Impacts of environmental weed invasion on arthropod biodiversity and associated community structure and processes

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Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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Claire Jane Stephens
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Frontispiece. An emergence trap (Chapter 4) situated in an extensive invasion of the environmental weed bridal creeper, *Asparagus asparagoides*. The invasion of exotic species is often a threat to native ecosystems, but can also be useful in the investigation and understanding of ecological patterns and processes (Crooks 2002).

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Abstract

Invasive exotic species frequently change natural patterns of biodiversity. This study investigated the effects of one of Australia's most serious environmental weeds, bridal creeper (*Asparagus asparagoides*), in remnant eucalypt woodland in South Australia. Research considered the impact of bridal creeper on different taxa and trophic groups (plants, arthropods and parasitic Hymenoptera), high-level (orders and families) and low-level (species) taxonomic assemblages, and ecological processes (parasitism and pollination). The impact of bridal creeper on the native plant community was overwhelmingly detrimental, undoubtedly due to direct interactions with the weed such as shading and root competition. It was predicted therefore, that the replacement of a species-rich and open ground-cover into a closed homogenous one would have flow-on effects to other biota in the habitat.

Despite the significantly adverse impact on the native plant community, a very abundant and diverse arthropod and wasp community occurred in bridal creeper invaded habitat. There was some evidence however, that the weed was not providing seasonally equivalent habitat to that of native vegetation for several herbivorous and nectar-feeding groups. Invaded areas were also being used for the reproduction and development of a diverse range of parasitic wasps and their hosts. However, the homogenous habitat produced by bridal creeper compared with native vegetation was reflected in the composition of the wasp assemblages occurring in invaded areas. Wasp functional group analysis based on host niche associations revealed the mobility and multi-habitat use of parasitic wasps and, presumably, their hosts. The collection from foliage of parasitoids of litter-associated arthropods and, in the absence of herbivores, the presence of parasitoids of plant-associated insects on bridal creeper, showed that many species used different habitat for juvenile development compared with that used by adults. The indirect effect of higher levels of leaf litter associated with bridal creeper invasion also resulted in greater numbers of litter-associated arthropods and their parasitoids and, in particular, the extreme abundance of one soil and litter parasitoid species which dominated the wasp assemblage that emerged from invaded habitat. Finally, the highly specific interaction between an orchid and its pollinator was not impacted upon by the presence of bridal creeper, and may have even been enhanced due the increase in the numbers of its soil/litter-associated pollinator in weed-invaded areas. Consequently, the ground-cover plant community that was so completely altered by bridal creeper was not as important as other components of the woodland habitat, such as the soil, leaf litter and canopy microhabitats, for the reproduction and development of the majority of arthropod taxa recorded.

The contrasting results for plant and arthropod diversity found in this study indicate that a plant community may always be negatively impacted by a successful weed due to direct interactions among plant species, such as competition that, in turn, reduce growth and fecundity. However, the impact of weed invasion on native fauna can be more complex. Direct (eg. provision of resources such as habitat) and indirect (eg. via increased leaf litter) interactions with the weed, species mobility, and multiple habitat use can influence the structure and composition of faunal communities. These findings are important not only for considering the effects of weed invasion on native biota, but also other disruptions where habitat structure and complexity, rather than simply plant diversity per se, are modified via changes in the plant community. This research has also highlighted the value of considering multi-species assemblages whose members comprise wide ranging taxonomic, trophic and ecological classifications to investigate the impacts of habitat change.

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Chapter 1

General introduction: biodiversity and environmental weeds

1.1 Introduction

Biodiversity is a significant and often influential catch-word. However, as a concept it remains crucial to ecological research, particularly when related to the current unprecedented levels of habitat change. Biological invasions are often considered one of the greatest threats to the integrity of natural ecosystems (Vitousek, *et al.* 1997). Released from their normal limiting factors, invasive species have the potential to consume, compete with and displace native species, resulting in a direct impact on biodiversity. However, the impacts of invasive species can be complex, and although invasive species undoubtedly change natural patterns of biodiversity, not all invaders have clear adverse consequences for all parts of the ecosystem. Furthermore, it is being increasingly realised that biodiversity cannot simply be reduced to a single number, such as species richness (eg. Purvis & Hector 2000), that previously has been the most common (and often useful) way to collect and present biodiversity data. Species diversity also has a functional component that is largely determined by interactions among species that facilitate energy and material flow, and maintain the functioning of ecosystems (Chapin, *et al.* 2000). Consequently, concern about changes to biodiversity needs to not only focus on the number of species impacted, but their associated ecological functions that are determined by their interactions within well-structured, often complex communities.

Extreme diversity, abundance and ubiquity make arthropods, and in particular insects, major contributors to the biodiversity of terrestrial ecosystems. Accordingly, within communities, arthropod-mediated interactions determine their 'functional roles' that contribute to various ecological processes (Miller 1993). In addition to species diversity and abundance, it is these interactions and associated processes that may be disrupted by biological invasions. In particular, it may be predicted that exotic plant invasion will not only directly impact on native plants (Groves & Willis 1999), but directly and indirectly affect plant-associated arthropod communities and their associated interactions and functions such as herbivory, pollination, seed dispersal, parasitism and predation. This chapter provides a review of the literature and focuses on arthropod biodiversity from the perspective of various community properties: species richness, abundance and trophic interactions among species. The impacts of habitat modifications, such as weed invasion, on biodiversity and community-level interactions are discussed, thus providing a background for the research presented in this thesis.

