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Urbanization affects the trophic structure of arboreal arthropod communities

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Abstract Urbanization is one of the most significant causes of habitat fragmentation on the planet, resulting in substantial losses of biodiversity and disruptions to ecological processes. We examined the effects of urbanization on the diversity and abundance of arboreal invertebrates in a dominant tree species (*Angophora costata*) in a highly urbanized landscape in Sydney, Australia, identifying the potential ecological consequences of shifts in diversity. We hypothesized that trophic structure would be influenced by landscape context with a greater richness and abundance of invertebrates in small remnants and edges. Canopy arthropods were sampled via beating from trees in 15 sites in three landscape contexts; five large patches of continuous vegetation, five edges of large patches and five small urban remnants. Trees in large patches supported fewer individuals compared to trees in small urban remnants and edge sites. The composition of assemblages and overall trophic structure also differed between edges and large patches, with a greater abundance of grazing insects in edges. No differences were detected between small urban remnants and edges, suggesting that observed differences might be attributed to an edge effect as opposed to an area effect *per se*. These changes in trophic structure, revealing a greater abundance of grazing herbivores and a reduced abundance of predators and parasitoids in edge sites, are consistent with work describing elevated levels of herbivory in edges of remnant vegetation. Future management of remnant urban vegetation and associated biodiversity

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requires not only an understanding of how trophic status influences the extent of responses by arboreal invertebrate communities, but also how these will affect ecosystem functioning.

Keywords Arboreal invertebrates · Urbanization · Trophic responses · Remnant vegetation

Introduction

Over half the world's population now live in urban areas, placing extensive pressures on remaining natural landscapes in cities (United Nations Population Fund 2007). Encroachment of human activities into our natural areas has led to significant fragmentation and degradation of native vegetation (Zipperer et al. 2000). Remaining patches of vegetation exist as urban remnants and are highly isolated, with little connectivity and are subject to increasing anthropogenic pressure from the surrounding urban matrix. Proximity to residential areas has facilitated the invasion of highly competitive species (Price et al. 1997; Bolger et al. 2000) and led to increased nutrient influx through urban run-off (Benson and Howell 1990; Leishman 2000; Zipperer et al 2000; King and Buckney 2002). Despite these influences, urban remnants are not only important for human well being and recreation (Magura et al. 2008a) they are capable of supporting a diverse flora and fauna and in some cases represent the last occurrences of communities of high conservation significance (Panzer 2003) as well as providing numerous ecosystem services (Colding 2007).

The effects of urbanized induced fragmentation on individual species however, have extended far beyond initial habitat loss (Liley and Clarke 2003). Although assessments of the ecological consequences of urbanization have historically been survey-based, with a strong bias towards vertebrates and dominant plants, there has been a recent shift in focus to determine the responses of terrestrial invertebrates (Nuckols and Connor 1995; Niemelä et al. 2002; Clarke et al. 2007; Scanlon and Petit 2008) as a means to understanding how urbanization affects ecosystem function. Invertebrate responses to urbanization have been found to be highly variable across taxa and are often linked to disruptions of ecological processes (Hatcher and Ayres 1997; McIntyre and Hostetler 2001; Rickman and Connor 2003; Christie and Hochuli 2009). For example, ecosystem functioning may be significantly affected by changes in arthropod communities as shifts occur in community composition (Bolger et al. 2000; Niemelä et al. 2000; McIntyre et al. 2001; Hochuli et al. 2004; Ryall and Fahrig 2005). A shift in community dynamics may be reflected by changes in ecosystem functioning as a result of trophic cascades, whereby significant changes in higher trophic groups influences assemblages at lower trophic levels in a "top–down" effect (Ricketts and Imhoff 2003). Alternatively, significant changes in lower trophic groups may result in shift in community dynamics of upper levels in a "bottom–up" effect. Understanding responses and interactions of trophic groups is an important step in predicting how disturbance events and increased degradation affects ecosystem functioning.

