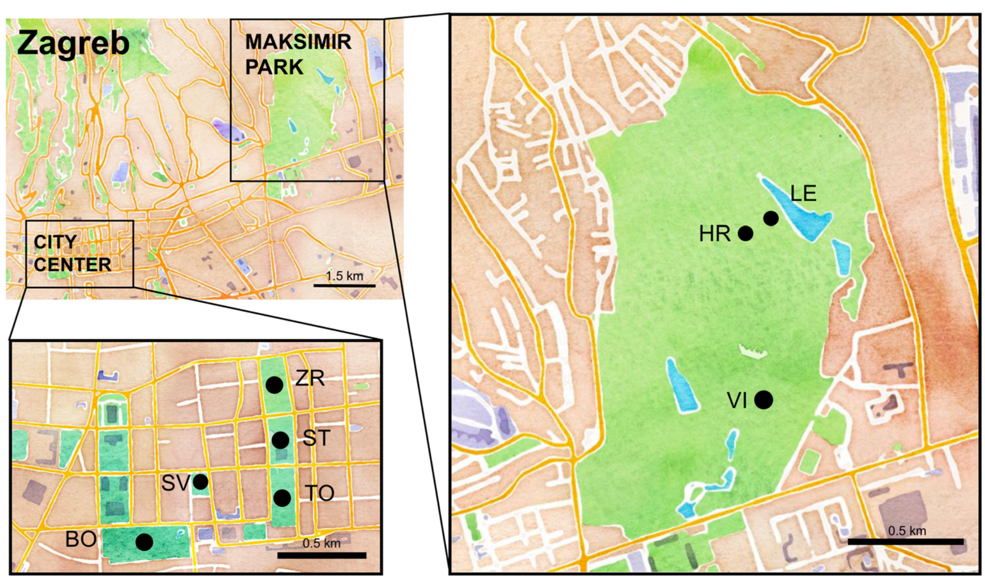

Fig. 1 Position of sampling localities in the city of Zagreb, Croatia. Black dots represent sampling localities; the name of localities are indicated by the two letter code. City center localities: BO- Botanical garden, SV- Petar Svačić Square, TO- King Tomislav Square, ST - JJ Strossmayer Park, ZR- Zrinjevac Park. Maksimir Park localities: VI - First meadow, LE - Second meadow, HR - oak forest. The map for this figure was prepared in QGIS v.3.4 (Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.org)

We baited ants using a 2 mL tube with a small piece of cotton at the bottom, soaked in a saturated honey solution. At each locality, we placed 15 baits on the ground, in a single linear transect, with 2 m between each bait. We measured ground temperature at the beginning and the end of each baiting period by aiming a portable IR thermometer to the ground (Fluke 62Max, Fluke Corporation, Everett, Washington, USA). We left baits on the ground for 60 min, after which we collected them with the ants inside. We conducted hand collecting during 60 min the baits were active. All ants were stored in 95% EtOH. All collected ants were identified to the species level under the stereomicroscope (XTL3400D) using the taxonomical keys (Radchenko and Elmes 2010; Wagner et al. 2017; Seifert 2018), and global ant specimen database Ant Web (https://www.antweb.org). All specimens are stored in the collection of the Croatian Myrmecological Society, Zagreb.

Measuring park characteristics To estimate the visitation intensity of parks we counted the number of people passing at one to two randomly chosen points within the park's paths or other areas where people walk, for 60 s, bi-monthly, for 3 months (Pacheco and Vasconcelos 2007). Using Google Earth Pro we measured surface area of the entire locality, total green spaces, wooded spaces (area covered with trees), open green spaces (areas with low vegetation), and vegetation-free urban surfaces (paved or gravel areas). We obtained average daily temperatures for all sampling months from the Croatian Hydrological and Meteorological Service (DHMZ), recorded at two measuring stations, Grič and Maksimir. Station Grič (GPS: 45.81468, 15.97196) is 600–1000 m away from the five city centre parks, and station Maksimir (GPS: 45.8213, 16.02594) is 500–1100 m away from the three sampling localities in Maksimir Park.

