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Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages

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Abstract

We investigated the effects of fragmentation due to urbanisation on the species composition and functional roles of ants, beetles, spiders, flies and wasps. The study was conducted in 21 fragments of heath and woodland in south-eastern Australia classed as either 'small' ($\leqslant$ 4 km^2) or 'large' ($\geqslant$ 80 km^2). Arthropods were pitfall-trapped and identified to family or genus and morphospecies and microhabitat characteristics were recorded. Large fragments did not support more species per unit area than small fragments for most arthropods, although there were more species of ants per sampling unit in small than large woodland fragments, mainly due to a higher frequency of generalist species in smaller fragments. Large and small habitat fragments contained different assemblages of spiders, wasps and ants, indicating that predators and parasitoids are affected more strongly than other trophic groups. Arthropod assemblages within larger fragments where grids were furthest apart were less similar than those within smaller fragments where grids were closer together in woodland, but not in heath. The responses of arthropods to fragmentation suggest that, in addition to effects of reduced area and proximity to the urban matrix, changes in fire regimes and the degradation of habitats resulting from urbanisation, may have a role in altering arthropod assemblages, particularly affecting those species belonging to higher trophic levels. Management goals for urban remnants should identify mechanisms for controlling fire and anthropogenic disturbance such that they closely resemble the levels of these factors in larger fragments.

Keywords: Habitat fragmentation; Fragment size; Indicator species; Wasps; Spiders; Beetles; Flies; Ants; Functional groups

1. Introduction

Clearing of native vegetation and the subsequent fragmentation of remaining habitat are considered an increasing threat to biodiversity in Australia (Commonwealth of Australia, 1996; Major et al., 1999) and other parts of the world (Harrison and Bruna, 1999). The division of continuous habitat into smaller, more isolated areas results in a loss of species through a reduction in remnant area, an increase in remnant isolation and edge, and a decrease in habitat connectivity (Andren, 1994; Didham et al., 1996; Harrison and Bruna, 1999). The equilibrium theory of island biogeography (MacArthur and Wilson, 1963, 1967) has often been used to explain the loss of species as a function of the loss of area and habitats resulting from habitat fragmentation (e.g. Klein, 1989; Andren, 1994; Kruess and Tscharntke, 1994; Didham et al., 1996). Preston (1962) predicts that, because the mainland supports many rare species that would not occur on islands, species richness will be greater on the mainland than on islands, not only for the whole mainland, but also in equal-sized quadrats.

Remnant habitat areas are different from oceanic islands as they are surrounded by an anthropogenic habitat (Andren, 1994) and are therefore exposed to greater anthropogenic disturbance, altered fire regimes (NPWS, 1998) and increased numbers of invading species (Yahner, 1988), and the new habitat allows generalist species to extend their ranges disproportionately (Yahner, 1988). These processes, whilst often leading to an increase in species richness within fragments, will generally lead to a decrease in species richness on a regional level as the species composition of the remnants

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changes (Gaston, 1996). Habitat fragmentation has not only been found to affect insect abundance and diversity, but may potentially alter interactions between insects and other organisms (Didham et al., 1996). In this study we address the differences in arthropod species richness, composition and functional groups in large and small habitat fragments.

In order to reduce the apparent complexity of a community and compare communities with little species overlap, community ecologists often classify species into guilds or functional groups (Terbough and Robinson, 1986; Didham et al., 1996; Andersen, 1997a, b) which recognize the ecological roles of organisms as well as their taxonomic affinities. Previous studies have shown the proportion of specialist to generalist arachnids and of arthropod predators and parasitoids to herbivores to be affected by habitat fragmentation (Webb and Hopkins, 1984; Kruess and Tscharntke, 1994). In this study, we examine effects of habitat fragmentation on several arthropod groups: spiders, which are predators; wasps which are parasitoids; ants which have a generalized diet; and flies and beetles which have more variable trophic functions. We also examine the effects of habitat fragmentation on ants with different ecological roles in more detail through the use of Andersen's (1990, 1995, 1997b) functional group classification for Australian ants. Like Grime's (1979) classification for plants, Andersen's classification is based on genus-level life-history strategies in response to stress and disturbance. It involves seven groups, the three most abundant of which are: the opportunists, which are rapid colonisers; the generalised myrmicines, which can exploit a wide pool of resources; and the dominant dolichoderines, which, due to their high abundance, activitiy and aggression are very competitive, but only under a low degree of environmental stress. These groups have been found to respond predictably to stress and disturbance in several regions in Australia (Andersen, 1990, 1995; Majer and de Kock, 1992; Majer and Nichols, 1998; York, 1994).