The short generation times and rapid response of invertebrates to changing environmental conditions makes them potential indicators of ecosystem health, however most research to date has focused on the response of ground-dwelling arthropods to urbanization (Pacheco and Vasconcelos 2007; Magura et al. 2008b). Canopy invertebrates have been largely overlooked despite their importance as indicators of forest health in other systems (Landsberg and Wylie 1983; Pitkänen et al. 2008). Arboreal invertebrates have been shown to have a close association with edges (Major et al. 2003) often evident by the high levels of leaf damage occurring in trees in edge habitats (Port and Thompson 1980; Lowman and Heatwole 1992;

Christie and Hochuli 2005). Outbreaks of defoliating insects are often seen as an indicator of a pre-existing stress and that disturbance events may predispose forests to outbreaks (Landsberg and Wylie 1983; Joern and Mole 2005). At coarser scales the diversity and abundance of canopy arthropods decreases at forest edges and is driven by increased disturbance and fragmentation (Ozanne et al. 1997). However, the effects of fragmentation on arboreal invertebrates and ecosystem functioning in what may be perceived as high stress urban environments is largely unknown (Tovar-Sánchez et al. 2003).

This research addresses this critical gap in our knowledge by investigating how urban fragmentation affects the richness and abundance of canopy arthropods of a dominant tree in urban forest remnants in Sydney, Australia's largest city. We examined the canopy fauna of *Angophora costata* (Gaertner) Britten (Boland et al 2006), a dominant tree in this system that suffers significantly higher levels of leaf damage in urban remnants (Christie and Hochuli 2005), comparing the fauna of small urban remnants and edges of large patches to the interior of large patches of vegetation. We tested two central hypotheses; that trees in small urban remnants and on the edges of large patches of vegetation would support a greater invertebrate assemblage (richness and abundance) compared to trees in larger, continuous patches of vegetation and that trees in the edges of large patches and in small patches would display a shift in trophic structure primarily through a greater richness and abundance of insect herbivores and a reduced richness and abundance of predators and parasitoids as a response to urbanization and increased disturbance.

Materials and methods

Study sites

The study was carried out in the remnant vegetation within and around the metropolitan area of Sydney, Australia. One of the areas most common remaining vegetation types exist on the soils of the Hawkesbury Sandstone which support the unique flora of Sandstone Gully Forest and Ridgetop Woodlands (Benson and Howell 1990). This vegetative assemblage persists as small urban reserves within the metropolitan area and is also well represented in the large national parks that border the city to the north south and west. Dominant canopy species of the community are *Angophora costata* (smooth-barked apple, family Myrtaceae) and *Corymbia gummifera* (red bloodwood). The understorey is comprised of a diverse flora from genera such as *Hakea, Acacia, Banksia*, and *Epacris*.

Fifteen study sites were selected from this vegetative assemblage (See Christie and Hochuli 2005). Five "small" remnants (<65 ha) were chosen from bushland reserves within the urban matrix. Five "interior" sites were located within large patches of continuous bushland in National Parks to the north and south of Sydney's central business district. Interior sites were all located more than 4 km from the woodland edge. A further five sites were "edge" sites and were located at the urban/woodland edge of large continuous patches of woodland. Edge sites were all located within 100 m of urban areas.

Tree selection and arboreal invertebrate collection

The study species selected was the canopy tree, *Angophora costata*. The genus *Angophora* is closely allied to *Corymbia* and *Eucalyptus* and superficially resembles trees from these genera (Boland et al. 2006). *A. costata* is common in open forests of Australia's east coast where it grows in association with *Eucalyptus* species. It is a large, spreading tree growing to a height of 25 m generally flowering in spring/summer (Costermans 1985). This species represented the dominant canopy tree in the study area although the invertebrate fauna of this species remains poorly known (Boland et al. 2006). In each of the fifteen study sites, canopy invertebrates were sampled from five mature trees of *A. costata* ranging in height from 10–18 m. Local council, access restrictions and the proximity of study sites to urban dwellings required the adoption of a novel sampling technique (tree climbing and branch beating) for invertebrate collection in this fragmented land system. This sampling methodology has more regularly been used in tropical forests and to our knowledge has not been adopted for research in urban areas. Given this, trees were selected on the basis that canopy foliage could be accessed with ropes and climbing equipment using the single rope technique (Perry 1978). Visually strong, healthy trees (minimum height 10 m) were selected where the canopy could be accessed using a climbing rope passed over at least two strong branches (in case of branch failure) following standard safety recommendations (Laman 1995). This was particularly important for this species which readily drops limbs. Safety lines were deployed when moving away from the main rope to access foliage.