Statistical analyses We used the number of sampled species with both hand collecting and pitfall traps, per month, for analyses of species richness. We calculated inverse Simpsons (*D*) and exponential Shannon (*expH'*) as diversity measures (Chao et al. 2014), using the pitfall data only (as the hand-collected samples do not provide a standardized abundance estimate). We standardized pitfall trap data from the Botanical garden (where we set up 15 instead of 10 traps) by randomly subsampling 10 out of 15 pitfalls. To illustrate differences in the ant communities between the localities we used the non-parametric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) based on pairwise distances (Bray-Curtis dissimilarity), using the pitfall data.

To test the effect of the total park area, wooded area, habitat loss, visitation, and sampling month on ant species richness we used generalized linear models (*glm* function in R). We included the month of sampling in our model to test for potential effect of seasonality (Herbers 1989). The total park area was highly correlated with both wooded area ($r = 0.93$, $p < 0.001$) and path area ($r = 0.81$, $p < 0.001$), so their contribution in explaining species richness was tested with separate models. As a proxy of habitat loss, we used the area of urban surfaces (paved or graveled) within each locality. To select the optimal model, we used an information theoretic approach (Burnham and Anderson 2002). After constructing our models, we ran a model comparison based on ΔAIC values—the difference of the AIC of the *i*-th model and the model with the lowest AIC value. To examine the differences in richness and diversity across parks we used Kruskal-Wallis test.

As an estimate of foraging activity, we calculated the proportion of baits occupied by ants. We first tested differences in ant occurrence across eight studied parks using a proportion test. We used GLM with binomial error distributions to test how ant activity varies with park characteristics. We included surface temperature, locality size, wooded area size, habitat loss, visitation and sampling month in our full model, and applied the same AIC model selection approach. All statistical analyses were run in R (R Core Team 2020), using package *vegan* (Oksanen 2019). The R code used for all analyses is available online at https://github.com/JelenaBujan/Zagreb-Urban-Ants.

Results

Wooded parks are species rich and diverse

Across eight localities, we collected 7595 ants, belonging to 30 species within 17 genera (Table 2). All of the collected species were native. Total species richness at a sampling locality ranged from 13 to 24 species. Localities containing larger wooded area had, on average, higher species richness (Fig. 2, Table S2a; GLM: $R^2 = 0.38$; $\beta = 2.27$, SE = 0.62, $p = 0.0015$). Both optimal models predicting species richness across Zagreb parks contained wooded area (within 2 AIC units). Although the second optimal model contained the number of visitors, only the wooded area was a significant predictor of species richness (Table S2a, $\beta = 2.5$, SE = 0.65, $p = 0.001$). The total park area was not a good predictor of species richness (Table S2a). Species richness differed across studied parks (Fig. 3a; Kruskal-Wallis: $\chi^2 = 18.41$, df = 7, $p = 0.010$) with the highest total species richness in the first meadow, VI (24 species), in Maksimir park. The Botanical garden had the highest species richness of the city-center parks (23 species), as well as the highest diversity ($D = 0.74$; *expH'* = 5.5) of all studied localities (Fig. 3, Table S1a). Both inverse Simpson (Fig. 3b; $\chi^2 = 16.76$, df = 7, $p = 0.019$) and exponential Shannon indices (Fig. 3c; $\chi^2 = 19.91$, df = 7, $p = 0.006$) differed across studied parks.

Table 2 The ant species collected in urban protected areas of Zagreb, presence-absence data per sampling locality. BO - Botanical garden, SV - Petar Svačić Square, TO - King Tomislav Square, ST - JJ Strossmayer Park, ZR - Zrinjevac Park, VI - First meadow, LE - Second meadow, HR - oak forest. * 1st record for Zagreb

