

Ecology of Sydney's urban fragments: has fragmentation taken the sting out of insect herbivory?

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ABSTRACT

The urban remnants of Sydney support a unique and diverse fauna and flora. Many are of high conservation value, despite being subjected to a range of anthropogenic disturbances that seemingly compromise their biodiversity value. We tested a suite of hypotheses associated with habitat fragmentation and urbanisation. We found that the composition of invertebrate fauna of small remnants was significantly different to that in larger continuous areas of similar vegetation, with higher trophic levels (predators and parasitoids) being most affected. Subsequent surveys on *Eucalyptus botryooides* revealed higher levels of herbivory in urban remnants, consistent with the hypothesis that herbivores in these remnants were released from pressures of parasitism and predation. The importance of higher trophic levels in regulating herbivory was demonstrated in field experiments excluding avian and insect predators from branches being used by a dominant herbivore on *E. botryooides*, *Doratifera casta* (Lepidoptera: Limacodidae). The declining state of urban remnants may be linked to a disruption of ecological processes associated with the loss of species from higher trophic levels, releasing herbivore populations from pressures of predation and parasitism. While this may be perceived as compromising the ecological integrity of urban remnants, it may also be an unavoidable consequence of habitat fragmentation and a factor that needs to be incorporated in the future management goals of urban remnants.

Key words: Habitat, fragmentation, urban insects, urban biodiversity, urban ecology.

Introduction

Clearing of native vegetation in Australia and the subsequent fragmentation of remaining habitat are considered an increasing threat to biodiversity at all levels (Australian State of the Environment Committee 2001; Major *et al.* 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 (Didham *et al.* 1996; Harrison and Bruna 1999). Much attention of the effects of habitat fragmentation in terrestrial ecosystems in Australia has focused on fragmentation associated with agriculture (Major *et al.* 1999) and forestry (Margules 1992; Davies and Margules 1998), although habitat destruction has probably been most complete in the areas surrounding our large cities.

Ecosystems in urban areas are often perceived as depauperate and highly modified owing to the apparent and pervasive anthropogenic impacts associated with the development and "maintenance" of cities (e.g. Davis 1982; McDonnell *et al.* 1993). The habitat remaining is often subjected to extreme anthropogenic pressures through disturbance and development (McDonnell *et al.* 1993) and the ecological history of remnants may also influence biota (Cam *et al.* 2000; Knick and Rotenberry 2000). Many urban remnants are actively managed for a range of often competing interests, including recreation, conservation and heritage values (Davies and Christie 2001; McDonald *et al.* 2002). Paradoxically, despite their complex ecological histories, urban remnants and bushland surrounding urban areas are often highly valued for their natural heritage values and

may support fauna and flora of considerable conservation significance (Benson and Howell 1990; Howell and Benson 2000; Banks 2004). Increased public awareness of biodiversity values, coupled with policies that increase roles for community involvement in the management of biodiversity (Lunney *et al.* 2002), have led to an urgent need to understand the ecology of these often understudied remnants, as well as an evaluation of the effectiveness of current and proposed approaches to their management.

In this paper we present an overview of work that considered the ecological impact of urban fragmentation in the Sydney region, linking the shifts in the composition of invertebrate fauna to the state of vegetation in urban remnants. The work is ongoing and is designed to evaluate the ecological consequences of habitat fragmentation by urbanisation, and how this may and should influence management goals for urban remnants. For each case, our findings are related to other work examining the ecology of urban remnants to identify any general principles of urban ecology.

Natural history of urban environments in the Sydney region

The remnant native vegetation on Hawkesbury sandstone in the Sydney Basin contains a diverse and unique flora and fauna (Benson and Howell 1990; Anon. 1997). The development of the city of Sydney has been associated with a rich history of disturbance and habitat degradation, its planning driven by a culture where historically "growth was seen as the natural order of things; the planner's role was to steer it to the right locations" (Freestone 2000,

p.122). Little is known of the original biodiversity of this area and its fine scale response to human land uses since 1788, other than the local extinctions of many fauna and the dramatic reductions in the extent of most vegetation types (Benson and Howell 1990). This has given rise to substantial conjecture about what constitutes its "natural" state (reviewed by Benson and Redpath 1997), a major priority for future research given the widespread recent public interest and commitment to the restoration of these bushland remnants (Davies and Christie 2001; McDonald *et al.* 2002). The remaining natural areas exist in a landscape matrix subjected to a multitude of uses and anthropogenic pressures, often with considerable public discourse on the merits of proposed developments and uses (Banks 2004).