Invertebrates were sampled at each site by beating canopy branches of five *A. costata* trees in Summer 2001. Four branches on each tree corresponding to the four compass points were chosen for sampling. Each branch was struck five times with a length of 2.5 cm diameter dowelling rod and dislodged invertebrates were collected in a 60 cm diameter beating tray. Active invertebrates were aspirated immediately into a collecting vial to prevent escape and debris was carefully sifted through to collect remaining arthropods. One tree sample consisted of the combined catch from four branches, giving a total of twenty branches from five trees per site. Aspirator vials were filled with 70% ethanol to kill specimens, and samples were transferred to sample vials containing tree, site and locality data. Sampling was only carried out on fine, still days to avoid collecting problems associated with wind and rain.

Arthropod classification

All arthropods were sorted to order, except for Hymenoptera that were further divided into ants and non-formicid Hymenoptera. Due to the high proportion of juveniles collected and the taxonomic difficulties associated with their identification, the majority of groups were only sorted to order. Arthropods were then grouped according to feeding guild under the following categories: ant, chewer, grazer, parasitoid, predator, omnivore, sucker, tourist, and unknown following Peeters (2002). In order to make feeding guild assignations some groups were further identified to Superfamily (Coleoptera) and Family level (Hemiptera, Hymenoptera (wasps only) and Diptera). Those groups whose members engaged a variety of feeding strategies were classed as omnivores. Due to the difficulties of assigning feeding guilds to hemipteran juveniles these specimens were not included in trophic level analyses. However, all juvenile spiders were assigned to the feeding guild “predator” as were neuropteran larvae. The omnivore, tourist, and unknown categories were combined for guild analyses due to the small number of arthropods collected for each of these groups.

Statistical analysis

One-way analysis of variance was used to test for differences in the abundance and ordinal richness of arboreal invertebrate fauna as well as differences in guild groupings. Prior to analysis we assessed assumptions of normality and homoscedasticity. As we were interested in changes at the treatment level (small edge, interior) and not at the tree level, sites were considered to be the sampling (experimental) unit. Therefore, tree data were pooled for each site, resulting in five replicates for each small, edge and interior treatments. Tukey HSD (honestly significant difference) pairwise comparison tests were used to determine the source of any differences observed.

To assess for compositional differences among treatment we used non-metric multi-dimensional scaling (nMDS) (1,000 restarts) using Bray Curtis similarities followed by an analysis of similarities (ANOSIM) (999 permutations). One-way ANOSIMs were used to test for an effect of treatment. Prior to the calculation of the similarity matrices data were 4th root transformed to allow for a more equal contribution of rare orders. Similarity Percentages (SIMPER) was used to determine the contribution of groups to observed differences (Clarke 1993), contributions were cut at 90%. All analyses investigating compositional differences were performed using Primer v5 (Clarke and Gorley 2001).

Analysis of covariance (ANCOVA) was used to test the hypothesis that there would be a shift in trophic structure as demonstrated through the number of individuals in the predator/parasitoid guilds relative to the herbivores among treatments.

Results

Arboreal invertebrate fauna of *A. costata*

A total of 1,718 arthropods from 16 orders were sampled, with four orders accounting for 81% of the specimens (Table 1). Araneae (spiders) was the dominant order comprising 42%

Table 1 Total abundance (adults and juveniles) of arboreal invertebrate orders (and feeding guild assignations) at each site treatment and results of ANOVA comparing abundances across sites. Numbers in parentheses represent the total number of sites each order occurred in

Order	Guild	Abundance	Small	Edge	Interior	F Ratio	*p*-value
Araneae	Predator	726	279 (5)	319 (5)	128 (5)	3.43	0.066
Hymenoptera-formicids	Ant	329	152 (5)	131 (5)	46 (5)	1.63	0.236
Hemiptera	Sucker	177	59 (5)	81 (5)	37 (5)	1.11	0.361
Coleoptera	Chewer	98	29 (5)	30 (5)	39 (5)	0.43	0.657
Hymenoptera- non ant	Parasitoid	65	33 (5)	22 (5)	10 (4)	1.52	0.257
Diptera	Predator	62	18 (4)	31 (4)	13 (4)	0.945	0.416
Collembola	Grazer	51	9 (5)	35 (5)	7 (2)	3.40	0.067
Blattodea	Omnivore	47	10 (4)	31 (5)	6 (2)	2.49	0.124
Acari	Omnivore	49	4 (3)	35 (5)	10 (4)	28.46	<0.005*
Lepidoptera	Chewer	41	20 (5)	13 (5)	8 (3)	3.57	0.061
Psocoptera	Grazer	36	18 (5)	16 (4)	2 (1)	1.70	0.223
Orthoptera	Chewer	15	9 (3)	5 (3)	1 (1)	0.97	0.107
Neuroptera	Predator	13	7 (3)	1 (1)	5 (2)	0.86	0.447
Mecoptera	Tourist	5	0 (0)	1 (1)	4 (2)	1.37	0.292
Mantodea	Predator	2	0 (0)	1 (1)	1 (1)	0.5	0.619
Thysanoptera	Omnivore	1	0 (0)	0 (0)	1 (1)	1.00	0.370
Trichoptera	Tourist	1	1 (1)	0 (0)	0 (0)	1.00	0.370