To test Preston's (1962) prediction (Gotelli and Graves, 1996, p. 232) that species richness in equal-sized areas will be greater in large than small 'islands', we used a fixed-sampling effort for all fragments. This also prevented more species being found in larger areas as a consequence of greater sampling effort, rather than as the result of biological processes (Connor and McCoy, 1979).

As the number and composition of species in an area also depends on habitat type (Rafe et al., 1985; Bauer, 1989), we compared different sized fragments belonging to a single habitat type (as advocated by Westman, 1983; Kelly et al., 1989; MacNally and Watson, 1997), a procedure which also allowed us to examine the effect of area independent of that of habitat heterogeneity.

We surveyed arthropod assemblages and microhabitats in fragments of different sizes in heath and woodland in the Sydney region of south-eastern Australia. Our hypotheses were that:

1. for equal sampling effort, the species richness of ants, beetles, spiders and wasps will be greater in large fragments than small;
2. opportunist and generalized ants will occur more frequently in traps in smaller than larger fragments whilst dominant ants will occur more frequently in larger fragments;
3. small and large habitat fragments support different assemblages of arthropods. Differences for taxa belonging to higher trophic levels, such as wasps, which are predominantly parasitic, and spiders, which are predators, will be greater than for ants, beetles and flies which have more variable trophic function;
4. arthropod assemblages in different grids within one fragment are most similar within the smaller fragments where transects are closest together, and least similar within larger fragments where the transects are furthest apart; and
5. small and large habitat fragments will contain different microhabitats.

2. Study sites

The original vegetation of the Sydney region (population approximately 3.7 million) in south-eastern Australia has become highly fragmented since European settlement in 1788 and all remaining fragments in this area have suffered anthropogenic disturbance, resulting in a change in the composition and structure of the remaining vegetation (Benson and Howell, 1990). We selected 10 areas of heath and 11 of woodland in 13 fragments of bushland within the Sydney region (Fig. 1, Table 1), ranging in size from 0.04 to 164.4 km^2, and surrounded by urban areas, for use in the study. Sites were chosen and assigned to vegetation types using a map of the natural vegetation of the Sydney region (1:100 000 map sheet, Benson and Howell, 1994), followed by inspection of the areas. The heath sites chosen were those classed as Coastal Sandstone Heath, dominated by plants such as *Hakea teretifolia, Allocasuarina distyla* and *Banksia ericifolia*. The 'woodland' sites chosen were dry, dominated by *Eucalyptus botryoides*, *Eucalyptus gummifera* and *Angophora costata* not taller than 20 m, and belonged to two similar classes: Sydney Sandstone Gully Forest and Sydney Sandstone Ridgetop Woodland. Previous work suggests that the arthropod assemblages in the finer scale vegetation classifications ridgetop and gully woodland do not differ in the Sydney region (Hochuli and Gibb unpublished data), whilst comparison of blackbutt-turpentine forest with protected bluegum high forest in the same region found no differences between arthropod fauna in the two habitat classifications (Dobbie, 1999), indicating that the coarse-scale examination is appropriate for our system. A vegetation map of Brisbane Water National Park (Benson and Fallding, 1981) was used to select heath and woodland sites north of Ku-ring-gai Chase National Park. Sites south of Botany Bay were selected by inspection of the area as no detailed vegetation map was available.