1.2 Biodiversity: names and numbers?

Biodiversity is, quite simply, biological diversity and is usually discussed at three nested levels: the genetic diversity contained in all biota, the number of species and the variety of ecosystems across landscapes (Harper & Hawksworth 1995; May 1995). Other definitions have included factors such as species abundance, phylogenetic diversity (or degree of relatedness), functional diversity, and species evenness or equality within a habitat (see Harper & Hawksworth (1995) for a review). Definitions and classifications aside, as a concept biodiversity has proven useful for ecological research, conservation, management and policy direction. Domestic crop enhancement, possible sources for human medicine and other products, and the direct harvesting of wild species for human use and consumption, has made genetic and species diversity economically important (Lovejoy 1995). Species richness counts are useful in research for detecting patterns among different communities, habitats and time periods for comparison and monitoring (Hammond & Miller 1998; Purvis & Hector 2000). However, when using species richness, issues relating to species abundance, equitability, heterogeneity, functional roles, complex life cycles and taxonomic difficulties need to be considered (Hawksworth 1995). Ecological diversity, which is probably the least commonly applied, has been used to identify unique locations for conservation, such as 'biodiversity hotspots', that are biogeographical areas with unique communities (Myers, *et al.* 2000).

Despite the recognition of these three levels of biodiversity, most biodiversity research focuses on the number of species observed or estimated in an area, ie. species richness (Gaston 2000). Through various extrapolative calculations, it is known that groups such as arthropods and fungi are extremely speciose, while others such as vertebrates have much lower species richness (Hawksworth 1991; Stork 1999). It is also well documented that species richness is distributed heterogeneously across the globe: generally high numbers of species are found in habitats such as tropical forests and coral reefs; overall low species richness is maintained in habitats such as some deserts; and others, such as temperate forests and grasslands have an intermediate number of species (Gaston 2000).

There is widespread evidence that the earth is losing biodiversity across all levels at unprecedented rates via human activity. Fragmentation of habitats can result in depleted genetic diversity within populations, habitat destruction results in species loss and the reduction of ecosystem diversity may cause disruptions across landscapes (Chapin, *et al.* 1992). However, as before, attention is largely focused on the loss of species richness. There are many empirical studies and estimates on the extent and rate of species extinctions (eg. Pimm & Raven 2000), and the lack of knowledge about most taxonomic groups makes it probable that a percentage of species will be lost due to human activities before they are even described (Chapin, *et al.* 1992). Recently however, an important question has emerged in biodiversity-related discussions, and that is, what are the ecological consequences of this loss? Or more simply, to what extent does biodiversity matter (Tilman 2000)? At the centre of this concept is the search for evidence to support the idea that stability, productivity and resilience of ecosystems are reliant on biodiversity (species richness) and, hence, what consequences may arise as species are deleted from communities.

1.2.1 Biodiversity and ecosystem functioning

It has been proposed that a more complete complement of a habitat's biodiversity results in greater ecosystem health. In more diverse systems, so-called 'ecosystem services' such as soil productivity and clean air and water, are maintained and systems are more likely to have a greater resistance and resilience (ecological stability (McCann 2000) to perturbations such as disease, pest outbreaks and invasion by exotic species (Elton 1958; Pimm 1994; Knops, *et al.* 1999; Naeem, *et al.* 2001). Much of this 'diversity-stability debate' (McCann 2000) remains theoretical, however the earliest, and probably best-studied, examples are the greatly simplified systems of cultivated agricultural land. Such agroecosystems are often more prone to large fluctuations in population densities, invasions and outbreaks compared with complex native communities, where co-evolved species naturally regulate populations and the resources available to invaders are limited due to fully utilised niche spaces (Elton 1958; McCann 2000).

To investigate the impact of species on ecosystem processes, the diversity-stability concept often employs the idea of functional groups, where species belong to assemblages in which they perform similar ecological functions within their communities (Chapin, *et al.* 1992). Community ecologists often recognise that species within a habitat can be grouped according to their common utilisation of particular environmental resources, such as food or habitat type, and have used the concept of functional groups to describe the ecological significance of species richness and abundance in surveys and other field research (Joern & Lawlor 1981; Simberloff & Dayan 1991; Andersen 1995; Lockwood, *et al.* 1996; Fisher 1998; Hövemeyer 1999; Andersen, *et al.* 2001; Davies 2002; Lassau, *et al.* 2005). Within the context of diversity and ecological processes, functional grouping has been used to suggest that within such groups, species are equivalent or redundant in their impact on ecosystem processes (Chapin, *et al.* 1992; Rosenfeld 2002). Two contrasting viewpoints on redundancy are commonly discussed: (1) the 'rivet hypothesis', where Ehrlich and Ehrlich (1981) compared the loss of individual species from an ecosystem like the gradual loss of rivets from the wing of a plane such that their removal progressively weakens the system; and (2) as discussed above, the 'redundant species hypothesis' that regards species richness as irrelevant in that an ecosystem has many species with ecologically overlapping functions, so that some species can be lost with little or no impact on ecosystem processes (Lawton & Brown 1994).

Recent reviews show that greater species diversity in plant communities have led to greater productivity and nutrient retention in ecosystems (Tilman 2000). Symstad, *et al.* (1998) found that the functional identity of individual plant species in a greenhouse grassland community influenced changes in productivity when species were experimentally removed. Alternately, Schwartz, *et al.* (2000) found little evidence of a link between species diversity and ecosystem function and that only 20-50% of species were needed to maintain most biogeochemical processes. They argue that evidence of an example where even the rarest species contribute to ecosystem function will be difficult to find. However, studies performed over greater temporal and spatial scales, rather than simply greenhouse or 'bottle ecosystem' experiments, may demonstrate that so-called redundant species do play some role and possibly even provide some 'insurance' against environmental change (Purvis & Hector 2000). Experimental studies have both supported and refuted the hypothesis that more diverse communities can resist invasion by exotic species (Prieur-Richard & Lavorel 2000; Dukes 2001; Kennedy, *et al.* 2002). It has been suggested that plant diversity may have an effect at local scales in resisting invasion, but may be overwhelmed by other ecological factors such as resource heterogeneity at regional scales (Levine 2000). Experiments that use animals in diversity-stability investigations are rare (however, see (Mikola & Setälä 1998), and the actual extent of redundancy in communities is largely unknown as there are very little data on the functional roles of most organisms (Chapin, *et al.* 1992). It is probable that the extent of redundancy may lie somewhere between the rivet and redundancy hypothesises depending on the system and the scale at which it is being examined (Chapin, *et al.* 1992).

