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Short Notes

Urbanization and plant pathogen infection interact to affect the outcome of ecological interactions in an experimental multitrophic system

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Abstract

Urbanization can change interactions in insect communities, and the few studies of tritrophic interactions in urban settings focus on interactions between plants, herbivorous insects and their mutualists and natural enemies. Plant pathogen infection is also widespread and common, and infection may also alter such interactions, but we have no understanding of whether the ecological consequences of pathogen infection vary with urbanization. Using replicated aphid colonies on experimental plants, we investigated how infection by the plant pathogen *Botrytis cinerea* influences interactions between plants, aphids and the aphid natural enemies and ant mutualists in highly urbanized, suburban and rural study sites. Aphid and natural enemy abundance were highest in the suburban site, while mutualist ants were most abundant in the urban site, reversing the usual positive density-dependent relationship between natural enemies and aphids. The effect of pathogen infection varied with trait and site, mediated by natural enemy preference for hosts or prey on uninfected plants. The effect of infection on aphid abundance was only seen in the suburban site, where natural enemies were most abundant on uninfected plants and aphid numbers were greatest on infected plants. In the urban site, there was no effect of infection, while in the rural site, aphid numbers were lower on infected plants. Uninfected plants were smaller than infected plants and differed between locations. This study suggests that the effects of urbanization on ecological interactions may become more complex and difficult to predict as we study ecological assemblages and communities at greater levels of structural complexity.

Key words: gray mold, natural enemy, plant-mediated indirect effects, plant pathogen, trophic cascade

Introduction

With over half of the world's people now living in towns and cities, urban areas have rapidly expanded to accommodate growing populations (Goddard, Dougill, and Benton 2010). Urban growth is associated with habitat loss and degradation, increased habitat heterogeneity, fragmentation, disturbance, the emergence of novel habitats and introduced species, and an increase in impervious surfaces (Goddard, Dougill, and Benton 2010; Kowarik 2011). These factors in turn greatly affect the abundance, distribution and patterns of ecological interactions between organisms, such as insects (Rocha and Fellowes 2018, 2020; Rocha et al. 2018). Insects provide excellent model systems for examining how urbanization affects ecological interactions between predators and prey, hosts and parasitoids, plants and herbivores, hosts and pathogens and between mutualistic species. Insects also lend themselves to more powerful experimental approaches to explore the effects of urbanization on ecological interactions.

The key drivers that alter insect community structures vary across urban areas. In heavily urbanized temperate areas, host plant scarcity and fragmentation drive a reduction in overall insect abundance, with specialist predators and parasitoids particularly affected (Peralta, Fenoglio, and Salvo 2011; Bennett and Gratton 2012; Turrini, Sanders, and Knop 2016; Rocha and Fellowes 2018, 2020). The diversity of host plants tends to reach a peak in suburban settings with high proportions of private domestic gardens, where ornamental species are widely planted (Thompson et al. 2003; McKinney 2008; Čepelová and Münzbergová 2012). As a result, suburban areas can have a remarkable diversity of insect herbivores (Owen and Owen 1975; Raupp, Shrewsbury, and Herms 2010), in turn driving increased numbers of natural enemies. As we reach peri-urban areas, a wide range of suitable habitats and less fragmented areas predominate, with increasing numbers of species such as butterflies (Tzortzakaki et al. 2019), before we move into heavily altered agricultural land, where insect diversity can decline.

It is not simply habitat availability that affects the structure of insect communities. Urbanization can have more subtle effects, modulating changes in insect (particularly herbivore) abundance through changes in host plant quality (Raupp, Shrewsbury, and Herms 2010). For example, urban heat island effects, the introduction of exotic plants, increased soil nitrification, pollution and plant drought stress (Raupp, Shrewsbury, and Herms 2010; Long, D'Amico, and Frank 2019) can change plant quality and therefore result in both positive and negative effects on insect herbivores (Herms 2002; Huberty and Denno 2004; Müller et al. 2005). Changes in herbivore traits can in turn affect their natural enemies (Vollhardt et al. 2019; Zhu et al. 2020).