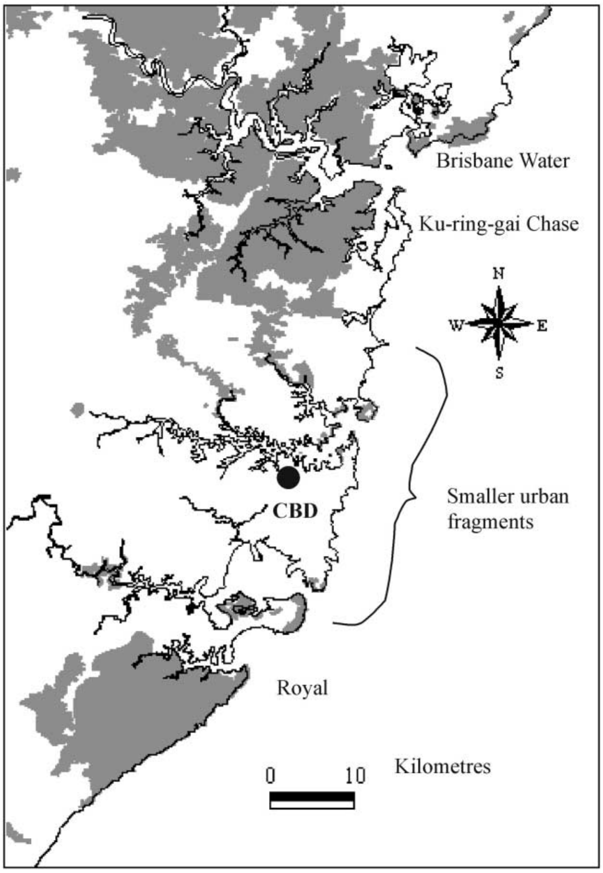

Fig. 1. Map of the Sydney region showing areas with original vegetation (grey), urban and agricultural landuse (white) and the central business district (●). The 'large' fragments are to the north and south of the central business district and the 'small' sites are in coastal areas between the large sites.

A division between the three larger National Parks and the smaller sites within the Sydney basin, such as those that make up Sydney Harbour National Park, was obvious, with no fragments being either larger than 500 ha or smaller than 8000 ha. This meant that no fragments of intermediate size were available. All fragments were characterised by numerous walking tracks and many also had bitumen roads running through them. Fragments smaller than 500 ha were referred to as 'small', whilst fragments larger than 8000 ha were referred to as 'large'. Four of the small sites consisted only of heath, and five consisted only of woodland. Another two sites, Botany Bay National Park and North Head, contained both heath and woodland. Three areas of heath and four areas of woodland within the three large areas were also chosen.

Fire frequency is a major source of variability in plant compositions within a community amongst Sydney sandstone communities (Morrison et al., 1995). The vegetation of the smaller fragments in this study, such as those within the Sydney Harbour National Park, has an altered fire regime, leading to unusually mature communities in some areas (NPWS, 1998). In urban areas where fires cause risk to life and property, efforts are made to prevent fires, resulting in decreased fire frequency in the smaller bushland remnants.

3. Methods

3.1. Trapping methods

Each fragment was divided into approximate thirds and a grid of insect traps was placed centrally in each third. This arrangement allowed us a good representation of the arthropod composition of the entire fragment,

Table 1
Macrohabitat-type and general size category of sites (L = large; S = small). Sites are ordered from northernmost to south. SHNP = Sydney Harbour National Park; NP = National Park

Heath	Area (km^2)	Woodland	Area (km^2)	Size
Brisbane Waters NP	84.1	Brisbane Waters NP	84.1	L
Ku-ring-gai Chase NP	156.1	Ku-ring-gai Chase NP	156.1	L
Dee Why Head	0.08	North Head (SHNP)	2.28	S
North Head SHNP	2.28	Wellings Reserve	0.07	S
Dobroyd Head SHNP	0.67	Parriwi Park	0.04	S
Malabar Rifle Range West	0.19	Middle Head (SHNP)	0.50	S
Malabar Rifle Range East	0.73	Bradley's Head (SHNP)	0.32	S
Botany Bay NP	4.05	Nielsen Park (SHNP)	0.21	S
		Botany Bay NP	4.05	S
Royal NP	164.4	Royal NP (Maianbar)	164.4	L

and ensured that larger fragments were not sampled more than smaller fragments which would have confounded the effects of area and sample size (Connor and McCoy, 1979). As edges often contain different faunal assemblages from the core habitat (Yahner, 1988), we placed all grids at least 20 m (the maximum distance possible in the smallest fragment) away from any paths or houses. We used pitfall traps (diameter 4 cm, depth 10.5 cm) half-filled with ethylene glycol to trap ground dwelling invertebrates such as ants, beetles and spiders (Majer, 1997) and yellow pan traps (yellow plastic bowls with internal diameter 15 cm, depth 4 cm) filled with water and a detergent to trap several groups of flying insects such as ichneumonid, diapriid and scelionid wasps, and dolichopodid flies, which are particularly attracted to yellow objects (Kirk, 1984; Mensah, 1997). Pitfall traps, in two rows of four traps each 10 m apart, were placed in the ground with their lids on over a period of about 3 weeks. All traps were closed for at least a week to avoid digging-in effects (Greenslade, 1964, 1973; Majer, 1997) before they were opened between 26 and 29 May 1997. A yellow pan trap was placed midway along the grid at each site when the pitfalls were opened. Only one yellow pan trap was used in each grid because they attract target insects, thus capturing a large number of arthropods from a wider area than pitfall traps (Mensah, 1997). All traps were left open for a period of 6 days before they were recovered between the 1 and 4 June 1997. Sampling of the intensity used in this study will not record all target species in the area, but standardized sampling allows us to obtain an estimate of the relative species richness and composition of different sites.