In reviews and studies of the relationship between biodiversity and ecosystem function, several authors have concluded that species richness should be included in the list of factors that influence ecosystem functioning, along with species composition, disturbance regime, soil type and climate (Naeem, *et al.* 1994; Hooper & Vitousek 1997; Tilman, *et al.* 1997;

Symstad, *et al.* 1998; Knops, *et al.* 1999; Tilman 2000). Importantly, Chapin, *et al.* (2000) highlight the interactions among species, as well as species richness, evenness, and composition, as factors that determine the functional importance of species diversity in regard to ecosystem processes (Figure 1.1). Indeed, Tilman (2000) maintains that it is from the interactions among individuals of different species that diversity is expected to impact on ecosystem processes, as it is these interactions that determine the functional roles species perform within their communities.

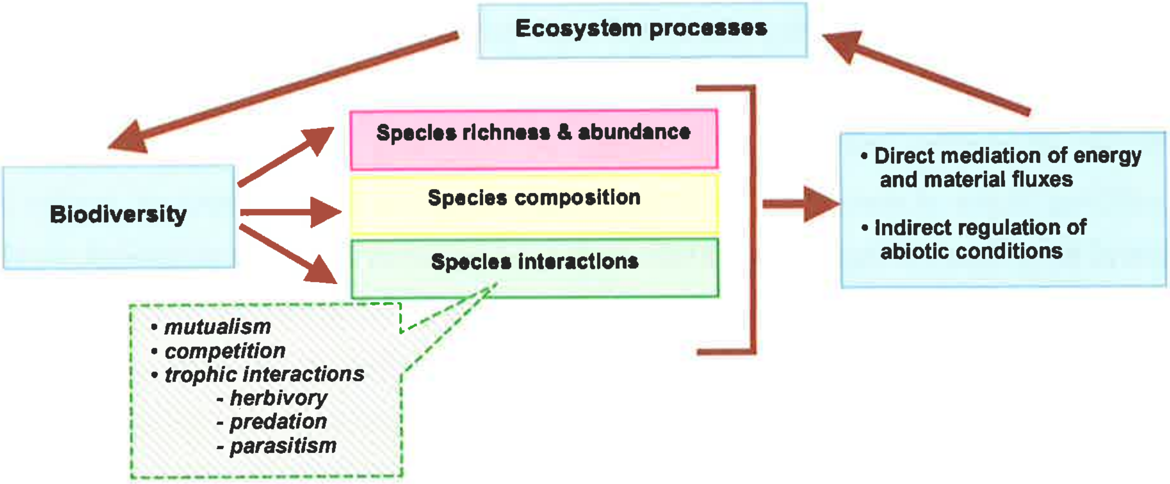


Figure 1.1 The components of species diversity that influence ecosystem processes (after Chapin, *et al.* 2000). Species richness, species abundance (or evenness), species composition and the interactions among species are the functional attributes of biodiversity that influence ecosystem processes, via direct energy and material flow through systems and indirect regulation of abiotic processes, such as disturbance and resource availability. Ecosystem processes contribute to biotic functioning and provide the system within which biodiversity is maintained.

1.2.2 Arthropod biodiversity and species interactions

As discussed above, a common and useful measure of biodiversity is species richness. Insects, for example, constitute around half of all species on Earth, exceeding that of any other class of animal with estimates ranging from 5-80 million species (Stork 1999; Gullan & Cranston 2004). Thus, in addition to their ubiquity, species richness and abundance make insects and other terrestrial arthropods an important, but poorly understood, contributor to biodiversity (Stork 1999). These measures provide standardised values that can be used to compare patterns across different populations, communities and habitats (Hammond & Miller 1998). However, as emphasised above, to understand the ecological importance of such statistics, species diversity and abundance should be discussed within a functional context.

Interactions among individuals and species, such as competition and mutualism, and the trophic interactions of predation, parasitism and detritivory, influence the structure and composition of a community and facilitate ecosystem processes (Figure 1.1). Within communities, it is these interactions that determine the 'functional roles' insects and other arthropods perform that maintain such ecosystem processes (Miller 1993). Insect-associated food webs have been studied in a diverse range of habitats, including plant galls, carrion, dung, tree holes, pitcher-plants and aquatic habitats (Schoenly, *et al.* 1991), highlighting their ubiquity and importance in ecological processes. As herbivores, predators, parasitoids, decomposers, and pollinators, insects disperse seeds, control populations of other insects, cycle nutrients, maintain soil structure and fertility, pollinate plants, and provide a major prey source for other taxa (Seastedt & Crossley Jr. 1984; Schoenly, *et al.* 1991). The mutualistic relationship between flowering plants and their pollinators form a complex community, without which many flowering plants would not reproduce sexually (Kearns, *et al.* 1998). Trophic interactions can have large effects on ecosystem processes by either directly modifying fluxes of energy and materials, or by influencing the abundance of species that control those fluxes (Chapin, *et al.* 2000). Arthropod predators and insect parasitoids regulate phytophagous insect populations, preventing herbivores from decimating plants by limiting population sizes (LaSalle 1993; Moran & Hurd 1998). The activities of soil and litter arthropods effects detritus decay rates, bacterial and fungal activities and nutrient supply that, in turn, strongly influences primary productivity (Seastedt & Crossley Jr. 1984; Wardle 1999; Moore, *et al.* 2004).