In many terrestrial ecosystems, plant pathogen infection can be an important direct (by reducing plant diversity and abundance) and indirect (by changing host plant quality and therefore influencing herbivore host choice and fitness) driver of insect community structure (Srisakrapikoop, Pirie, and Fellowes 2020). For example, the fungal pathogen *Hymenoscyphus fraxineus* causes devastating ash dieback on European ash (*Fraxinus excelsior*) and this effect cascades to associated species (Hultberg et al. 2020). Furthermore, plant pathogen presence and infection are also likely to be affected by urbanization given the effects of air pollution on plant susceptibility and pathogen population dynamics (Heagle 1973; Manning 1975; Bearchell et al. 2005). What is unstudied is whether urbanization alters the effects of plant pathogen infection on insect community structure.

Botrytis species are among the most important plant pathogens, and they have a worldwide distribution (Williamson et al. 2007). *Botrytis cinerea* is a widespread necrotrophic pathogen causing soft rot in host plants and infects more than 200 species of host plants, causing pre- and post-harvest damage (plant disease and rotting) to many commercial plants, including ornamentals, fruits and vegetables, as well as stored and transported agricultural products (Elad et al. 2004; Williamson et al. 2007). It is suggested that *B. cinerea* growth rates are reduced by some air pollutants, including SO_2 (Couey and Uota 1961; Xue and Yi 2018) and ozone (Violini 1995), and so infection may be less frequent in urban areas.

Both urbanization and plant pathogens have been shown to influence ecological interactions at higher trophic levels, and the pathways that determine this influence are likely to be different. In aphid systems, urbanization (but not always, given increased diversity recorded in suburban domestic gardens; e.g. Raupp, Shrewsbury, and Herms 2010; Rocha et al. 2018) is associated with a reduction in the diversity and abundance of natural enemies, and an increase in mutualists (Rocha and Fellowes 2018, 2020), while infection by *B. cinerea* has variable effects on aphid herbivores (Srisakrapikoop, Pirie, and Fellowes 2021), and aphid natural enemies such as parasitoids prefer uninfected plants (Desurmont, Xu, and Turlings 2016; Lin et al. 2016; Ngah et al. 2018). In turn, *B. cinerea* infection also changes plant growth (Ait Barka et al. 2002; Ngah et al. 2018), while changes in herbivore numbers associated with urbanization are also likely to affect plant biomass (Turrini, Sanders, and Knop 2016). To date, how urbanization affects ecological interactions in systems that include plant pathogens has not been studied. We hypothesize that the presence of plant pathogens may alter the observed effects of urbanization on interactions between aphids, their host plants and their natural enemies and mutualists. To address this gap in knowledge, we performed a field experiment using a model plant-aphid-plant pathogen system to investigate the respective and possibly interacting effects of urbanization and plant pathogen infection on interactions between an aphid, its host plant, natural enemies and mutualists.

Methods

Study sites

The three study sites were located on grounds belonging to the University of Reading, Berkshire, UK. The London Road campus (UoRL), Whiteknights campus (UoRW) and Centre for Dairy Research (CEDAR), representing urban, suburban and rural habitats, respectively. The urban site is located in Reading town center (51°26'58.0″N, 0°57'43.6″W) and is surrounded by impervious surfaces made up of buildings and roads. The planted area is predominantly grass lawn, with ornamental shrubs and some large deciduous trees. The UoRW (51°26'13.1″N, 0°56'31.6″W) site is in mature suburbs and is surrounded by a mix of impervious surfaces and domestic gardens and mixed-use green space. The campus landscape is composed of meadows, urban woodland and diverse ornamental planting. CEDAR (51°24'46.3″N, 0°54'37.6″W) is largely dairy farmland situated south of the suburbs and is largely surrounded by agricultural pastureland and hedgerows.

Study system

A single Black bean aphid, *Aphis fabae*, was collected in July 2018 from the University of Reading Whiteknights campus. A monoculture was reared and maintained on Broad bean, *Vicia faba* (Fabaceae, cv. Sutton Dwarf) in a laboratory with ambient temperature and light. A monoclonal culture was used to avoid the variation in predator–prey interactions seen between aphid clones (Hazell and Fellowes 2009).

Botrytis cinerea pepper isolate (Denby, Kumar, and Kliebenstein 2004) was cultured on apricot halves in grape juice (Del Monte®) and incubated at 20°C with 12 hours of UV light and 12 hours of dark cycle to encourage the fungus to produce spores.