	Locality							
Species	BO	SV	TO	ST	ZR	VI	LE	HR
Aphaenogaster subterranea	1	1	0	1	0	1	1	1
*Camponotus fallax**	1	1	0	1	1	1	0	0
Camponotus vagus	0	0	0	0	0	0	1	0
Colobopsis truncata	1	1	1	1	1	1	0	1
Crematogaster schmidti	1	1	1	1	1	1	1	1
Dolichoderus quadripunctatus	0	1	1	1	1	1	0	1
Formica cunicularia	1	0	1	1	1	1	1	0
Formica fusca	1	0	0	0	0	1	1	1
*Lasius brunneus**	1	1	0	1	1	1	0	1
Lasius emarginatus	1	1	1	1	1	1	0	1
*Lasius flavus**	1	0	0	0	0	1	1	0
Lasius fuliginosus	1	0	0	0	0	1	0	0
Lasius myops	0	0	1	0	1	1	1	0
Lasius niger	1	1	1	1	1	1	1	1
Liometopum microcephalum	1	1	1	1	1	0	1	1
*Myrmecina graminicola**	1	0	1	1	0	0	0	1
Myrmica curvithorax	0	0	0	0	0	0	1	1
Myrmica scabrinodis	1	0	0	1	0	1	1	1
*Plagiolepis pygmaea**	1	1	0	0	0	1	0	0
Ponera coarctata	1	0	0	0	0	0	0	1
*Ponera testacea**	1	0	0	0	0	1	0	0
Prenolepis nitens	1	0	1	0	0	1	0	0
Solenopsis fugax	1	1	1	1	1	1	1	0
*Tapinoma subboreale**	1	1	1	1	1	1	0	0
Temnothorax affinis	0	0	0	1	0	0	0	0
*Temnothorax clypeatus**	0	0	0	1	0	1	0	0
*Temnothorax crassispinus**	0	0	0	0	0	1	0	1
*Temnothorax tergestinus**	1	1	0	1	1	1	0	1
*Temnothorax turcicus**	1	1	0	1	0	1	0	0
Tetramorium caespitum	1	1	1	1	1	1	1	0
Total species number	**23**	**15**	**13**	**19**	**14**	**24**	**13**	**15**

Distinct community composition at three localities

Four city center parks (SV, TO, ST, ZR) and one Maksimir Park locality (VI), had similar ant community composition, indicated by their close clustering in the NMDS ordination (Fig. 4; stress value: 0.087, Shepard plot non-metric $R^2 = 0.994$). Complementing the NMDS, ANOSIM analysis indicated a significant difference between the communities ($p = 0.0001$, Fig. 4). The remaining two localities from Maksimir Park (oak forest, HR and second meadow, LE), and the Botanical Garden (BO) show distinct ant communities, not similar to any of other sampled localities (Fig. 4). The most common species, collected across most localities, were thermophilic and opportunistic species of European cities, such as *Lasius niger, Tetramorium caespitum, Formica cunicularia,* and *Crematogaster schmidti.* Based on the pitfall trap data the most abundant species was *L. niger* (57.3% of total ant abundance), followed by *Solenopsis fugax* (15.1%), *Myrmica scabrinodis* (6%), *Formica cunicularia* (5.8%), and *Tetramorium caespitum* (4.6%). Out of 25 species for which such ecological data exists 22 species (80%) are thermophilic and 13 (52%) are dry adapted (Table S1b). Most of the species (20/30, 66.6%) are habitat generalists, with a smaller number of open habitat specialists (5/30, 16.6%) and woodland species (5/30, 16.6%) (Table S1b).

Although they were less common and less abundant, we also found indicators of mature habitat, and species of conservation interest, endangered at the regional or national level in Europe (Falk 1991; Glowacinski et al. 2002; Sturm and Distler 2003; Witkowski et al. 2003; Farkac et al. 2005; Gärdenfors 2010; Kålås et al. 2010; Rassi et al. 2010; Binot-Hafke et al. 2011), such as *Aphaenogaster subterranea*, *Camponotus vagus*, *Colobopsis truncata*, *Ponera testacea*, *Myrmecina graminicola* (Table S1b). An exception was the European velvet tree ant, *Liometopum microcephalum*, a species of conservation interest in Europe (Petráková et al. 2017), which was abundant and which occurred across seven out of eight localities.

Activity is higher in larger, wooded parks at lower temperatures

Ants occurred on 35% of total baits (Table S1e), and their occurrence was significantly different across parks (Fig. 5a; $\chi^2 = 31.65$, df = 7, $p < 0.0001$). The best predictor of ant activity was the average ground temperature, followed by the wooded area and total park area (Table S2b). The two optimal models together predicted 85% of variation in ant activity. In the range of sampled temperatures (20–47 °C), we found a negative relationship between ant activity and temperature (Fig. 5b; GLM: $R^2 = 0.34$, $\beta = -0.13$, SE = 0.02, $p < 0.0001$).