We removed ants, beetles and spiders from the pitfall traps and flies, wasps, ants, beetles and spiders from the water traps. We identified beetles, spiders, flies and wasps to family (using CSIRO, 1991, Goulet and Huber, 1993, and an unpublished key to the spider families of the Sydney region; A. Low, The University of Sydney) and morphospecies—recognizable taxonomic unit based on the external appearance of specimens and commonly used as a surrogate for species diversity. For ants and some families of beetles and spiders, morphospecies correlates strongly with species, even for the naïve sorter (Oliver and Beattie, 1996). Ants were identified to genus (using Shattuck, 1999) and morphospecies and then allocated to functional groups (Andersen, 1990, 1997a). Phorids and several of the most abundant nematoceran flies in the region: the cecidomyiids, sciarids, and chironomids, are very difficult to classify to morphospecies (David Britton, personal communication), so all morphospecies within each of these families were combined into a single morphospecies for the analyses. A total of 504 morphospecies were collected. The reference collection is stored at The University of Sydney.

3.2. *Microhabitat assessment*

Within each site, each of the three grids was characterised on the basis of 'microhabitat' features. These included characteristics of the ground, such as leaf litter, ground cover, debris and rock cover, the dominant understorey species and height of the plant understoreys, as well as inclination and disturbance levels. At each grid, we assessed these characters in three 5×5 m quadrats drawn in the middle and at both ends of the grid. The average of results for three quadrats was used to characterise the entire grid.

Slope was recorded on an ordinal scale of 1–5, with 1 being flat to 5 being the steepest site at an angle of 24 degrees (Akuna Bay in Ku-ring-gai Chase National Park). Aspect was evenly distributed amongst large and small fragments. Disturbance by humans was assessed by determining the proximity of paths and their size and usage, as well as by looking for any accumulated rubbish. Anthropogenic disturbance was ranked from 1 to 5, with 1 being relatively undisturbed (with no obvious recent anthropogenic use), and 5 being the most apparently disturbed site, crossed by many small paths and having obvious accumulated rubbish. Leaf litter, ground, rock and debris cover were estimated as a percentage. The sum of their percentages may have exceeded 100% if debris covered leaf litter or ground cover, or leaf litter had fallen on the surface of the rock. Understorey cover was estimated visually as the percentage of sky obscured by smaller trees or shrubs greater than 1 m in height. All estimates were made by the same observer.

3.3. *Data analyses*

All analyses were performed separately for the Diptera, Coleoptera, non-formicid Hymenoptera, Araneae and Formicidae and it's three major functional groups. The abundance of ants was analysed using percent positive traps rather than total abundance as traps near nests often trap excessive numbers of one species. As comparisons were planned and the hypotheses referred explicitly to each group of arthropods, and each functional group, we did not make corrections for multiple hypothesis tests on the same data or hypothesis (Rice, 1989; Snedecor and Cochran, 1989).

3.3.1. *Associations with vegetation type*

We tested the predictions regarding differences in arthropod assemblages and microhabitats in heath and woodland fragments using ANOSIM (analysis of similarities; Clarke, 1993; with a maximum of 5000 permutations) in the program PRIMER (Anon, 1994). For all arthropod data we used a 4th-root transformation which reduces the weighting of abundant species but preserves relative abundance information (Clarke, 1993). The program constructs a similarity matrix between samples using the Bray-Curtis similarity measure that is not affected by joint absences. This similarity measure also gives more weight to abundant than to rare species (Field et al., 1982).

We tested for differences in dissimilarities of assemblages of ants, beetles, spiders, flies and wasps between heath and woodland fragments. As the analyses showed arthropod assemblages and microhabitats in heath and woodland were significantly different, the two vegetation types were treated separately in all large–small comparisons.

When the ANOSIM was significant, SIMPER breakdowns (Clarke, 1993) were conducted to determine which species were primarily responsible for the differences. Species with low proportional abundances ($<0.5\%$) were omitted from this analysis as the full data set exceeded the limitations of the PRIMER program (Smith, 1996).