Vicia faba (Fabaceae, cv. Sutton Dwarf) plants were grown individually in 1-l pots with pot/bedding peat compost (Clover®) in a controlled environment (CE) room with 16:8 L:D light cycle at 60% relative humidity. When the plants had four true leaves, they were divided into two groups. One group of 150 plants was left uninfected (treated only with water) and the other 150 were inoculated with 0.1 ml of 10^5 conidia/ml of *B. cinerea* suspension on adaxial surface with a paint brush to produce the infected

Table 1: Species of natural enemies found at each study site

Site	Family	Species
Rural-CEDAR	Diptera: Syrphidae	*Syrphus ribesii* (Linnaeus) *Episyrphus balteatus* (De Geer)
	Coleoptera: Coccinellidae	*Harmonia axyridis* (Pallas) *Coccinella septempunctata* (Linnaeus) *Propylea quatuordecimpunctata* (Linnaeus)
	Neuroptera: Chrysopidae	*Chrysoperla carnea* (Stephens)
Suburban-UoRW	Diptera: Syrphidae	*Syrphus ribesii* (Linnaeus) *Episyrphus balteatus* (De Geer) *Epistrophe eligans* (Harris)
	Coleoptera: Coccinellidae	*Harmonia axyridis* (Pallas) *Coccinella septempunctata* (Linnaeus) *Propylea quatuordecimpunctata* (Linnaeus)
	Coleoptera: Staphylinidae	*Tachyporus* sp.
	Hemiptera: Anthocoridae	*Anthocoris nemorum* (Linnaeus)
	Hymenoptera: Aphidiinae	*Praon volucre* (Haliday) *Lysiphlebus fabarum* (Marshall)
	Charipinae	*Alloxysta* sp.
Urban-UoRL	Diptera: Syrphidae	*Syrphus ribesii* (Linnaeus) *Episyrphus balteatus* (De Geer)
	Coleoptera: Coccinellidae	*Harmonia axyridis* (Pallas) *Propylea quatuordecimpunctata* (Linnaeus)
	Hymenoptera: Aphidiinae	*Praon volucre* (Haliday)

CEDAR, University of Reading Centre for Dairy Research; UoRL, Reading London Road campus; UoRW, University of Reading Whiteknights campus.

group. Each plant was kept in an individually sealed polythene bag at 20°C for 48 hours to encourage spore germination. Three adult aphids were placed on every uninfected and infected plants and were then kept in the CE room for 7 days before moving them to the study sites.

The study was conducted in May 2019. One hundred plants (50 infected and 50 uninfected) were randomly selected for each site, and then each plant was randomly placed within a grid one meter apart at the site. Plants in the CEDAR and UoRL sites were placed in the field on the same day, and for logistical reasons, plants in UoRW were placed in the field the next day. Each plant was enclosed by a cylinder (50 cm in height) made of chicken wire (25-mm mesh) to prevent access by vertebrate herbivores. The aphids and plants were left to acclimatize for 3 days before data collection began. Data from each plant in each site were collected five times every 4 days, rotating from CEDAR, UoRL and UoRW, with the fourth day taken as a break. Each set of three consecutive days before a break day are termed a session. The number of aphids, ants, predators and mummified aphids was recorded on each day of counting. Predators were identified using appropriate keys (Rotheray 1989, 1993; Roy and Brown 2018). Mummified aphids were collected and kept separately in an Eppendorf tube. Emerged parasitoids were sorted into morphospecies and sent to the Natural History Museum London for formal identification.

The chlorophyll content index (a measure of plant quality: Curran, Dungan, and Gholz 1990; Filella et al. 1995) of each plant was measured once using a chlorophyll content meter (Hansatech Instruments, Model CL-01) in the field at the end of the experiment before the above ground parts of the plants were harvested. All the plants were removed on the same day from all sites a month after they were placed *in situ*. They were put in a hot air oven at 70°C until they reached constant mass. Each plant was weighed to get the above ground plant dry mass.

Data analysis

All statistical analyses were performed using R 4.0.3 (R Core Team 2021). Some plants and some aphid colonies died before the end of data collection; these replicates were excluded from the data analyses, yielding 91 plants at CEDAR (46 uninfected and 45 infected plants), 87 plants at UoRL (45 uninfected and 42 infected plants) and 90 plants at UoRW (44 uninfected and 46 infected plants).