The temperature in the city centre was on average 0.93 °C higher than in Maksimir Park for all sampling months except May (Fig. S1, Table S1f). The baits in the city centre localities also had a higher average number of ants on baits (607 compared to 92.3 in Maksimir), and they differed in dominant species. The city centre was dominated by *Tetramorium caespitum* (87.5%), while in Maksimir localities *Lasius niger* and *Crematogaster schmidti* were the dominant species. Ant activity was positively correlated with the total area ($\beta = 0.46$, SE = 0.11, $p < 0.0001$) and the wooded area in the park ($\beta = 0.84$, SE = 0.62, $p < 0.0001$, Table S2b). We recorded the highest activity in the Botanical garden (BO), and lowest at first meadow (VI) in Maksimir Park (Fig. 5a). The species

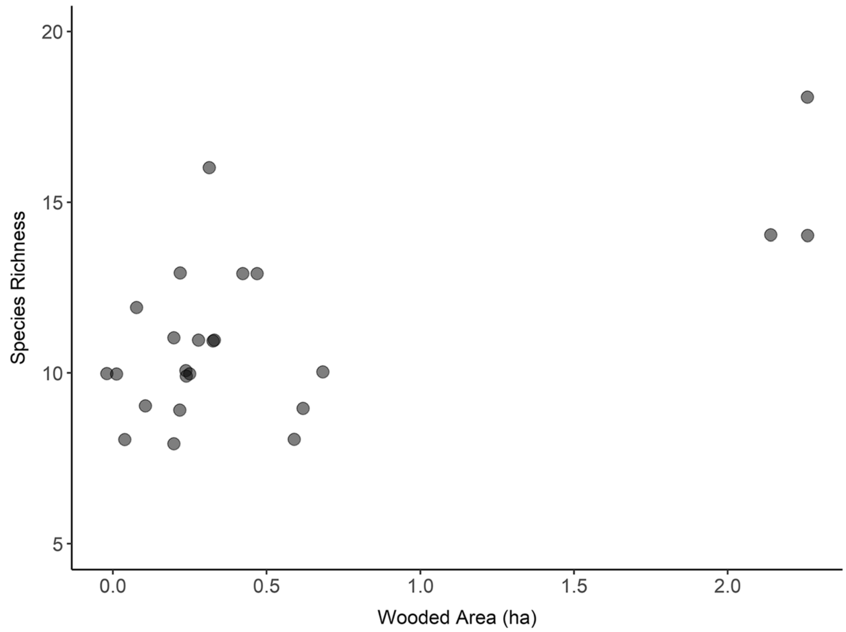

Fig. 2 Relationship between wooded area of Zagreb parks and ant species richness

most commonly occurring on baits was *Tetramorium caespitum,* accounting for 47% of total occurrences, all recorded at the city center localities.

Discussion

We tested how certain habitat characteristics impact ant species richness, activity, and community composition in protected urban areas. We found that the parks with larger wooded area support more species, in line with our hypothesis. We did not find support for our hypothesis that larger parks will have higher species richness. Ant activity was best explained by the ground temperature, as predicted. Thermophilic species and habitat generalist were most common and most abundant across the sampled localities. However, three of the sampled localities had distinct ant communities. Some sampled protected urban areas hold species of conservation interest, endangered at the regional or national level, suggesting that urban protected areas in Zagreb have the capacity to serve in species conservation.

The wooded area is the best predictor of ant species richness

Our results are in accordance with previous studies showing that forest fragments (Uno et al. 2010; Slipinski et al. 2012; Fattorini and Galassi 2016), and single trees in open habitats