3.3.2. *Associations of arthropod assemblages with fragment size*

We used *t*-tests assuming unequal variances to compare species richness of ants, beetles, spiders, flies and wasps; and the frequency of capture of the three major ant functional groups in small and large fragments of heath and woodland.

We used ANOSIM, as described above, to test for differences in dissimilarities of assemblages of ants, beetles, spiders, flies and wasps between large and small fragments fragments of heath and woodland. SIMPER breakdowns were performed to determine which species were primarily responsible for differences.

3.3.3. *Similarities of arthropod assemblages within sites*

We tested the hypothesis that arthropod assemblages within small fragments, where the distance between grids was smaller, would be more similar than in larger fragments where the distance between grids was greater. A measure of the overall similarity of the pitfall-trapped arthropod assemblages between all combinations of grids within each site was obtained from the similarity matrices obtained using PRIMER. The mean Bray-Curtis similarities of each paired comparison of the three grids at each site were regressed against the common log of the site area which was used as a correlate for distance between grids. All Bray-Curtis similarities were arcsine transformed before analysis.

3.3.4. *Comparison of microhabitats in small and large fragments*

We used *t*-tests assuming unequal variances to compare mean understorey height and overstorey height (for woodland only), as well as arcsine transformed percentage overstorey and understorey cover (for woodland), leaf litter, and ground, rock and debris cover between large and small fragments for heath and woodland. We used the Wilcoxon rank sum test to compare slope and disturbance levels in small and large fragments of heath and woodland.

4. Results

4.1. *Association of arthropod assemblages with vegetation type*

Assemblages of ants, beetles, spiders, flies and wasps were significantly different between woodland and heath sites (ANOSIM always with $P<0.01$; Table 2), indicating that heath and woodland should be analysed separately in the remainder of the study.

4.2. *Associations of arthropod assemblages with fragment size*

There was no difference in species richness between small and large fragments in heath, and woodland for most taxa. The species richness of ants in woodland, however, was greatest in small fragments (Table 3). Within the ant functional groups, the Generalised Myrmicinae occurred significantly more frequently in small fragments in woodland (Table 4). Opportunist species were also more common in small than large woodland fragments, and Dominant Dolichoderinae were more common in large than small heath fragments although neither of these results were quite significant (Table 4).

Assemblages of spiders were different in small and large fragments in both heath and woodland, while ant assemblages were different only in small and large woodland (Table 5). Wasp assemblages were different in small and large heath and the difference was close to significant in woodland ($P=0.061$). The SIMPER analysis showed that only one species contributed to more than 5% of the differences in any of the taxa. Zodariidae X (3.4%) and Diapriidae A (3.5%) contributed most to differences between large and small heath and were both more common in the small fragments.

Table 2
Analysis of similarities of arthropod asssemblages in heath and woodland

Taxon	Global *R*	*P* value
Ants	0.513	<0.001
Spiders	0.386	<0.001
Beetles	0.290	0.002
Flies	0.262	0.001
Wasps	0.207	0.001

Table 3
t-tests with unequal variance on species richness in large and small fragments in heath (d.f. = 8) and woodland (d.f. = 10)

Taxon	Heath		Woodland	
	t-Statistic	*P*-value	*t*-Statistic	*P*-value
Ants	1.74	0.2223	−2.76	0.0246
Beetles	0.90	0.4036	1.95	0.1084
Spiders	−0.54	0.6438	−0.19	0.8584
Flies	−0.67	0.5309	0.97	0.3765
Wasps	−0.21	0.8416	1.16	0.2804

Table 4
t-Tests with unequal variance for the the frequency of capture for ant functional groups and fragment area in heath (d.f. = 8) and woodland (d.f. = 10)

Functional group	Heath		Woodland	
	t-Statistic	*P*-value	*t*-Statistic	*P*-value
Dominant Dolichoderinae	2.82	0.0668	1.58	0.1891
Opportunists	0.94	0.4000	−2.13	0.0654
Generalized Myrmicinae	0.57	0.5906	−2.93	0.0168

Pheidole A (5.2%) and Pisauridae B (4.5%) contributed most the differences in woodland and were also more common in smaller fragments.

4.3. *Influence of spatial scale on similarity*

At grids within sites in woodland, the Bray-Curtis similarities of all arthropod taxa within sites were significantly negatively related to fragment area ($F_{(1,10)}=5.44$; $P=0.0446$; $r^2=0.38$), whilst those of heath were not ($F_{(1,9)}=0.37$; $P=0.7985$; $r^2=0.01$; Fig. 2).