Aphid abundance

Aphid abundance was analyzed using a generalized linear mixed model (GLMM) with negative-binomial distribution family (nbinom2) with a log link, using the *glmmTMB* package (Brooks et al. 2017). Infection status, site, number of ants and natural enemies were used as fixed effects and session was treated as a random effect.

Ant and natural enemy abundance

To deal with excessive zeros in the ant and natural enemy models, and as our experimental design included data recording session as a nested repeated measure, a zero-inflated generalized linear mixed model (ZIGLMM) in the *glmmTMB* package (Brooks et al. 2017) was adopted with a negative binomial distribution family (nbinom2) for the count part, and with a binomial distribution with a logit link for the binary part. Session was also used as a random effect for the count part, while session and site were used for the binary part. Adding the binary part did enhance model fit by reducing the AIC value. Zeros can be accounted for in both the count part (true zeros), and binary part to explain the probability of false zeros that may occur from design, survey and observer errors (Zuur, Ieno, and Smith 2009).

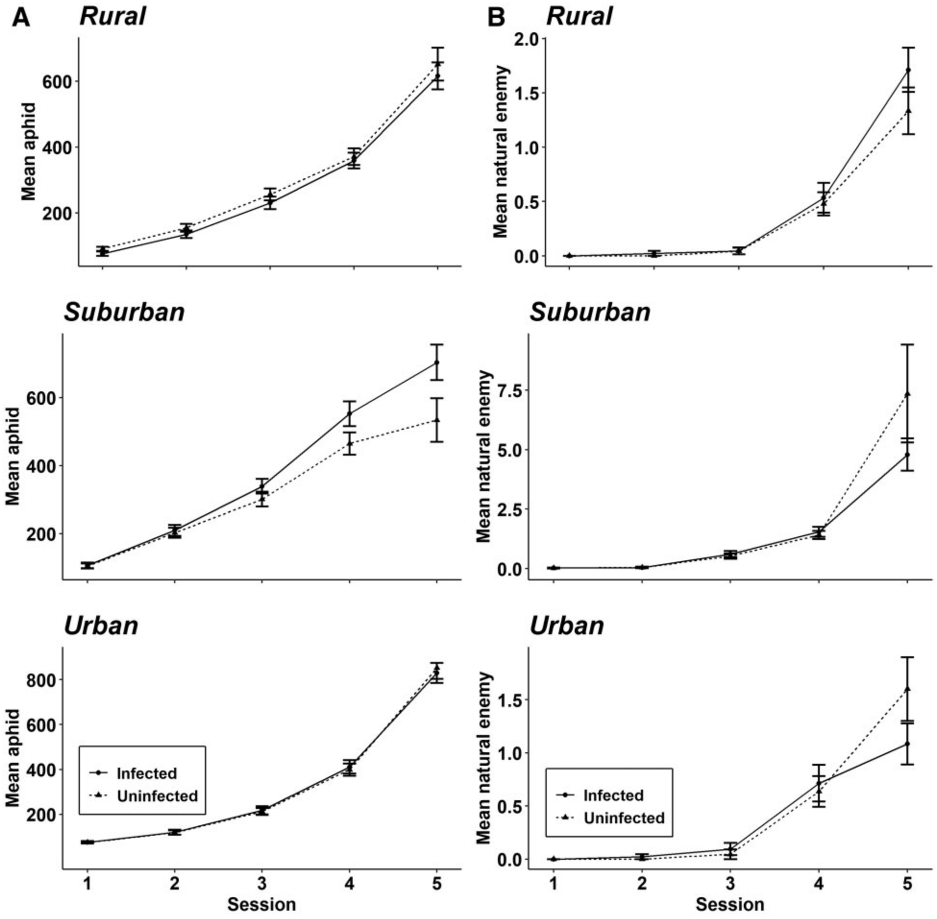

Figure 1: Mean ± SE (a) aphid and (b) natural enemy recorded on *B. cinerea* infected and uninfected plants in three study sites over five sampling sessions.

Chlorophyll content index and above ground plant dry mass

Plant chlorophyll content index was compared between uninfected and infected groups using independent-sample *t*-tests. Plant dry mass was modeled using a generalized linear model (GLM) with a Gamma distribution with the identity link with infection status, site and the cumulative numbers of natural enemy and aphid as fixed effects in a global model.