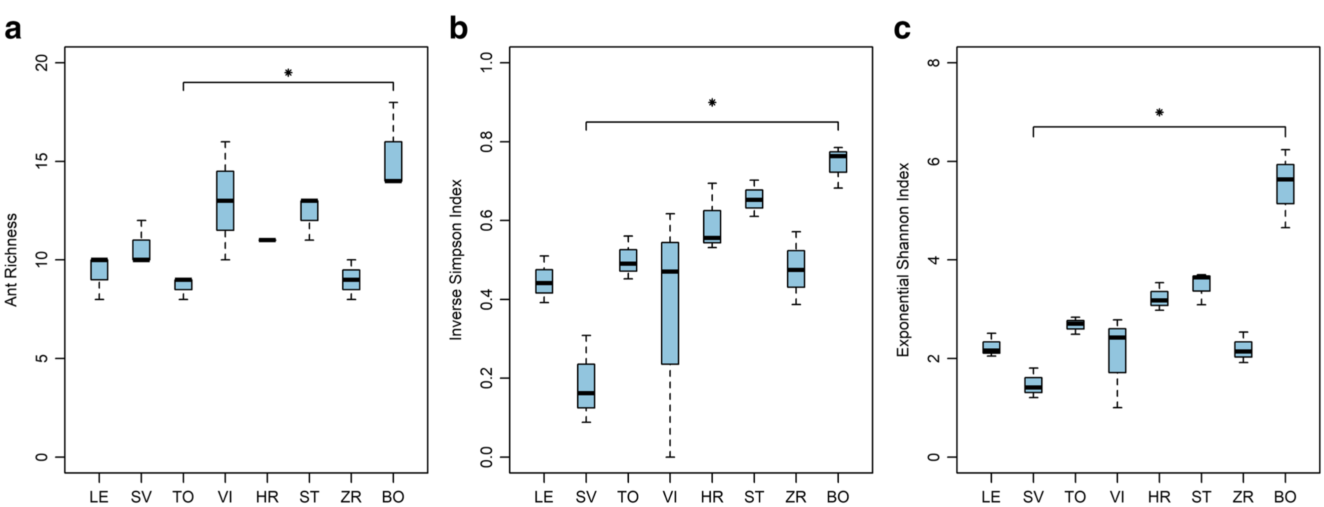

Fig. 3 Ant richness and diversity: Ant species richness (**a**), inverse Simpson index (**b**), and exponential Shannon (**c**). The localities on are ordered along x axis by the size of their wooded spaces, from smallest to largest. Significant differences between parks after pairwise comparisons is marked with an * ($\alpha = 0.05$). City center localities: BO - Botanical garden, SV - Petar Svačić Square, TO - King Tomislav Square, ST - JJ Strossmayer Park, ZR - Zrinjevac Park. Maksimir Park localities: VI - First meadow, LE - Second meadow, HR - oak forest

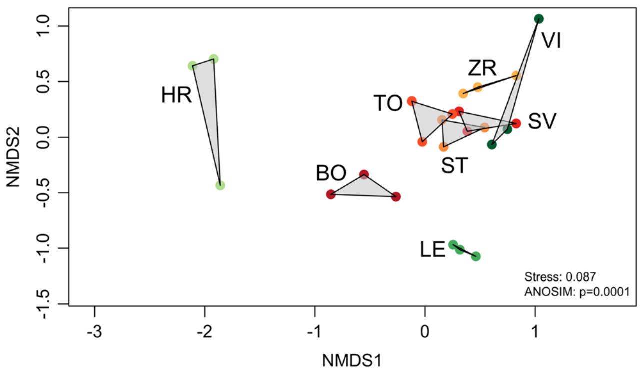

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination of ant communities in different localities. City center localities (in red colors): BO - Botanical garden, SV - Petar Svačić Square, TO - King Tomislav Square, ST - JJ Strossmayer Park, ZR - Zrinjevac Park. Maksimir Park localities (in green colors): VI - First meadow, LE - Second meadow, HR - oak forest

promote ant species richness (Majer and Delabie 1999; Manning et al. 2006; Yasuda and Koike 2009; Frizzo and Vasconcelos 2013; Prevedello et al. 2018), as well as richness of other arthropods, birds, and plants (Guevara et al. 1992; Dunn 2000; Manning et al. 2006; Martin et al. 2009). In open and disturbed habitats, such as urban and agricultural areas, trees provide nesting sites, food, and a distinct microclimate. The accumulation of leaf litter and deadwood material on the ground surrounding the trees provides additional microhabitats for leaf-litter species (Vepsäläinen et al. 2008). At the landscape scale trees increase habitat heterogeneity and ecological connectivity (Manning et al. 2006; Lindenmayer and Laurance 2017). However, not all trees have the same impact: native, older, and larger trees ("veteran trees") have a stronger positive effect on biodiversity than non-native or young trees (Majer and Delabie 1999; Manning et al. 2006; Hall and Bunce 2011; Frizzo and Vasconcelos 2013; Horák 2017). Within our study sites, old trees with the hollow or rotten trunks were especially important for species *Liometopum microcephalum, Lasius fuliginosus* and *Dolichoderus quadripunctatus,* as their essential nesting site (Petráková et al. 2017; Miklín et al. 2017; Seifert 2018), as well as for other arboreal ant species (40% of all recorded species, Table S1b).