Some interactions among species are disproportionately strong and as such, species that control and facilitate these interactions play an important role in the structure of a community. These influential species have been labelled 'keystones'. The presence of a keystones species is crucial for maintaining the organisation and diversity of their ecological community (Mills, *et al.* 1993). The impact of such a species on its community or ecosystem is disproportionately large relative to its abundance (Power, *et al.* 1996). Keystones can impact on other species, not only via trophic interactions like consumption, but also through other interactions such as competition and mutualism, and via habitat modification such as physical disturbance and rates of nutrient transfer (Bond 1994). The presence or absence of insects is important to the distribution, abundance and diversity of many plants and animals due to their interaction-driven roles as providers, eliminators and facilitators (Miller 1993). As such, many insect species have been reported to function as keystones. For example, studies have found how interactions involving insects, such as herbivory and parasitism, can produce a measurable change throughout the entire community. Preferential herbivory by a specialist beetle species decreased competition between plant species, resulting in increased diversity and abundance of non-host species (Carson & Root 2000). Host switching by a polyphagous parasitoid species changed mortality rates, and hence the structure, of a multi-species parasitoid community due to increased inter-specific competition (Kato 1994). Bees are considered to be among the most important of all keystone insects as they are essential for the maintenance of many flowering plant communities via pollination (LaSalle & Gauld 1993; Kearns, *et al.* 1998). Therefore, the loss of insects and other arthropod species from habitats can potentially have community-wide consequences (see also Section 1.2.4).

Interactions can be direct between two species, such as those between a predator and its prey or competing pairs. However, species can also indirectly affect other species (Wootton 1994), leading to secondary interactions (Chapin, *et al.* 2000). Within communities, species indirectly affects other species via interaction chains or by changing the interaction between species (Figure 1.2). Such indirect effects are an important property of multi-species assemblages, but can be complex and difficult to identify in natural systems (Wootton 1994).

Figure 1.2 Two ways in which species can indirectly affect another in multi-species interactions; **(i)** an interaction chain, where species C affects species A through a chain of direct interactions involving a change in the abundance of species B (trophic effects); and **(ii)** an interaction modification, where species C indirectly affects species A by modifying how species A interacts with species B (behavioural effects) (from Wootton 1994).

1.2 Environmental weeds and biodiversity

1.2.1 Habitat disturbance and modification

Ecosystems, their communities and populations continually undergo disruption via physical disturbances such as tree-falls, seasonal fires, floods and droughts, and day-to-day tides (eg. (Hobbs 1989). Such natural disturbance regimes are thought to maintain species diversity in habitats (eg. the intermediate disturbance hypothesis (Connell 1978; Petraitis, *et al.* 1989) and may be vital to the normal functioning and continued stability of many systems (Vitousek 1990). Fire and periodic insect or pathogen outbreaks can affect ecosystems in similar ways to anthropogenic disturbance, but over a longer time scale these disturbances are often cyclic and driven by factors within the ecosystem (eg. fuel accumulation or nutrient deficiency) (Vitousek 1990). However, in many systems, anthropogenic-based disturbances, such as habitat fragmentation, cropping and grazing, pesticide and herbicide use and the invasion of alien species are now the main driving forces behind habitat modification. These usually differ from natural disturbance regimes in intensity and timing, often causing a more gradual change to individual species, communities and ecosystem processes (Vitousek 1990).

The impact of habitat change on individual species will depend somewhat on how specific its resource requirements are. For a specialist, the loss or change of resources may lead to severe reduction in population numbers or even extinction. For example, the Richmond birdwing butterfly (*Ornithoptera richmondia)* is threatened with extinction due to the loss of its specific larval food plant (Sands, *et al.* 1997). However, species with more general requirements may be relatively insensitive to the removal of one or more resources, or may have the ability to adapt to a variety of environmental conditions (eg. Ehrlich & Mooney 1983; Mcintyre & Lavorel 1994; Valladares & Salvo 2001). The intensity of the modification must also be considered when assessing its impact. In a study of the effects of grazing pressure and water availability on native plants, reptiles, birds and ants in Australian rangelands, Landsberg, *et al.* (1997) found that species could be classified into three groups based on their abundance at different distances from stock watering points, and hence their response to different levels of grazing pressure. These were described as 'increasers', which were species that increased in abundance in relation to increasing grazing pressure; 'decreasers', which were those that showed an opposite trend; and 'neutral species' that had no obvious response (Landsberg, *et al.* 1997).

Species found to have measurable responses to habitat modification have been used as indicators of habitat change and intensity. Insect populations can rapidly change in abundance over relatively short time scales in response to ecological changes as their small size and reproductive capacity allows them to colonise new habitats and exploit favourable conditions or new resources quickly (Schowalter 2000). In addition to having an inherent potential for rapid responses to changes in their habitat, insects and other arthropods are also particularly useful indicator taxa as they span a variety of ecological, distributional and functional niches, and are often sufficiently abundant to provide statistical rigour (Kremen, *et al.* 1993). The response of various arthropod assemblages and, in particular functional groups (Section 1.2.1), to disturbance has proven useful to indicate ecological changes associated with habitat quality, management and rehabilitation success (Andersen 1990; Burbidge, *et al.* 1992; Lockwood, *et al.* 1996).

The impact of habitat modification on an arthropod community will also vary according to trophic level. In studies of insect communities in fragmented habitats, herbivores and detrivores were found to be unaffected by habitat fragmentation, whereas numbers of higher trophic levels such as predators and the rates of parasitism were reduced (Didham, *et al.* 1998; Dubbert, *et al.* 1998; Zabel & Tscharntke 1998). Generally, higher trophic levels, such as predators and parasitoids, take much longer to recover from low population numbers compared to herbivores, making them more prone to population disruptions due to habitat change (LaSalle 1993; Didham, *et al.* 1996; Polis, *et al.* 1996; Komonen, *et al.* 2000). For example, Cohen, *et al.* (1994), in a comparison of arthropod food webs from pesticide treated and untreated agroecosystems, found a significant reduction in the abundance of predators and parasitoids in treated plots that led to a four-fold increase in herbivorous pests.