The aphid and plant above ground dry weight models were generated by using the dredge function in the *MuMIn* package (Barton 2019), from the global models. Model selection was then based on Akaike's Information Criteria (AIC) by comparing all candidate models (Burnham and Anderson 2003). This was not done for ant and natural enemy models due to the complex structure of ZIGLMM containing two parts to model excessive zeros. Instead, these models were built by adding all independent variables, then dropping the non-significant terms and adding the ecologically meaningful interactions to see if the interaction terms did improve AIC values.

For all models with multiple candidate models, models with a delta AIC within 2 units ($\Delta_i < 2$) from the lowest AIC (best model) were considered as candidate models. Akaike weights were also calculated, which can suggest the overall importance of a model. A higher weighting signifies a greater probability the model is the best model (Anderson, Burnham, and Thompson 2000).

In all of the analyses, *multcomp* (Hothorn, Bretz, and Westfall 2008) or *emmeans* (Lenth 2021) packages with *post hoc* Tukey tests were used to determine the significant differences between means of dependent variables across study sites. Independent variables were checked for collinearity through checking variance inflation factors (VIFs). If VIF values were higher than 3, it indicated that there was collinearity between independent variables (Zuur et al. 2007). From our data, collinearity was not detected as VIF values ranged from 1.02 to 1.22.

Results

During the study, 398 586 aphids, 2039 ants and 861 insect natural enemies [746 predators (86.64%) and 115 parasitoids (13.36%)] were recorded. All ants attending aphids were black garden ants (*Lasius niger*). Hoverfly larvae (Diptera: Syrphidae) were the most abundant predators (75.91%), followed by parasitoids (13.45%; Hymenoptera), 7-spot ladybirds (4.21%; *Coccinella septempunctata*), harlequin ladybirds (3.74%; *Harmonia axyridis*), common flower bugs (1.75%; *Anthocoris nemorum*), 14-spot ladybirds (0.58%; *Propylea quattuordecimpunctata*), lacewings (0.23%; Family: Chrysopidae) and rove beetles (0.12%; Coleoptera: Staphylinidae). In terms of natural enemy species richness, UoRW had the most diversity, followed by CEDAR and UoRL, respectively (Table 1).

Aphid abundance

Although there were two candidate models, the first model showed the lowest AIC with substantial Akaike weight support (Supplementary Table S1). The mean aphid number on infected

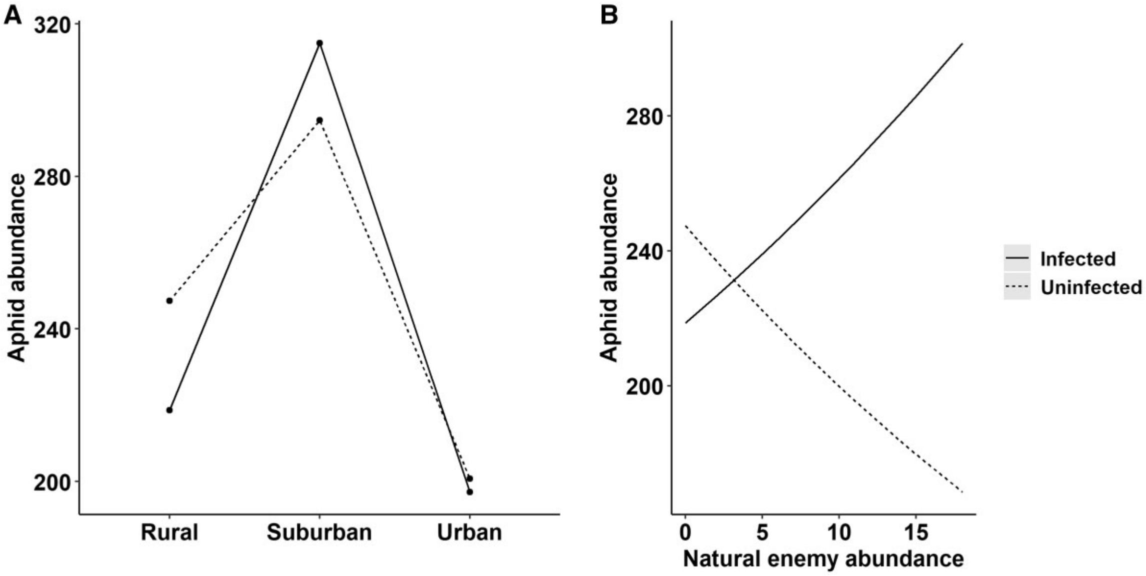

Figure 2: The interaction plot between (a) site and infection status on aphid abundance and (b) natural enemy abundance and infection status on aphid abundance on *B. cinerea* infected and uninfected plants.