Despite being situated in Australia's largest city, the biodiversity of most of Sydney's bushland remnants has not been systematically surveyed (Anon. 1997). There is a considerable body of literature examining various components of the fauna and flora (Edmonds and Webb 1986; Roberts 1993; Carolin and Tindale 1994; Fairley and Moore, 1995; Leonard 1997; Griffiths

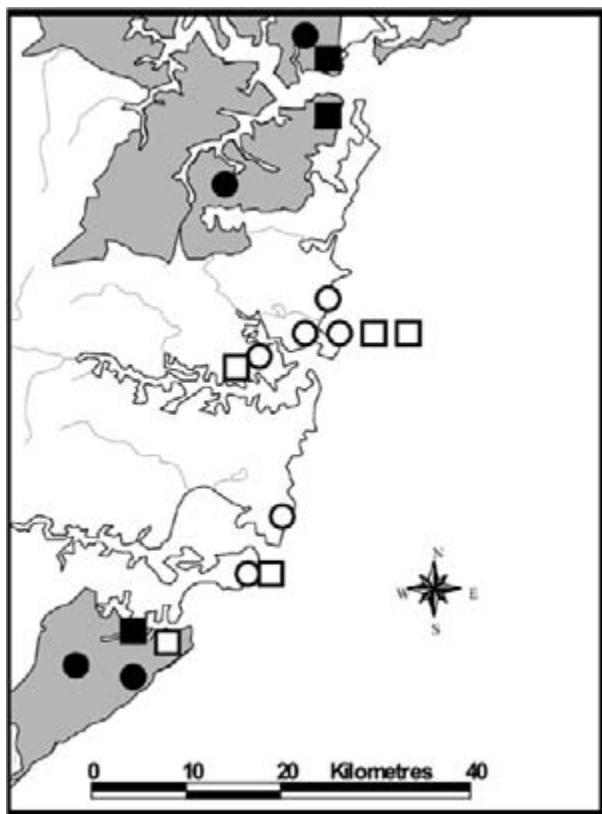


Figure 1. Location of study sites for invertebrate surveys and dieback assessment in the Sydney region. The 'large' fragments (closed circles) are in Brisbane Water and Kuring-gai Chase National Parks to the north and in Royal National Park to the south of the central business district. The 'small' sites (open circles, 6 heath and 7 woodland) are in coastal areas between the large sites. Squares represent areas where factors associated with dieback were assessed; closed squares are areas where *Eucalyptus botryoides* was not suffering dieback and open squares represent areas suffering extensive dieback. Full details of sites are given in Gibb and Hochuli (2002) and Burrows (1999).

1997; Fairley 2001) although much of this body of work is in the form of field guides for the devoted group of natural historians in the region. A recent study targeting bushland biodiversity in western Sydney surveyed flora, mammals, birds, reptiles, amphibians, and aquatic macroinvertebrates (Anon. 1997) revealed considerable biodiversity value in many remnants. This study also revealed that the major threats to biodiversity in these urban remnants were habitat loss, fragmentation and degradation and that there was an urgent need to actively manage and restore these habitats at regional scales. The setting of appropriate targets for restoration of urban bushland created the need for specific collection and assessment of local information and the placing of that information into the appropriate environmental context (Kleiman *et al.* 2000).

The landscape-level work described in this paper was undertaken mainly in remnants dominated by Sydney sandstone woodlands (Sydney sandstone gully forest and ridgetop woodland) and coastal sandstone heathlands (Benson and Howell 1994). We examined these vegetation types because they were distinct and clearly mapped and readily available in small remnants as well as in larger, continuous areas, a critical part of the design required for our initial questions on the composition of invertebrate fauna in urban remnants. For these questions we needed to compare the faunal compositions and levels of herbivory in small remnants to those found in areas not affected by habitat fragmentation, large areas in Ku-ring-gai Chase National Park (N.P.), Royal N.P. and Brisbane Water N.P. (Figure 1).