The df for all ANOVAs is (2, 12)

*indicates significance at $p=0.005$

of specimens followed by Hymenoptera—ants (23%), Hemiptera (10%), Coleoptera (6%), Hymenoptera—non ant (4%) and Diptera (4%). A high number of juveniles (47%) were collected, primarily from the Hemiptera (69% of total Hemiptera) and Araneae (82% of total Araneae). All orders were represented in each treatment (small, edge and interior) except those orders for which less than six individuals were collected (e.g. Mecoptera, Mantodea, Thysanoptera and Trichoptera).

The mean ordinal richness of arthropods did not differ between treatments ($F_{2,12}=1.67$, $p=0.230$) (Fig. 1a). However, the abundance of arboreal arthropods was significantly different between treatments (Fig. 1b) ($F_{2,12}=11.31$, $p=0.002$) with interior sites supporting fewer invertebrates than small and edge sites and edges supporting the greatest overall abundance of invertebrates. No differences were detected in the abundance within each order except for the Acari which were more abundant in edge sites ($F_{2,12}=28.46$, $p<0.001$) (Table 1).

Ordinal and trophic composition

The assemblages at interior sites were significantly different to those of small and edge sites (Global $R=0.207$, $p=0.008$) (Fig. 2). SIMPER analysis showed that the orders Psocoptera, Collembola and Blattodea contributed to more than 30% of the dissimilarity and were all less abundant in interior sites compared to both edge and small sites.

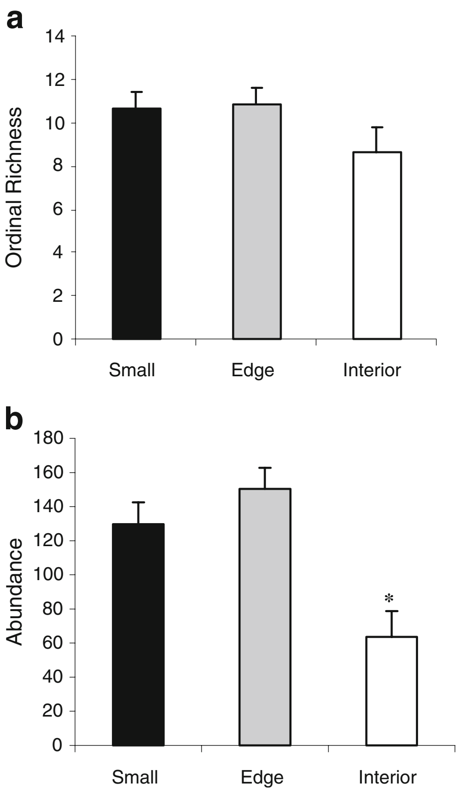

Fig. 1 **a** Mean ordinal richness of arboreal invertebrates at small, edge and interior sites; **b** Mean abundance of arboreal invertebrates at small edge and interior sites. *Error bars* represent the standard error of the mean ($n=5$); *denotes significantly different at $p=0.05$

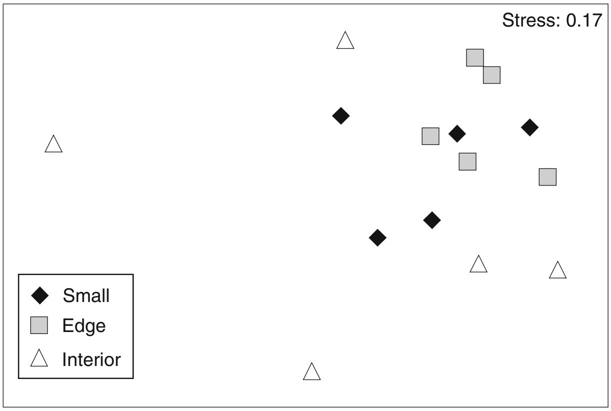

Fig. 2 Ordination (nMDS) plot of fourth root transformed data of arboreal invertebrate assemblages