1.2.2 Biological invasions and environmental weeds

Over millions of years, species ranges and the composition of habitats change naturally via events such as continental drift and climate change (di Castri 1989). Biological invasions are an important source of speciation, for example, invasion of islands by exotic species via rafting on vegetation across oceans and rivers, or crossing mountain ranges by long distance wind transport (di Castri 1989). However, such invasions rarely cause large, lasting decreases in species richness or ecological damage (Brown & Sax 2004). As human globalisation has increased, the rate of deliberate and accidental introductions of plants and animals into new habitats outside their natural range has dramatically accelerated (Lodge 1993). Such invasions have been viewed as homogenising or reducing the geographic distinctness of the Earth's biota by breaking down the geographic boundaries that created and maintained the unique biota of different regions (Lodge 1993; Vitousek, *et al.* 1997; Olden & Poff 2003). When combined with other forms of habitat change, biological invasions are undoubtedly placing ecosystems under significant pressure (McCann 2000). As discussed above, habitat disturbance is typically defined as a relatively discrete event in time that removes organisms and opens up space that can be recolonised. The habitat modification caused by a successful invader generally results in a more gradual change. Biological invasions can perhaps be more appropriately described as 'ecosystem engineering', as an invader can provide new resources as well as the removal or structural modification of habitats, whereas disturbance mainly results in removal or habitat damage (Crooks 2002).

Plants are one of the most common biological invaders as they are actively transported outside their natural ranges for agricultural and horticultural purposes. The term 'environmental weed' has been coined to distinguish those species that have become established in native habitats and pose a threat to environmental values, compared to those that cause economic loss to agricultural production (Adair & Groves 1998). Around 15% (approximately 2500 species) of the total Australian vascular flora has been introduced from elsewhere over the last 200 years and around ten new plant species are added to the naturalised flora every year (Adair & Groves 1998). Vitousek, *et al.* (1997) provide a summary of equivalent global statistics. Invasive plant species that persist to become weeds may have experienced a decrease in regulation by herbivores and other natural enemies (the 'enemy release hypothesis' (Keane & Crawley 2002), but see Colautti, *et al.* (2004)), and be able to out-compete the native species due to higher seed producing abilities, better seed dispersal, greater seedling survival or better growth rates, resulting in an increase in distribution and abundance (Elton 1958; van der Sommen 1986; Blossey, *et al.* 2001).

Many plant invasions also succeed due to earlier habitat change (Elton 1958; Vitousek, *et al.* 1997). The establishment of these species is often facilitated through the disruption of natural communities, such as soil disturbance, grazing or fire, that provides opportunities for colonisation and naturalisation due to the loss of resident individuals and species (Loope, *et al.* 1988; Hobbs 1989; Knops, *et al.* 1995; Adair & Groves 1998; Knops, *et al.* 1999). As some other type of habitat modification often facilitates the invasion of many environmental weeds, the latter are rarely the only threat to biota and are often considered a problem when combined with habitat fragmentation and other disruptions (Leigh & Briggs 1992; Groves & Willis 1999; Gurevitch & Padilla 2004). Indeed, Samways (1994) claims (in the context of Southern Hemisphere insects) that "weeds are rarely either particularly fragmenting to populations or the cause of extinctions". This may be the case where habitat perturbations have resulted in depleted and often isolated populations in fragmented habitats that are then threatened by weed invasion. For example, populations of endangered native plant species already threatened by fragmentation in remnant habitats are in further danger of individual losses due to weed invasion (Sorensen & Jusaitis 1995; Groves & Willis 1999).

1.2.3 Impacts of environmental weed invasion

Invaders will have the largest impact when they modify ecosystems by changing the availability or quality of resources (eg. food, living space, water, heat or light), that cause direct and indirect effects for associated plants and animals (Crooks 2002). As discussed above, such species have been termed 'ecosystem engineers' as they cause physical changes to the structure and complexity of habitats (Crooks 2002). Invasive plant species can cause considerable change to habitat structure, making them one of the most common ecosystem engineers. For example, the invasion of *Mimosa pigra* in northern Australia changes the structure of the invaded habitat from grassy sedgeland to tall woody shrubland (Braithwaite, *et al.* 1989).

Ecosystems are made up of a wide range of species belonging to different trophic groups and, as such, the impact of an environmental weed on native biota in the same habitat often varies depending on the species and groups examined (Groves & Willis 1999). Successful weeds generally have detrimental effects on native plant communities. Such species reduce the number and abundance of native plants through direct competition or by changing natural disturbance regimes or ecological conditions, which results in the formation of monospecific stands, or depauperate assemblages of tolerant species (Braithwaite, *et al.* 1989; Griffin, *et al.* 1989; Clouse 1999; Blossey, *et al.* 2001; Gurevitch & Padilla 2004). Determining the specific impact of weed invasion on native fauna, and the processes behind it, can be more complex and cannot be as clearly classified as 'negative' or 'positive'. In a South African grassland, areas planted with exotic conifers resulted in an increase in grasshopper abundance and diversity, whereas exotic pine trees had an adverse effect on the same assemblage due to the different shading patterns produced (Samways & Moore 1991). In *Acacia*-invaded fynbos in South Africa, differences in abundance and composition were detected in seed-collecting ant communities, yet ant species were found to have no preference of native seeds over those of *Acacia* (French & Major 2001). In several studies, the impact of weed invasion was found have both negative and positive effects on the numbers of plants, birds, frogs, reptiles and mammals (Braithwaite, *et al.* 1989; Griffin, *et al.* 1989). Weeds that that significantly reduce native plant diveristy have been found to have little or no effect on the number of arthropod species present in an invaded habtiat (Samways, *et al.* 1996; French & Eardley 1997; Toft, *et al.* 2001; Costello, *et al.* 2003; Harris, *et al.* 2004; Standish 2004). Such studies provide good examples of the inadequacy of only using certain species, groups or trophic levels when investigating the effects of weed invasion on biodiversity (Groves & Willis 1999).