4.4. *Comparision of microhabitats in small and large fragments*

Small and large fragments of both heath and woodland showed differences in several of the microhabitat characteristics measured (Tables 6 and 7). Small fragments of both heath and woodland had thicker understorey cover, with *Pittosporum undulatum* being a dominant species in most small, but no large woodland remnants. Small heath fragments had significantly less ground cover, more debris cover, higher levels of anthropogenic disturbance and were flatter (the difference in slope was close to significant at $P=0.0648$) than large fragments. Small woodland fragments had significantly more leaf litter, a higher understorey and higher levels of disturbance (although this was not quite significant at $P=0.0649$).

Table 5
Analysis of similarities of arthropod assemblages in large and small fragments of heath and woodland

Taxon	Heath		Woodland	
	Global *R*	*P* value	Global *R*	*P* value
Ants	0.296	0.107	0.431	0.021
Spiders	0.407	0.024	0.421	0.015
Beetles	0.025	0.417	0.177	0.148
Flies	0.136	0.286	0.299	0.133
Wasps	0.309	0.048	0.266	0.061

5. Discussion

The key finding of this study is that arthropod assemblages show a strong compositional response to urban fragmentation in the Sydney region. Importantly, this response occurred in both major habitat types for several major taxa, although responses in heath and woodland were not always consistent.

The species richness per unit sampling area of almost all taxa examined, in both heath and woodland, was not greater in large than small fragments, in contrast to predictions of the area per se hypothesis (Preston, 1960, 1962), but in agreement with previous studies (Westman, 1983; Kelly et al., 1989; Woinarski et al., 2000). Examination of the composition and ecological function of the species may therefore reveal more clearly the effects of fragmentation. Large and small fragments of heath supported significantly different assemblages of spiders and wasps, whilst large and small fragments of woodland supported significantly different assemblages of spiders and ants. Assemblages in the smaller fragments were not subsets of those in the larger fragments (see Gibb and Hochuli, 1999) and the difference between microhabitats in small and large habitat fragments indicates that habitat alteration occurs after fragmentation, resulting in a change in arthropod species. Higher trophic levels such as predators and parasitoids show the strongest compositional differences, while generalized species have become more common in the highly disturbed smaller fragments.

While the equilibrium theory of island biogeography (MacArthur and Wilson, 1963, 1967) makes no prediction about the composition of species on an island, it does imply that species persisting on smaller remnants are likely to be better dispersers or longer lived than those that become extinct (Margules et al., 1994). Small, isolated habitats are more likely to have a higher proportion of vagrant and ephemeral species (Webb and Hopkins, 1984), with particular ‘weedy’ characteristics being required to colonise small ‘islands’ (Diamond, 1975). Thus the effects of habitat fragmentation depend on characteristics of individual species such that the patterns observed for each taxonomic group reflect a combination of different responses from different species.