Contrary to our predictions we did not find higher number of ant species in larger parks. This finding is in contrast with some previous studies (Yamaguchi 2005; Pacheco and Vasconcelos 2007; Carpintero and Reyes-López 2014; Fattorini et al. 2018) and with the theory of island biogeography (MacArthur and Wilson 1967), often applied to urban green spaces (Fattorini et al. 2018). However, some research shows that the habitat size does not have a strong influence on ant species richness (Smith et al. 2006; Clarke et al. 2008), and that smaller fragments can have higher species richness than larger areas (Gibb and Hochuli 2002). In general, our understanding of the minimal habitat size requirements for most invertebrate taxa is much poorer than for vertebrates (Cardoso et al. 2011). Some ant species can establish populations on very small green areas, such as road medians of Broadway, New York (Pećarević et al. 2010; Savage et al. 2015). Most ant species are good dispersers, which enables them to colonize isolated habitat patches (Holldobler and Wilson 1990).

Although our results are in line with some of the previous research, we would like to point out that studied localities and wooded spaces had relatively small variation in size (Table 1) and that variation was unevenly distributed (e.g., none of the localities had the wooded space size between 1 and 2 ha). In this study we were restricted by choosing to investigate only the urban protected areas in Zagreb. A study that would include a larger gradient in sizes of urban parks and its wooded spaces could have a different result.

Community composition is distinct at three localities Ant community composition in over 60% of our localities was

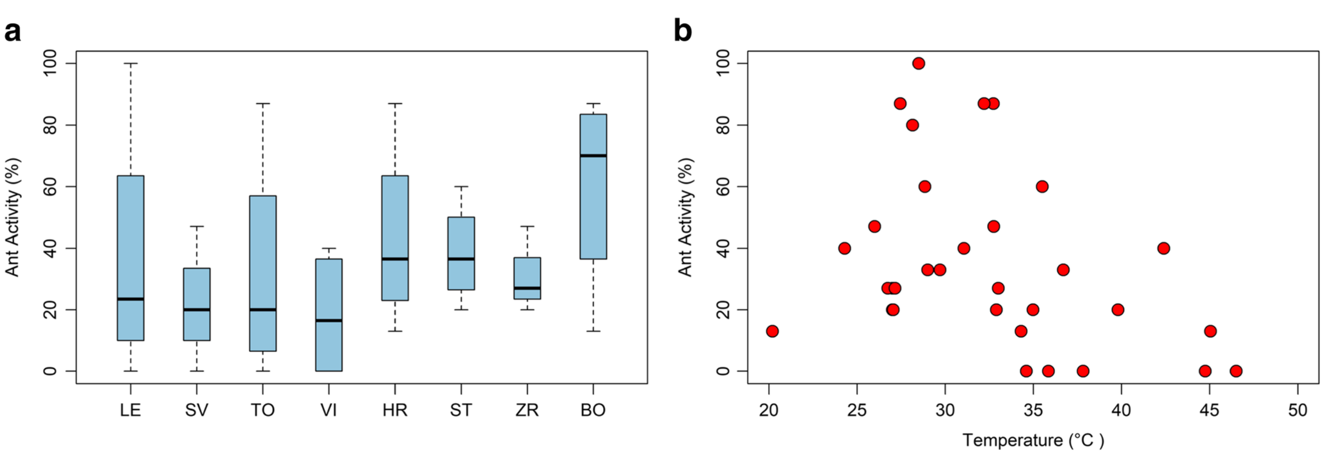

Fig. 5 Ant activity across Zagreb parks. Ant activity per locality (**a**). Ant activity was positively correlated with temperature (**b**). City center localities: BO- Botanical garden, SV- Petar Svačić Square, TO- King Tomislav Square, ST - JJ Strossmayer Park, ZR- Zrinjevac Park. Maksimir Park localities: VI- First meadow, LE- Second meadow, HR- oak forest

homogeneous, dominated by the common opportunistic, thermophilic, dry-adapted species of European urban habitats. These species are indicative of higher environmental stress on those localities (Savage et al. 2015) frequently found in urban areas (Vepsäläinen et al. 2008; Uno et al. 2010; Menke et al. 2011; Santos 2016; Seifert 2018). The remaining three localities had distinct ant communities, reflecting different habitat types: urban botanical garden (BO), the oak forest (HR), and the semi-natural meadow (LE). These localities supported rare species, species considered indicators of mature habitats, and species of conservation interest. All species we collected were native, which was surprising because Zagreb has a well-established international trade and there are about 40 alien ant species known in Europe (Rabitsch 2011). This result indicates that alien ant species are either not present in studied parks or they are currently at very low population densities. If this changes in future, our study will provide baseline data for comparative post-invasion studies.