Responses of insect assemblages to urban fragmentation

A major criticism of previous assessments of urban biodiversity is that one of the major functional groups, the terrestrial invertebrates, were not considered (Kremen *et al.* 1993; Yen and Butcher 1997). Given the importance of these animals in indicating the state of many ecosystems, there is a need to develop methods by which these organisms can be incorporated into similar studies to the urban bushland biodiversity survey (Anon. 1997).

Terrestrial invertebrates are affected by habitat fragmentation and subsequent disturbance in many systems and can be used as tools to evaluate the state of natural areas and the success of any restoration efforts (De Vries *et al.* 1996). Terrestrial invertebrates are also a valuable potential measure of the ecological integrity of these areas, as they are involved in key ecological processes occurring in remnants (e.g. pollination, seed dispersal, decomposition) and generally form strong associations with plant assemblages (Panzer and Schwarz 1998). As such, they make practical indicator taxa and suitable units for assessing appropriate milestones or 'endpoints' of restoration and rehabilitation efforts (Kremen *et al.* 1993). However, to be able to use these taxa in this way, their patterns in distribution and abundance and the basic factors underlying these need to be identified.

Terrestrial arthropods may respond to habitat fragmentation in urban environments in a number of ways; smaller remnants may support fewer species and smaller populations (Blaire and Launer 1997; Miyahshita *et al.* 1998; Bolger *et al.* 2000); effects are stronger for higher trophic levels (McGeoch and Chown 1997); invasion by introduced species may be facilitated (Suarez *et al.* 1998); and assemblages may exhibit classic responses to “edge effects” (Didham 1998), with some native species responding positively to fragmentation (Port and Thompson 1980; Bolger *et al.* 2000). Although generalisations about responses to habitat fragmentation for other taxa have been fraught with exceptions (Robinson *et al.* 1992), they provide the framework for which hypotheses about responses to urban fragmentation can be generated.

We surveyed heath and woodland remnants using several trapping techniques and compared the composition of assemblages in urban remnants and larger continuous areas of the same vegetation type. Our work (Table 1; summarised in detail in Gibb and Hochuli 1999, 2002) has shown that not only is there a change in the species composition of urban remnants, but also that the response of fauna to fragmentation is uneven, with higher trophic levels more likely to respond (Table 1). Our findings were consistent with previous work, which predicted a complex suite of responses (Miyahshita *et al.* 1998; Bolger *et al.* 2000). Changes in the functional composition of fauna affect the extent to which they interact and have potentially significant consequences for fundamental ecological processes in urban remnants.

The presumed sensitivity of higher trophic levels to fragmentation increases the likelihood that biotic controls on lower trophic levels may be relaxed in urban

remnants through the loss of predators and parasites (Miyahshita *et al.* 1998; Ruzsyczk 1996), although these patterns are not always apparent (Bolger *et al.* 2000). Gall occupancy, larval density and species richness for fungus, gall-inhabiting lepidopterans using acacias in urban remnants in South Africa were lowest at the most disturbed, city sites (McGeoch and Chown 1997). Thus, simple predictions of urbanisation-driven, top-down effects on herbivores and levels of herbivory needed to be tested specifically for individual systems (Nuckols and Connor 1995; Bolger *et al.* 2000).

Patterns of insect herbivory in *Eucalyptus botryoides* in urban fragments

The vegetation of urban remnants is also subjected to the effects of habitat fragmentation, characterised by exposure to altered disturbance regimes and hydrological conditions which may facilitate the establishment of invasive plants (King and Buckney 2002). There is also potential for vegetation in these remnants to be subjected to biotic pressures not found in larger continuous landscapes, through alterations to the extent of top-down processes exerted by herbivores and the release of herbivores from the pressures of predation and parasitism.