Weeds can adversely impact native fauna if invasion results in the loss of resources and/or unfavourably modifies the habitat. Alternately, weeds can prove advantageous if the invader provides new resources, such as food and habitat (Stansbury 1996; Adair & Groves 1998; Memmott & Wasner 2002). The host-range expansion of many native phytophagous insects onto introduced plants illustrates how weed invasion can be beneficial for some native fauna by providing new resources (Strong 1974; Andow & Imura 1994; Fraser & Lawton 1994; Yela & Lawton 1997). However, evidence suggests that animals which can take advantage of new resources provided by weeds are often generalist species that also use many other plants species in the habitat (eg. (Stansbury 1996; Memmott, *et al.* 2000; Memmott & Wasner 2002). Such species may also simply be 'tourist fauna' that occupy the invaded habitat as resting and hunting spaces and do not consume the weed (French & Eardley 1997). Samways (1996) suggests that the likelihood of native arthropod species becoming established in exotic vegetation patches can depend on how close the patches are to large areas of similarly structured native vegetation and how long the exotics have been established (see also Andow & Imura 1994).

The processes behind changes in species richness and abundance will vary depending on the types of species and habitats involved. However, there is evidence that invaders that increase habitat complexity or heterogeneity increase species abundance and/or richness, whereas those that simplify the habitat or reduce its complexity tend to have the reverse effect (Crooks 2002; Sax, *et al.* 2005). A positive relationship between habitat complexity and species richness and abundance is a well-documented phenomenon for arthropods with habitat structure influencing available resources such as such as food, shelter from predators, display and hunting areas, access to alternative prey and suitable microclimate (Joern 1982; Lawton 1983; Marino & Landis 1996; Sanchez & Parmenter 2002; Sax 2002; Kruess 2003; Langellotto & Denno 2004; Lassau & Hochuli 2005). The simplified habitat in willow-invaded riparian zones due to loss of a shrub layer was suggested to be a cause of lower abundance and diversity of terrestrial arthropods (Greenwood, *et al.* 2004). However, an increase in structural complexity can sometimes also negatively influence the movement, foraging efficiency and other activities of some arthropod species (eg. Coll & Bottrell 1996). Indeed, it has been suggested that one of the impacts of invasive plants with thick, impenetrable growth is to impede the flight of insects (Samways, *et al.* 1996). For example, in South Africa, savanna dung beetle diversity, density and overall biomass was lower in dense thickets of exotic mesquite (*Prosopis glandulosa*) due to the thick plant growth impeding beetle flying, searching and dung-rolling abilities (Steenkamp & Chown 1996).

Detecting the effects of weed invasion may be observed as changes in community composition before changes in the number of species can be detected, because species abundances often respond more rapidly to disturbance than do changes in species richness (Adair & Groves 1998; Chapin, *et al.* 2000). Furthermore, the dominance of an exotic plant species in habitat will not necessarily result in a reduction in the number of species present, however species composition (or the identity of the species present) will often be changed (Sax 2002; Sax, *et al.* 2005). For example, differences in community composition were detected in bird (French & Zubovic 1997) and arthropod communities (Samways, *et al.* 1996; French & Eardley 1997; Harris, *et al.* 2004; Standish 2004) between weed invaded and non-invaded habitats, whereas no significant differences in species richness were found.

1.2.4 Community-level changes

Changes to a native habitat, such as those caused by weed invasion, go beyond a direct negative or positive impact on biodiversity, for example, changing the abundance and distribution of a particular species by removing or adding habitat resources. These changes will also cause a 'ripple effect' (Miller 1993) throughout the community via indirect interactions (Figure 1.2). There is a strong indication that many effects of species alterations due to habitat modification are mediated through food webs (Winemiller & Polis 1996). The differential loss of species from trophic levels will have a large destabilising effect on food web structure and hence, associated ecological processes (Didham, *et al.* 1998). Similarly, because keystone species (Section 1.2.2) interact with a large number of other species in a community, the removal of a keystone can have significant community- and ecosystem-wide consequences (Tscharntke 1992; Fisher 1998; Komonen, *et al.* 2000). In mutualistic interactions, the loss of one partner, such as a plant or pollinator, could subsequently cause disruptions, possibly even extinctions, throughout the community (Rathcke & Jules 1993). For example, habitat fragmentation and isolation has been shown to reduce the abundance and species richness of flower-visiting bees and, in turn, decrease the seed set of associated plant species (Steffan-Dewenter & Tscharntke 1999). The disruption of insect species interactions via habitat change has also been shown to impact on seed dispersal (French & Major 2001), decomposition (French & Eardley 1997), and natural biocontrol regimes (Dubbert, *et al.* 1998). The invasion of an exotic grass was shown to change the composition of a habitat matrix by 'filling-in' inter-patch spaces (mudflat) that increased habitat patch connectivity and hence movement of both a grass-feeding insect herbivore (Hemiptera, Delphacidae) and its egg parasitoid (Hymenoptera: Mymaridae) (Cronin & Haynes 2004). The increased emigration out of host-plant patches resulted in lower densities and greater spatial dispersion of both planthopper and parasitoid. In turn, this led to significant changes in host-parasitoid associations, including a reduction in parasitism rates and population persistence in habitat patches, particularly for the mymarid, which had three times the extinction rate of the planthopper in a weed-dominated landscape (Cronin & Haynes 2004).