Management intensity most likely caused the difference between the localities with homogeneous and with unique ant communities. All five localities with homogeneous ant communities had intensive mowing regime of open areas (~bimonthly), while the remaining three localities had either none or low mowing regime across at least some percentage of their area. Urban forest habitat, such as locality HR, are in general less managed than the open green spaces. The meadow (LE) is mowed only twice a year, and the Botanical garden (BO) has some of its areas left unmoved for most of the year, a part of their "Let it Grow" natural management project. Our study did not specifically test the mowing regime's influence, but we suggest that it could be important in structuring ant communities. The mowing regime has been recognized as important for the management of the open habitats (Smith et al. 2015; Leston and Koper 2017; Unterweger et al. 2017), as reduction of mowing intensity has a positive effect on diversity and biomass of plants, vertebrates, and invertebrates (Fischer et al. 2013; Leston and Koper 2017; Unterweger et al. 2017), including ants (Elmes et al. 1998).

Temperature is the best predictor of ant activity The best predictor of the ant activity, measured by ant occurrence on baits, was the temperature, and wooded area and park size to a lesser extent. Ants are ectotherms, and the temperature is a major factor influencing their abundance, activity, and community composition in both natural (Cerdá et al. 1998; Jenkins et al. 2011), and urban environments (Menke et al. 2011; Gippet et al. 2017). Ants will stop foraging at temperatures that are either too high or too low compared to their thermal optimum, so ant activity often has a unimodal relationship with temperature (Porter and Tschinkel 1987; Cerdá et al. 1997; Cerdá et al. 1998). We found that thermal optimum (maximum foraging activity) of urban ants was at 28.5 °C after which with temperature increase ant activity decreases. Considering that our ants are adapted to a moderate temperate continental climate, temperatures above 29 °C are likely stressful, and this is why activity levels decline at higher temperatures. In cities, the temperature is consistently higher than in adjacent rural areas (Oke 1973, 1982), acting as an environmental filter (Menke et al. 2011; Gippet et al. 2017). Although *Lasius niger* was the most abundant species in our pitfalls (57%), *Tetramorium caespitum* was dominating resources in strictly urban areas, consistent with previous studies (Pećarević et al. 2010; Savage et al. 2015; Wagner et al. 2017).

Implications for conservation In conclusion, our results demonstrate that small green spaces within highly urbanized areas have the capacity to support diverse ant fauna, including species of conservation interest. Although urbanization has demonstrated negative impact on insect diversity (Fattorini 2011a), previous studies also found that urban green spaces can support populations of protected, endemic, and rare species (Fattorini and Galassi 2016; Angold et al. 2006; Theodorou et al. 2020). Urban biodiversity also has an important role in raising the awareness, and projects that achieve synergy between research and education, more common in urban ecosystems, can serve this role (Braschler et al. 2010; Dunn et al. 2006).

Habitat characteristics of urban green spaces, especially the size of the wooded area and tree age, should be taken into consideration in the management planning of urban parks. The conservation of old trees in city centres, often because of their symbolic or aesthetic value, promotes habitat quality for rare insect species (Nieto and Alexander 2010; Seifert 2018), but also for other wood-dependent and arboreal taxa such as tree-nesting birds and bats (Poulsen 2002; Lučan et al. 2009; Dietz et al. 2018). For ant species of conservation interest inhabiting urban green spaces of Zagreb, conservation measures should include protection of old trees with partially hollow or rotten trunk, decrease of management practices which remove tree stumps and larger branches (Lindenmayer and Laurance 2017), as well as reduced mowing regime of open spaces (Seifert 2018; Diacon et al. 2011, Unterweger et al. 2017). As with many insect taxa, ant conservation is often limited by data deficiency (Seifert 2018). Even for known key-stone species with recognized decline very little is known about their natural history (Petráková et al. 2017; Seifert 2018). Further studies that would investigate species-specific responses to habitat changes for urban species of conservation interest (Fattorini 2011b) are important for advancing concrete, science-informed insect conservation planning.

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