Herbivory may be associated with substantial dieback in urban remnants. Observations of urban dieback of dominant trees in woodland in the Sydney region have alarmed the public for some time (e.g. Bradleys Head, Woodford 2000) and efforts to manage the dieback have been frustrated by a lack of knowledge of the causal mechanisms. Dieback of forest trees is regarded as a

Table 1. Summary of invertebrate responses to habitat fragmentation in the Sydney region. Comparisons between large continuous areas and small areas were made for species richness (using one way ANOVA) and assemblage composition (using ANOSIM), and nesting analysis used a nestedness temperature calculator (Atmar and Patterson 1993). Full details can be found in Gibb and Hochuli (1999, 2002).

Comparison of large and Small Heath fragments (N=10 Sites)				
Taxon	# of species	Species richness*	Assemblage composition	Degree of nestedness
all	319	No difference	Significantly different	random
ants	62	No difference	No difference	random
beetles	39	No difference	No difference	random
spiders	79	No difference	Significantly different	random
flies	53	No difference	Significantly different	significantly nested
wasps	86	No difference	No difference	significantly unnested

Comparison of large and Small Woodland fragments (N=11 Sites)				
Taxon	# of species	Species richness	Assemblage composition	Degree of nestedness
all	329	No difference	Significantly different	random
ants	57	No difference	Significantly different	random
beetles	33	No difference	No difference	random
spiders	82	No difference	Significantly different	random
flies	43	No difference	No difference	random
wasps	114	No difference	Significantly different	random

*species richness/per unit area

multi-causative phenomenon associated with a range of anthropogenic, physical and biotic pressures (Heatwole and Lowman 1986; Old 2000; Stone 2000). Dieback occurs in many contexts, however, the focus of much previous research in Australia has been on rural dieback at relatively coarse scales (e.g. Lansberg 1990a,b,c; Old 2000). Such studies have examined the extent of dieback and associations with possible causal factors, as well as identifying the likely causal mechanisms associated with disruptions to ecological process through changes to faunal composition and biotic invasions (Stone 2000). As an environmental problem, the complex nature of dieback, coupled with the likelihood that it is a response to long-term exposure to a range of disturbances, represents a major challenge to ecologists seeking to identify its causes and develop strategies to combat it (Heatwole and Lowman 1986).

Insect damage is commonly associated with eucalypt dieback as either a cause or consequence (Landsberg 1990c). Recent assessment of levels of insect herbivory on Bangalay *E. botryoides* in urban forest remnants within the Sydney Basin (Burrows 1999) revealed that trees at sites supporting trees suffering dieback exhibited higher levels of herbivory than those in control sites (Figure 2) and that levels of herbivory increased as the levels of dieback for individual trees increased. Preliminary analyses of levels of herbivory on Sydney Red Gum *Angophora costata* suggested that the pattern of elevated levels of herbivory in urban remnants may also be generalised to other dominant trees (*A. costata*, Christie, pers. obs.).

Seasonal variation in levels of damage of *E. botryoides* followed a predictable trend that was independent of the level of dieback, with new growth in spring being subjected to higher levels of herbivory (Burrows 1999). Interestingly, the type of damage at urban remnants was highly variable, with localised outbreaks of insects from different taxa implicated in causing the damage at different sites. Within a 10 km radius, three different herbivores caused substantial damage; the gumleaf skeletoniser (*Uraba lugens*, Lepidoptera: Noctuidae) was most prominent at North Head, the black slug cup moth (*Doratifera casta*, Lepidoptera: Limacodidae) caused most of the damage observed at Middle Head and psyllids (Hemiptera: Psyllidae) caused most of the damage at Bradleys Head.

The loss of higher trophic levels from remnants may release herbivores from the pressures of parasitism and predation to cause elevated levels of herbivory, although plants in these remnants may not be healthy enough to defend themselves from herbivory (White 1984). For example, outbreaks of herbivorous insects along motorways in the United Kingdom have been associated with changes in the composition and status of foliage (Port and Thompson 1980). Furthermore, Nuckols and Connor (1995) found no evidence for the contention that urban or ornamental plantings are more susceptible to insect attack and receive more damage to foliage by herbivores than trees in natural forests. Fine scale studies, targeting the causal mechanisms by which levels of herbivory are affected, are required to support general arguments for the disruption of ecological processes in urban remnants (Debinski and Holt 2000).