Experimental manipulations also provide insight into the potential direct and indirect effects of habitat change on trophic interactions and community structure. Knops, *et al.* (1999) found that experimental manipulation of the basal level of a grassland community impacted throughout the entire system, where a decrease in plant diversity resulted in reduced numbers and abundance of herbivorous insects and in turn, insect predators and parasitoids. In a study on a tri-trophic community, Gómez (1994) experimentally excluded the parasitoids of seed-predating weevils that resulted in reduced seed production of a woody shrub. The addition of a top predator (a beetle) to an understorey shrub species caused a reduction in the beetle's prey (a predatory ant), resulting in increased herbivory and reduced leaf area (Dyer & Letourneau 1999). The latter two studies are examples of trophic cascades, which are an important type of indirect effect within communities (Wootton 1994; Müller & Godfray 1999). Trophic cascades result in inverse patterns in abundance or biomass across more than one trophic link in a food web (Pace, *et al.* 1999). 'Top-down' trophic cascades occur when changes in the abundance of a top predator results in lower numbers of midlevel consumers and a higher abundance of basal producers. Alternately, 'bottom-up' cascades occur when changes in primary productivity effects associated herbivores and predators (Polis 1994). Trophic cascades in perturbed systems are a well-documented phenomenon, where the disruption itself may result in a cascade or reveal amplified natural cascades (eg. Pace, *et al.* 1999).

When the productivity of producers influences consumers (ie. when the system is under 'bottom-up' control), ecological theory predicts that changes to the base of an ecosystem can impact on the entire system (Polis 1994; Siemann 1998; Knops, *et al.* 1999). As such, it has been suggested that the adverse impacts of an invasive weed on the bottom of a food web (ie. the plan community) may be of particular significance due to such 'bottom-up' effects through the food web (Groves & Willis 1999). Changes in species diversity and the physical structure of a habitat due to weed invasion has also been shown to disrupt ecosystem functioning by altering processes such as primary production, hydrology, nutrient cycling, soil development and disturbance regimes (Vitousek 1986; D'Antonio & Vitousek 1992; Stock, *et al.* 1995; Mack & D'Antonio 1998). Extensive research on the impacts of the exotic purple loosestrife (*Lythrum salicaria*) in North American wetlands illustrates some of the complex direct and indirect effects weed invasion can have on native biota and ecosystem processes and functioning. In invaded wetlands, purple loosestrife directly competes with native species by producing more seeds with higher germination and growth rates. This decreases wetland plant diversity and, in turn, reduces bird habitat and alters decomposition rates and nutrient cycling (Blossey, *et al.* 2001). Purple loosestrife also modifies the interaction between a related native species and its insect pollinators by competing for pollination services. Pollinator visitation to natives is reduced and, due to pollen transfer between species, pollen quantity and quality is also reduced, resulting in decreased seed production (Brown & Mitchell 2001). Thus, by competing with native plants (eg. Groves & Willis 1999; Blossey, *et al.* 2001), changing habitat composition and structure (eg. Braithwaite, *et al.* 1989; Greenwood, *et al.* 2004), and providing new resources (eg. Stansbury 1996; Memmott & Wasner 2002), the presence of a successful weed in a native habitat can be predicted to cause significant and complex changes to native biodiversity and associated species interactions across multiple trophic levels. These changes can then impact on ecological processes and ecosystem functioning.

1.3 Thesis outline

There is very little known about the effects of many of Australia's most serious environmental weeds with calls for research into their impacts on biodiversity, community structure and ecosystem processes (Adair & Groves 1998). This thesis reports research that investigated the impacts of environmental weed invasion on native plant and arthropod diversity in remnant *Eucalyptus* woodland invaded by one of Australia's most serious environmental weeds, bridal creeper (*Asparagus asparagoides* (L) Druce (Asparagaceae)). Bridal creeper is a climbing geophyte that can smother large areas of ground with dense, twinning foliage. As such, the weed was predicted to be modifying the ground-cover habitat and associated native biota via both direct and indirect interactions among species. As highlighted throughout this chapter, biodiversity cannot simply be reduced to a single number, such as species richness. Biodiversity also has a functional component that is largely determined by interactions among species. Accordingly, this research aimed to determine the effects of weed invasion on the abundance, distribution and functioning of native biodiversity by investigating the impact of bridal creeper on the abundance and diversity of native plants and associated arthropod communities and the functional interactions among parasitic Hymenoptera and their hosts, and a flowering plant and its insect pollinator.

The results are reported in four chapters:

(i) Chapter 2 describes the impact of bridal creeper on the native ground-cover plant community and associated habitat structure. This chapter also introduces the woodland study system and provides the background for the research reported in subsequent chapters.

(ii) Chapter 3 reports the effect of bridal creeper on arthropod communities associated with the ground-cover vegetation, and in particular parasitic wasps, whose abundance and species-richness were placed in an ecological context by examining host niche associations.

(iii) Chapter 4 examines the effects of habitat changes caused by the invasion of bridal creeper on the reproduction and development of the arthropod community. The emergence of parasitic wasps and their hosts from ground-cover vegetation, litter and soil habitats were recorded and used to examine parasitoid and host developmental habitat associations.

(iv) Chapter 5 considers the effect of bridal creeper on another important species-level interaction and ecological process, insect pollination. The pollination success of an endangered orchid species was investigated in habitat invaded and free of bridal creeper. This chapter also reports the identification of a possible pollinator and its distribution and abundance associated with the presence of bridal creeper in the habitat.

Chapter 6 provides a summary and general discussion of this research, particularly in the context of the more general assumptions about habitat modification, including that caused by weed invasion. As the invasion of an exotic species represents an opportunity to gain insights into the invaded ecosystem (Crooks 2002), this chapter also discusses the structure, functioning and complexity of the studied woodland habitat. The value of using such multiple species assemblages, and in particular parasitic wasps, for the investigation of habitat modification is also considered. Lastly, using the current study as a baseline for further work, the final chapter of this thesis also highlights further research that could be undertaken.