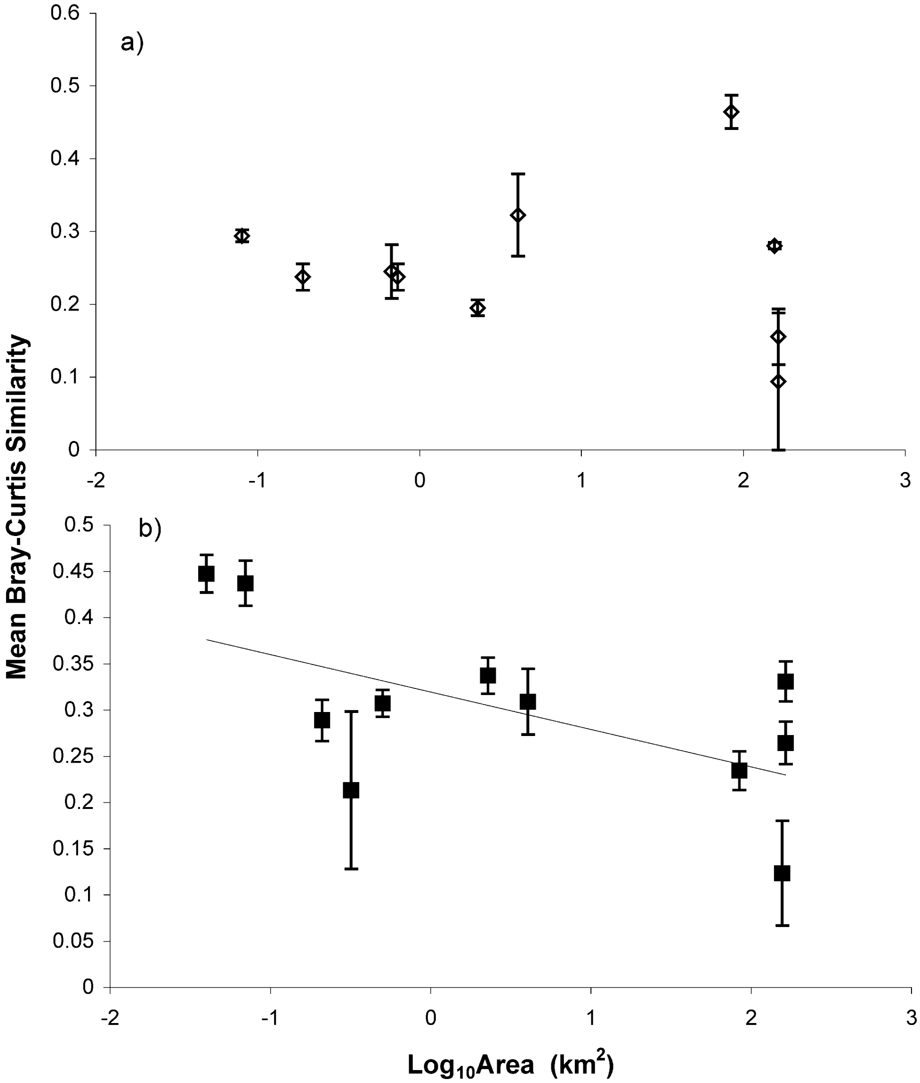

Fig. 2. Mean (±S.E.) Bray-Curtis similarities of arthropod assemblages for grids within each site in (a) heath and (b) woodland.

Table 6
t-Tests with unequal variance on microhabitat variables in large and small fragments of heath (d.f. = 8) and woodland (d.f. = 10)

Character	Heath			Woodland		
	t	*P*-value	Greater in	*t*	*P*-value	Greater in
Leaf litter	−1.98	0.1052	–	−3.06	0.0183	Small
Ground cover	2.37	0.0493	Large	0.57	0.6021	–
Rock cover	0.12	0.9112	–	1.01	0.3580	–
Debris cover	−3.01	0.0394	Small	−0.83	0.4268	–
Understorey cover	−6.43	0.0007	Small	−3.31	0.0129	Small
Understorey height	−1.15	0.3337	–	−2.54	0.0443	Small
Overstorey cover	–	–	–	0.69	0.5112	–

Habitat fragmentation has a greater effect on higher trophic levels such as predators and parasitoids than on their prey, and they are therefore more likely to show a strong response to fragmentation (Kruess and Tscharntke, 1994; Didham et al., 1996). In this study, spiders, which are predators, showed a strong association with fragment size, while patterns for other taxa were less consistent. Assemblages of wasps, which are predominantly parasitic and predatory (Naumann, 1991), were significantly different in small and large heath, and almost so in woodland ($P = 0.061$). In an analysis of nestedness of the same data (Gibb and Hochuli, 1999),

Table 7
Wilcoxon ranked sums test on disturbance and slope in large and small fragments of heath (d.f. = 8) and woodland (d.f. = 10)

Character	Heath			Woodland		
	Chi-square	*P*-value	Greater in	Chi-square	*P*-value	Greater in
Disturbance	5.90	0.0151	Small	3.409	0.0649	Small
Slope	3.41	0.0648	Small	0.424	0.5151	–

wasp species compositions were found to be negatively nested, implying that smaller, more disturbed fragments did not support a subset, but a completely different wasp fauna from larger, less disturbed fragments. Parasitoids are known to lag behind their hosts in colonising or recolonising habitat patches (Kruess and Tscharntke, 1994) and may be more sensitive to environmental fluctuations such as anthropogenic disturbance than less specialised species due to their close association with their host species and often complicated life cycles (Naumann, 1991). They may therefore be more vulnerable to changes resulting from habitat fragmentation.