Table 2: Mean ant numbers recorded on each plant for each of the three study sites

Dependent variable	Site	Mean ± SE
Ants	Rural-CEDAR	0.011 ± 0.005^a
	Suburban-UORW	1.135 ± 0.118^c
	Urban-UORL	3.705 ± 0.219^b

Superscript alphabets indicated significant differences between groups calculated from *post hoc* Tukey tests.

and uninfected plants in three different sites over five sampling sessions is shown (Fig. 1a). There was a positive relationship between aphid abundance and ant numbers. The interaction between site and infection on aphid abundance is also significant (Fig. 2a), suggesting that the effect of infection depends on study site. The significant interaction term between natural enemies and *B. cinerea* infection on aphid abundance (Fig. 2b) suggests that the positive density-dependent effects of aphid numbers on natural enemy abundance is reversed on infected plants.

Ant abundance

At the rural site, ants were found tending aphids on 3 out of 91 plants (3.30%), at the suburban site on 66 out of 90 plants (73.33%), and at the urban site on 82 out of 87 plants (94.25%). The best model included the number of aphids, site, number of natural enemies, interaction between site and number of natural enemies, and interaction between site and number of aphids as independent variables (Supplementary Table S2). Aphid number was positively associated with ant numbers, while the number of ants was significantly different across the study sites, ant abundance was highest at the urban site (UoRL) followed by suburban (UoRW) and rural (CEDAR) (Table 2).

Natural enemy abundance

Site, ant number and the interaction between aphid and site were included in the best model, in which ant abundance had a negative effect on natural enemy numbers (Supplementary Table S3). The mean natural enemy number on infected and uninfected plants in three different sites over five sampling sessions is shown (Fig. 1b). The effect of aphids on natural enemy abundance also depended on location (Fig. 3); positive associations between natural enemy and aphid abundance were seen in the rural and suburban sites, while in the urban area we found a negative relationship, most likely a result of the high abundance of mutualistic ants.

Chlorophyll content index and above ground plant dry mass

There was no significant difference found in chlorophyll content index between uninfected (31.5 ± 0.57) and infected (31.2 ± 0.53) plants ($t_{257} = 0.34$, $P = 0.74$). However, above ground plant dry mass did vary across study sites. The best candidate model for above ground plant dry mass included aphid number, infection status, site, interaction between aphid number and infection status and interaction between site and infection status (Supplementary Table S4). The interaction between aphid abundance and infection suggests that at low aphid abundance infection caused indirect positive effects on plants, but once the aphid abundance was high, this effect was lost (Fig. 4). The dry mass of plants with different infection status in three different sites is shown in Fig. 5.

Discussion

The abundance and diversity of insects are both affected by urbanization, but the majority of studies are observational studies of single (or limited numbers of) species. If we are to understand how urbanization affects insect ecology, then experimental studies of interacting species provide a powerful approach, but there are very few such studies to date. Here, we use replicated colonies of aphids on experimental plants that are either infected or uninfected by a ubiquitous plant pathogen, to examine how urbanization affects the recruitment of natural enemies and mutualists, which in turn will feed back and affect aphid abundance and hence plant traits.