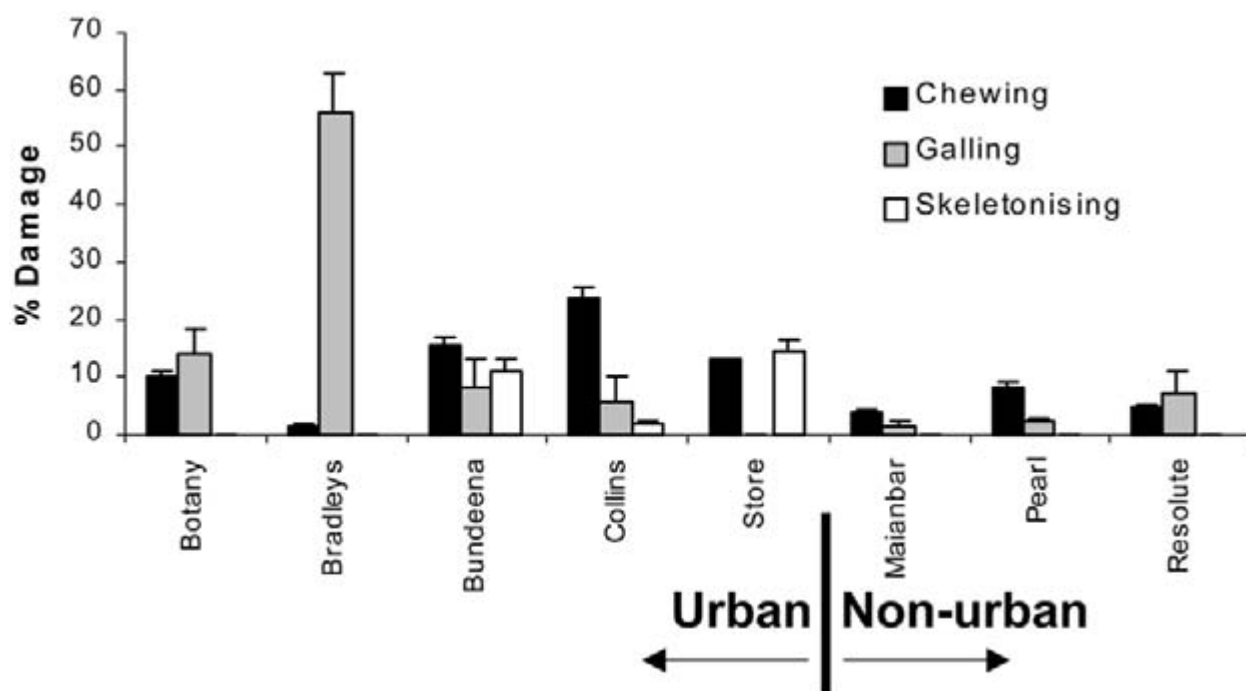


Figure 2. Levels of insect damage on *Eucalyptus botryoides* compared for trees at sites with dieback associated with urban development (1st five sites from left) and sites not suffering dieback. Data are mean levels of damage per tree (n=5 trees, with each tree being assessed from 4 branches from which 25 leaves each were taken), \pm standard error. Full details of methods are given in Burrows (1999).

Elevated herbivory in urban remnants: causal mechanisms and alternative explanations

Regulation of insect herbivore populations by higher order predators and parasites has been predicted in numerous systems but experimentally demonstrated in relatively few (reviewed by Rosenheim 1998). Fine scale exclusion experiments show that the release of insect herbivores from predation and parasitism results in higher levels of herbivory (Marquis 1984; Marquis and Whelan 1994; Dial and Roughgarden 1995) and re-introductions of predators at coarser scales caused dramatic reductions in levels of insect herbivory (Clarke and Schedvin 1999). The extent to which predator and parasites regulate herbivore populations in urban remnants has been subjected to considerable speculation, with evidence for any general effect of urbanisation on ecological processes equivocal (Nuckols and Connor 1995, McGeoch and Chown, 1997, Gunnarson and Hake 1999, Harrison and Bruna 1999). In any case, the changes in the diversity of parasitic wasps (Gibb and Hochuli 2002) and some insectivorous birds (Christie, pers. obs.) in Sydney's urban remnants create a context where the hypothesis is clearly worth testing.