Generalist and opportunist species respond more successfully to change than specialists (Didham et al., 1996) and they are often able to survive in the landscape outside the remnant habitat. Ant species richness was significantly greater in small than large woodland fragments and this response was driven by the two most common functional groups. The functional groups ‘opportunists’ and ‘generalised myrmicines’ occurred more frequently in small than in large fragments. This is consistent with the hypothesis that these groups compete more successfully against dominant ants in areas with higher levels of disturbance (Andersen, 1995). However, the ‘Dominant Dolichoderinae’ were much rarer in woodland than heath, probably due to a preference for warmer temperatures (Andersen, 1990), so competition may not have been a major regulator in woodland. It is more likely that these highly adaptable species invade the fragment from the urban matrix and are therefore more common in small fragments which have a high proportion of edge relative to area. The dominant Dolichoderinae, considered to be highly successful competitors in areas with low to moderate disturbance (Andersen, 1990, 1995), were more common in large fragments of heath and woodland, but the differences were not significant, possibly because the study was conducted in winter when their activity is relatively low.

Large and small fragments of both heath and woodland showed differences in several of the microhabitat characteristics examined. Anthropogenic disturbance level, estimated by quantities of rubbish and numbers of tracks was higher in small than large fragments for both heath and woodland. Changes in vegetation structure, microclimate and habitat suitability which may result from anthropogenic disturbance have been shown to occur in remnants after fragmentation (Lovejoy et al., 1986; Kapos, 1989; de Souza and Brown, 1994) and these changes may affect arthropod populations, particularly at habitat edges (Klein, 1989; Cappuccino and Martin, 1997).

Remnant bushland in older suburbs in the Sydney region is typified by invasive exotic species and *Pittosporum undulatum*, a dominant plant in all small, and no large woodland fragments in this study, and these species are mesic, fire-sensitive, shade-tolerant and adapted to relatively moist conditions (Rose and Fairweather, 1997). In Sydney Harbour National Park, remnant bushland is affected by high nutrient runoff where stormwater is directed into the park, resulting in gullying, siltation, pollution and weed introduction (NPWS, 1998). A reduced incidence of fire, such as that in these small remnants, has been found to alter vegetation, leading to unusually mature communities and low species diversity (Morrison et al., 1995; NPWS, 1998). The greater understorey cover and height and leaf litter cover in small fragments are all likely to be the result of a reduced fire frequency. Different structural characteristics of vegetation result in different microclimates (Kapos, 1989), and changes in humidity and temperature conditions have been shown to alter the development of insects under laboratory (Bailey, 1976) and field conditions (Ehrlich et al., 1980), thus affecting insect populations. Habitat alteration through anthropogenic disturbance and changes in microhabitat resulting from the protection of urban remnants from fire is thus likely to have contributed to the differences in arthropod assemblages between small and large fragments.

Arthropod assemblages were less similar with increasing distance between grids within fragments in woodland, but not in heath. The finding for woodland is consistent with that of Ferrier et al. (1999) who found that the similarity of spider assemblages is strongly influenced by geographic distance. It also indicates that the geographic spread of reserves is an important factor in conserving arthropod diversity. Reduced fire frequency in smaller fragments may result in a more uniform habitat rather than the mosaic of age since fire seen in larger fragments and this may lead to a more uniform arthropod fauna throughout the entire remnant.

6. Conservation implications

Urban remnants in the Sydney region often represent the last examples of once-common vegetation types and, despite high levels of anthropogenic disturbance, are of substantial conservation significance (Benson and Howell, 1990). Although overall patterns in heath and woodland were similar, different taxa and ant functional groups responded to fragmentation differently in the two vegetation types. We therefore recommend that future studies considering the biotic characteristics and ecology of urban remnants look not only at different taxa, but also different habitat types when evaluating the general effects of disturbances, especially at coarse scales. The differences in the composition of arthropod assemblages in small and large fragments also imply that species richness alone (e.g. as used by Panzer and Schwartz, 1998) is too simplistic a measure of diversity to use when evaluating the complex changes occurring after fragmentation.

The different fauna found in small urban fragments may be a consequence of any of a number of pressures associated with fragmentation and urbanisation, including decreased fire frequency, increased anthropogenic disturbance, reduced area, loss of hosts, invasion of new species and release from natural enemies (Yahner, 1988). Because they are subject to many of the processes which result in lower numbers of species on smaller islands, fragments in urban environments may never resemble larger, less disturbed remnants. Management goals for small urban remnants should focus on those factors which have potential to be disentangled from the effect of island size, such as anthropogenic disturbance and altered fire regimes and their biotic consequences. Given the strong response of functional groups to urban fragmentation, assessments of conservation status, and especially restoration programs, in urban remnants should focus on functional characteristics of faunal responses, rather than simple taxonomic measures.

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