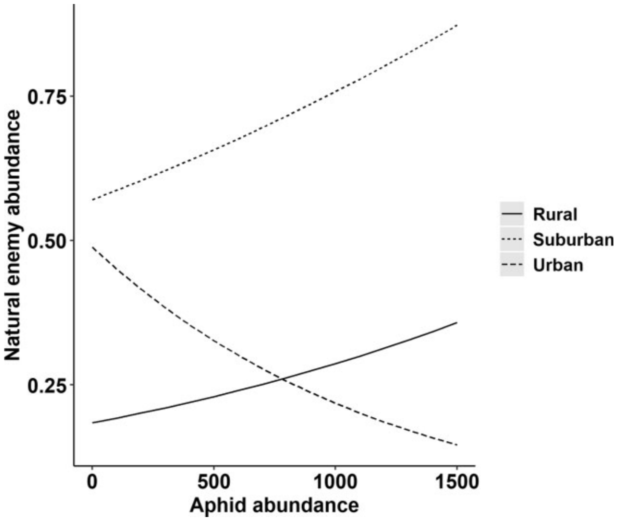

Figure 3: Plot of the interaction between aphid abundance and site on natural enemy abundance.

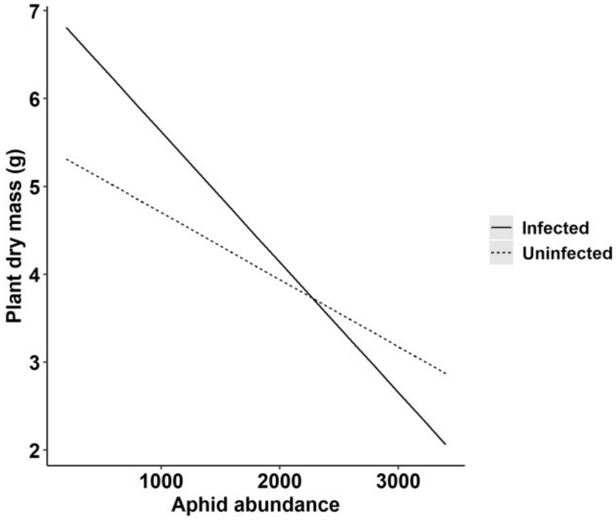

Figure 4: Plot of the interaction between aphid abundance and *B. cinerea* infection status on above-ground plant dry mass.

We found that natural enemy abundance varied across study sites and depended on aphid abundance. The differences in size between infected and uninfected plants was greatest in the suburban site, reflecting differences in aphid numbers. The urban site had the highest number of mutualist ants, and this appears to result in top-down regulation being limited. There was no effect of plant infection on aphid numbers in the urban site. Natural enemy abundance was highest at the suburban site, while at the rural site with the low abundance of natural enemies and the absence of ant mutualists resulted in aphid abundance being similar on both infected and uninfected plants.

Aphis fabae abundance was affected by symptomatic infection of *B. cinerea*, but the effects varied across study sites, with aphids being more abundant on uninfected plants in the rural site, less abundant on uninfected plants in the suburban site, but no difference in the urban site (Fig. 2a). It should be noted that while overall more aphids were found on infected plants in the suburban site, this seems to result from greater initial population growth rates in that site, rather than the aphid population size on the final census, which was highest in the urban site (Fig. 1a). Part this is likely to be explained by the significantly higher number of natural enemies in the suburban site, which showed a preference for attacking aphids on uninfected plants (Ngah et al. 2018). This hypothesis is supported by the experimental data, as aphid populations on uninfected plants in the suburban site were starting to fall due to predation, unlike the other two sites, with fewer natural enemies (Fig. 1a, b), and the relationship between natural enemy and aphid abundance differed between infected and uninfected host plants (Fig. 2b). Both results suggest that natural enemy foraging behavior is affected by host plant infection status.

Some ant and aphid species form mutualistic relationships, both of which receive reciprocal benefits (Stadler, Dixon, and Kindlmann 2002; Styrsky and Eubanks 2007; Nielsen, Agrawal, and Hajek 2010; Novgorodova and Kryukov 2017; Senft, Weisser, and Zytynska 2017). We found a positive relationship between ant numbers and aphid density, as reported in previous studies (Kaplan and Eubanks 2005; Yoo, Kizner, and Holway 2013). Ant abundance differed between sites, with the highest abundance present in urban followed by the suburban and then rural sites, and such patterns have been previously reported (Rocha and Fellowes 2018, 2020).