The abundance of arthropods within each feeding guild did not differ between treatments. However, interior sites supported a different trophic assemblage to edge sites (Global $R=0.157$, $p=0.038$) (Fig. 3). SIMPER revealed that a greater abundance of grazers (Collembola and Psocoptera) in edge sites contributed to 31% of the observed differences. We found no difference in the abundance of phytophagous (combined chewers, suckers and grazers) invertebrates between the treatments, although interior sites generally had fewer individuals ($F_{2,12}=3.08$, $p=0.083$). There was a significant difference in the abundance of the combined predator and parasitoid guilds with interior sites having significantly fewer individuals than both small and edge sites (Fig. 4) ($F_{2,12}=4.16$, $p=0.042$).

The abundance of predator/parasitoids and the abundance of herbivores did not differ between treatments, there was a putative interaction between covariate and treatment ($F_{2,9}=3.76$, $p=0.065$) (Fig. 5, Table 2), suggesting that ratio of predator/parasites to herbivores may be affected by landscape context.

Fig. 3 Ordination (nMDS) plot of fourth root transformed data based on arboreal invertebrate guilds

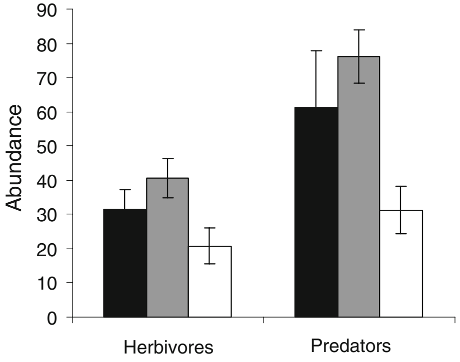

Fig. 4 Mean abundance of arboreal invertebrate herbivores (chewer, sucker, grazer guilds) and predators (predator and parasitoid guilds) in small (■); edge (▨) and interior (□) sites. *Error bars* represent the standard error of the mean

Discussion

Dominant trees in small urban remnants and edges of large remnants supported a significantly different arthropod community from trees in the interior of large remnants. Despite sharing a comparable number of invertebrate orders, interior trees also supported significantly fewer individuals than trees in other sites. Although these findings are consistent with previous work on ground-dwelling arthropods in this region showing a strong compositional response to urban fragmentation (Gibb and Hochuli 2002), they contrast responses by wasp assemblages examined at finer taxonomic resolutions (Christie and Hochuli 2009). This highlights the variable responses of functionally different taxa to urbanization. There was also a significant shift in trophic structure of arboreal invertebrates between treatments with edge sites supporting a more abundant herbivore fauna than interior sites. The ecological consequences of this response is supported by the high levels of leaf damage observed in this system in edge and small sites compared to interior sites (Christie and Hochuli 2005). Although the frequency of leaf damage in this study was consistent across treatments, trees in edges suffered approximately three times as much damage as trees in interior sites (Christie and Hochuli 2005). These findings indicate that these patterns may be the result of shifts in arboreal assemblages between sites.

Based on predictions of higher trophic groups being more sensitive to fragmentation, we would have expected fewer predators and parasitoids in edge and small sites. However, this was not the case and observed differences may be driven by the greater abundance of prey and host fauna (herbivorous insects) detected in small and edge sites. Furthermore, parasitic

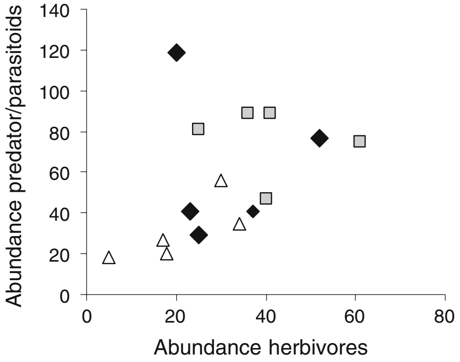

Fig. 5 Relationship between the total abundance of arboreal invertebrate herbivores versus predators/parasitoids (♦=small, □=edge, Δ=interior)

Table 2 Analysis of covariance of the effect of treatment on the herbivores by predator/parasitoid relationship

Source	SS	df	F ratio	*p*-value
Treatment	0.5755	2	1.850	0.212
Log herbivores	0.0004	1	0.003	0.958
Treatment*log herbivores	1.1684	2	3.757	0.065
Error	1.3997	9		

* Denotes interaction

wasps in this system have been found to be highly resilient to urbanization (Christie and Hochuli 2009) and it appears that fragmentation alone is not driving patterns observed between these groups and secondary impacts of urbanization may be responsible.