The fact that extensive damage of trees in Sydney's urban remnants is caused by a range of herbivores limits the extent to which general experimental approaches can be applied to remnants at landscape scales. We examined some of the potential mechanisms that may have 'released' the population of *D. casta* at Middle Head to outbreak proportions, evaluating the effects of plant nutrient status, as well as carrying out a series of experiments examining the roles of predators and parasites (Reader and Hochuli 2003). We have made numerous observations of parasitism of larvae by hymenopterans (primarily ichneumonids) and dipterans (primarily tachinids) and found that exposure to predation and parasitism increased mortality significantly (Reader and Hochuli 2003), resulting in substantially less leaf damage on experimental branches.

There is an urgent need to assess the extent to which ecological processes have been disrupted in urban remnants and identify whether these are part of the intrinsic character of an urban remnant or a management problem needing to be solved. Understanding the roles played by different invertebrates in these remnants will also lead to the development of these organisms as a tool for those assessing the biological status of urban remnants.

Urban fragments and "high quality" vegetation: implications for management?

High levels of disturbance and herbivory in urban remnants raise questions over their ecological integrity and whether they can be managed to sustain their biodiversity values. Small urban remnants have high edge/interior ratios and are thus susceptible to a suite of edge effects (Ozanne *et al.* 1997; Bolger *et al.* 2000), which decrease habitat quality for many species (Debinski and Holt 2000). The different fauna found in small urban fragments may be a consequence of any number of pressures associated with

fragmentation and urbanisation, including increased anthropogenic disturbance, reduced area, loss of hosts, invasion of new species and release from natural enemies, most of which are difficult to ameliorate. If urban remnants are inherently and irrevocably altered as a result of these varied anthropogenic and ecological pressures, it is critical that we revise the goals for managing these types of reserves to accommodate these changes. These issues are critical when setting and assessing the goals for restoration in these remnants, as appropriate control and reference sites will need to incorporate any constraints imposed by the remnants in their landscape context.

Urban remnants in the Sydney region often represent the last examples of once-common vegetation types and, despite high levels of disturbance, are of substantial conservation significance. These remnants often require active management to deal with the diverse range of threats faced by fauna and flora through disturbance, invasive species and competing uses (Kendle and Forbes 1997), as well as to ameliorate the potential stochastic pressures generally faced by small populations (Caughley and Gunn 1996). Many goals for the management of biodiversity in urban remnants focus on "charismatic" fauna (e.g. Banks 2004; Recher 2004; Ward and Close 2004; van der Ree 2004) or flora (Howell and Benson 2000) as these capture the public's imagination. The complex response of arthropods to urbanisation and fragmentation in the Sydney region suggests that management goals for smaller remnants should focus on the functional roles of invertebrates, rather than on specific target taxa identified from surveys of larger, undisturbed remnants (Gibb and Hochuli 2002).

Furthermore, urban remnants cannot be considered without acknowledging the multiple uses for which they must be managed (Kendle and Forbes 1997). The value of urban remnants needs to be considered in their broader context; in addition to acting as refugia for flora and fauna they also provide valuable opportunities for research and education (Davies and Christie 2001) and have even been implicated as sources of psychological well-being for jaded urban dwellers (Kaplan 1997). The true value of urban habitat remnants is thus a function of the value that communities place on them intrinsically and the simple fact that they still persist in the urban matrix, despite harbouring what may be perceived as compromised states of "naturalness" with respect to their constituent flora and fauna and the ecological interactions in which they engage.

Conclusions

Disruptions to ecological processes in urban remnants are a likely consequence of the loss of species from higher trophic levels and the invasion of new species capable of tolerating shifts in disturbance regimes and conditions common in urban remnants. The composition of terrestrial invertebrates in urban remnants, a major component of biodiversity in these remnants, is likely to provide an indicator of the ecological state of remnants. Finally, an understanding of the extent to which their ecological roles are being manifested will provide insights into the sustainability of remnants and the degree to which 'natural' processes are being maintained in urban remnants.

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