At the same time, mutualistic ants reduce rates of insect natural enemy attack experienced by aphid colonies, and these ants also affect other insects sharing the same host plant, such as unattended aphids, pollinators, and other herbivorous insects (Kaplan and Eubanks 2005; Mooney and Agrawal 2008; Oliver et al. 2008; Yoo, Kizner, and Holway 2013; Assunção, Torezan-Silingardi, and Del-Claro 2014; Adachi and Yano 2017). In this study, most insect natural enemies were predators rather than parasitoid wasps and the number of natural enemies was negatively associated with increased numbers of ants. Hoverfly larvae were the most abundant of the aphids' insect natural enemies. The presence of ants reduces the survival rate of hoverfly larvae and alters adult hoverfly oviposition behavior (Amiri-Jami, Sadeghi-Namaghi, and Gilbert 2017). This study reinforces the evidence that urbanization can affect ecological patterns by modifying the likelihood of finding mutualistic interactions.

Site as a proxy for urbanization had a strong effect on natural enemy interactions with other insects. Insect predators and parasitoids are more abundant in less fragmented habitats with more complex vegetation, and nectar and pollen resources, which are important food sources for some adult insects (Root 1973). This explains why natural enemy abundance was greatest at the suburban site which had greater plant diversity than the urban site (surrounded by impervious surfaces) and the rural site (surrounded by grass pasture). Previous studies also found an increase in natural enemy abundance with increasing vegetation complexity in urban areas (Langellotto and Denno 2004; Thomson and Hoffmann 2009; Martin et al. 2015; Rocha et al. 2018). Taken together, our study demonstrates that site affected the recruitment of natural enemies (Fig. 3). In suburban and rural areas, natural enemy abundance increased with aphid abundance, but with different magnitudes. In contrast, we found the opposite pattern in the urban area, where high ant abundance limits an already lower population of natural enemies (Rocha and Fellowes 2018, 2020).

Symptomatic infection also affected host plant traits. Increased herbivore (aphid) numbers were negatively associated with plant dry mass, and aphid numbers on infected plants were significantly lower than those feeding on uninfected

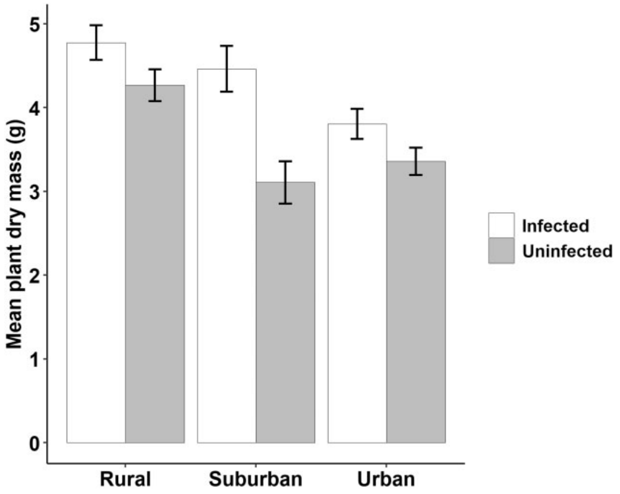

Figure 5: Mean ± SE dry mass of *B. cinerea* infected and uninfected plants at the three study sites.

plants. Infection by *B. cinerea* had a (albeit likely short term) positive indirect effect on the host plant by inhibiting aphid damage (Fig. 4). Once aphid population size grows beyond a threshold, infected plants are more damaged by herbivory. It seems that plant pathogen infection slows early aphid population growth (as shown in term of plant dry mass) and influences natural enemy foraging behavior.

It is important to note a caveat with this study. For sound logistical reasons (access, time, security of experimental plants), this study was completed at three sites, clearly differentiated by location (heavily urbanized, suburban, rural). Following Davies and Gray (2015), we are careful to acknowledge this issue and defend our approach as it provides insight into how the possible (and ecologically reasonable) effects of plant pathogen infection on tritrophic and mutualistic interactions may vary with urbanization. The great value in this study is in its novelty, and the understanding that emerges from the work, which we hope will encourage further consideration of this topic.

Conclusion

This is the first study that investigates the effects of plant pathogen infection and urbanization simultaneously, introducing further complexity into an experimental approach to understanding the effects of urbanization on a complex web of interactions. Our study showed that both factors have roles in altering insect community structure. While urbanization emerged as a dominant factor determining changes in ecological dynamics, food webs are complex, and it is only by examining key interactions that we will be able to understand how and why urbanization alters the structure of ecological communities.

Supplementary data

Supplementary data are available at *JUECOL* online.

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Conflict of interest statement. None declared.

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