Several hypotheses may explain the greater abundance of arboreal invertebrates on trees from edges and small remnants. Firstly, trees in urban situations are often subject to increased nutrient levels, resulting in increased foliar nutrients (Port and Thompson 1980). Foliar nutrients, in particular nitrogen, can limit factor the performance and fecundity of invertebrate herbivores (White 1984; Landsberg 1990; Peeters 2002). Close proximity to urban areas has subjected remnant vegetation to storm-water and urban run-off, which has led to significant increases in soil nutrient levels within the Sydney basin (King and Buckney 2002).

Secondly, arboreal invertebrates in small and edge sites may be released from predation pressure owing to the decline in insectivorous birds in small and edge sites in our study area (Christie 2004). Insectivorous birds play a dominant role in the regulation of invertebrates with their loss from systems leading to increased abundance of invertebrates (Marquis and Whelan 1998; Lill and Marquis 2001). The responses found here are consistent with those from other fragmented land systems (Grey et al. 1997; Piper and Catterall 2003).

Abiotic effects, such as differences in microclimate between edges and interior sites may also account for the differences observed. It has been well shown that there are increased total light levels as well as increased daily temperatures at edges compared to forest interiors (Foggo et al. 2001). This may mean an increase in the amount of overall time in which minimum temperature ranges for activity of insects are met, leading to a greater fecundity and abundance of individuals. Determining such effect was however, beyond the scope of the current study.

Differences in plant community composition and structure have been shown to be key determinants of invertebrate community composition (Ozanne et al. 1997). We attempted to control for differences in plant community composition and structure during the site selection process by controlling for the presence of key understory and canopy species, canopy height, shrub and canopy cover. That said individual taxa are well known to respond differently to subtle differences in habitat (Dangerfield et al. 2003) and it is likely that differences may in part be driven by floristic and structural differences.

Finally, the composition and abundance of invertebrates were consistently similar at edge and small sites. Small urban remnants also have a high edge to area ratio and may be considered edge habitat as they generally lack the core habitat associated with larger patches of vegetation (Murcia 1995). Given this they are more vulnerable to the edge effects from the surrounding urban environment such as invasion by weed species and nutrient enrichment (Price et al. 1997). These results suggest that an edge rather than an area effect may have accounted for the differences observed as has been found previously (Major et al. 2003).

Little is currently known regarding the invertebrate canopy fauna of *A. costata*, which may simply naturally support a depauperate fauna, compared to other phylogenetically aligned tree species such *Eucalyptus*. The low abundance of invertebrates encountered on this species reflects the low levels of leaf herbivory (<8%) (Christie and Hochuli 2005). Future work on the ecological interactions in the area of canopy sampling close to urban and residential areas is essential, although the difficulties of applying conventional techniques for canopy surveys may limit the efficacy of sampling. Whilst beating is the most effective way of sampling phytophagous insects among arboreal fauna (Wade et al. 2006), tree climbing is a labor intensive technique and small sample sizes reflect the shortcomings of this technique. However, it is still the most appropriate approach given the perceived public safety risks precluding the use of alternative sampling techniques such as shot samples or insecticidal canopy fogging.

Conclusions

The arboreal fauna of remnant vegetation in Sydney has shown a strong compositional response to urbanization with a significant shift in functional groupings. Results indicate that urbanization affects the trophic structure of arboreal invertebrates in small and edge sites, diverging from the distinct interior fauna of arboreal invertebrates of *A. costata*. The consequence of higher invertebrate herbivore loads in small and edge habitat has implications for remnant health. High invertebrate abundances and increased leaf damage in dominant trees of small remnants as well as a loss of insectivorous bird species may have significant effects on the long-term persistence and health of small urban remnants. Under predictions of global population increases we can assume that these last vestiges of biodiversity within the urban matrix will continue to be impacted by anthropogenic actions. Understanding the ecology and functioning of remnant urban vegetation and the mechanisms driving shifts in community composition is central to their long-term sustainability and preservation, particularly as many areas of remnant vegetation are of high conservation significance (Benson and Howell 1990). Management of the ecological consequences of such shifts in both faunal and floral assemblages requires that we not only treat the symptoms (e.g. elevated levels of herbivory), but also the causes.

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