Chapter 2

The impact of bridal creeper on native habitat

2.1 Introduction

Exotic plants that invade and naturalise in native habitats are considered to be one of the greatest threats to natural ecosystems worldwide (Vitousek, *et al.*; Groves & Willis 1999; Dukes & Mooney 2003). Much of this concern is due to widespread evidence that invasive plant species generally have a detrimental impact on native plant communities. Through direct competition with native plant species or by changing ecological conditions to the detriment of natives, weeds can reduce the number of endemic plant species in communities resulting in the formation of monospecific stands, or depauperate assemblages of tolerant species (eg. Braithwaite, *et al.* 1989; Griffin, *et al.* 1989; Clouse 1999; Blossey, *et al.* 2001).

Asparagus asparagoides (L) Druce (Asparagaceae) was introduced into Australia from South Africa in the late 19th Century as an ornamental garden plant. The species is commonly known as bridal creeper due to the once popular use of its foliage for floral arrangements, particularly bridal bouquets. Now considered a 'Weed of National Significance', bridal creeper has naturalised in a range of soil and habitat types including wet and dry sclerophyll forests, mallee shrubland, creek and river banks and coastal vegetation across south-western Western Australia, South Australia, Victoria and coastal NSW (Groves & Willis 1999; Agriculture & Resource Management Council of Australia & New Zealand 2001). The species is a creeping geophyte with an extensive root system of tuber-bearing rhizomes that has the potential to cover large areas of ground with dense foliage, also often growing up shrubs and tree trunks (Figure 2.1a). The network of rhizomatous roots form a dense mat up to 10cm deep in the soil (Raymond 1999). Small, white flowers open in late winter to early spring (Figure 2.1b), followed by fleshy red berries (Figure 2.1c,d). Both native and exotic frugivorous birds consume the fruit, and can disperse seeds over considerable distances. This mode of dispersal leads to the invasion of undisturbed habitats where, unlike the majority of environmental weeds (Chapter 1: Section 2.2.2), it will successfully germinate without any type of soil disturbance (Stansbury 1996; Raymond 1999). The bird-dispersal of seeds also results in a characteristic invasion pattern where bridal creeper growth is often most noticeable and extensive under tree canopies used by birds (Stansbury 1996).

Figure 2.1 Bridal creeper (*Asparagus asparagoides*): **(a)** growth; **(b)** flowering shoots (image: (Agriculture & Resource Management Council of Australia & New Zealand 2001); **(c)** green fruit; **(d)** red fruit; **(e)** senescing; and **(f)** re-shooting.

In South Australia, and other regions with a winter rainfall pattern, the above-ground biomass senesces in early summer (Figure 2.1e) leaving the root system which shoots again in autumn (Figure 2.1f). Seeds also germinate over autumn and winter and plants take at least three years to flower (Raymond 1999; Agriculture & Resource Management Council of Australia & New Zealand 2001). Current management of bridal creeper is via manual removal, herbicide use (glyphosate and metasulfuron-methyl), and three biological control agents: a rust fungus (*Puccinia myrsiphylli*) and two foliage-feeding insects, a leafhopper, *Zygina* sp. (Hemiptera: Cicadellidae) and a leaf beetle, *Crioceris* sp. (Coeloptera: Chrysomelidae) (Agriculture & Resource Management Council of Australia & New Zealand 2001; CSIRO 2003).

There is very little known about the effects of many of Australia's most serious environmental weeds with calls for research into their impacts on biodiversity, community structure and ecosystem processes (Adair & Groves 1998). Raymond's (1999) comprehensive ecological study of bridal creeper led her to conclude that eradicating the weed from Australia would be a difficult, if not impossible task. As such, a thorough understanding of its possible impacts is clearly needed. As it can smother large areas, bridal creeper was predicted to be modifying the ground-cover habitat, thus effecting associated native biota. Indeed, bridal creeper is considered a threat to a range of native herbs, lilies and orchids across southern Australia (Sorensen & Jusaitis 1995; Groves & Willis 1999; Agriculture & Resource Management Council of Australia & New Zealand 2001; Bickerton 2001). Therefore, this study aimed to determine the impact of bridal creeper on the native plant community and associated habitat variables, in *Eucalyptus* woodland typical of the type of native habitat invaded by the weed in southern Australia. This chapter also introduces the woodland study system and provides the background for the research reported in subsequent chapters.

2.2 Methods

2.2.1 Study site

The site for this research was Mount Billy Conservation Park (CP) (35°25'72"S 138°35'82"E) on the Fleurieu Peninsula, South Australia (Figure 2.2a). The park is 208ha, with an elevation ranging from 100-216m. The region surrounding the park is cleared grazing land, except for the southern end that adjoins an uncleared area surrounding the Hindmarsh Valley Reservoir. Mean maximum summer temperatures range from 24-27°C and mean maximum winter temperatures from 13-15°C (Figure 2.3). The area has a strong winter rainfall pattern (Figure 2.3) with a mean annual rainfall of 766 mm (Bureau of Meteorology, Melbourne).

Mt Billy CP contains both mallee, woodland and forest habitats and, due to its history as a fenced-off catchment for a drinking-water reservoir, has remained in a relatively natural state with minimum disruption. Over 430 native plant species have been recorded in the park, with a particularly high diversity of ground-cover herbs, ferns, lilies and orchids (R. Taylor, 'Friends of Mt Billy CP' pers. comm. 2000). The habitat within Mt Billy CP used for this study was medium-height eucalypt woodland with a moderately open canopy of *Eucalyptus leucoxylon* (South Australian blue gum) and *E. fasciculosa* (pink gum), a sparse mid-story of *Acacia pycnantha* (golden wattle), *Dodonaea viscosa* (sticky hop-bush), and *Xanthorrhoea semiplana* (flat-leafed grass-tree), and a diverse, low ground-cover of native herbs and grasses (Figure 2.2b). Bridal creeper was by far the dominant weed, and undoubtedly the most serious issue for management and conservation, in this area of the park.

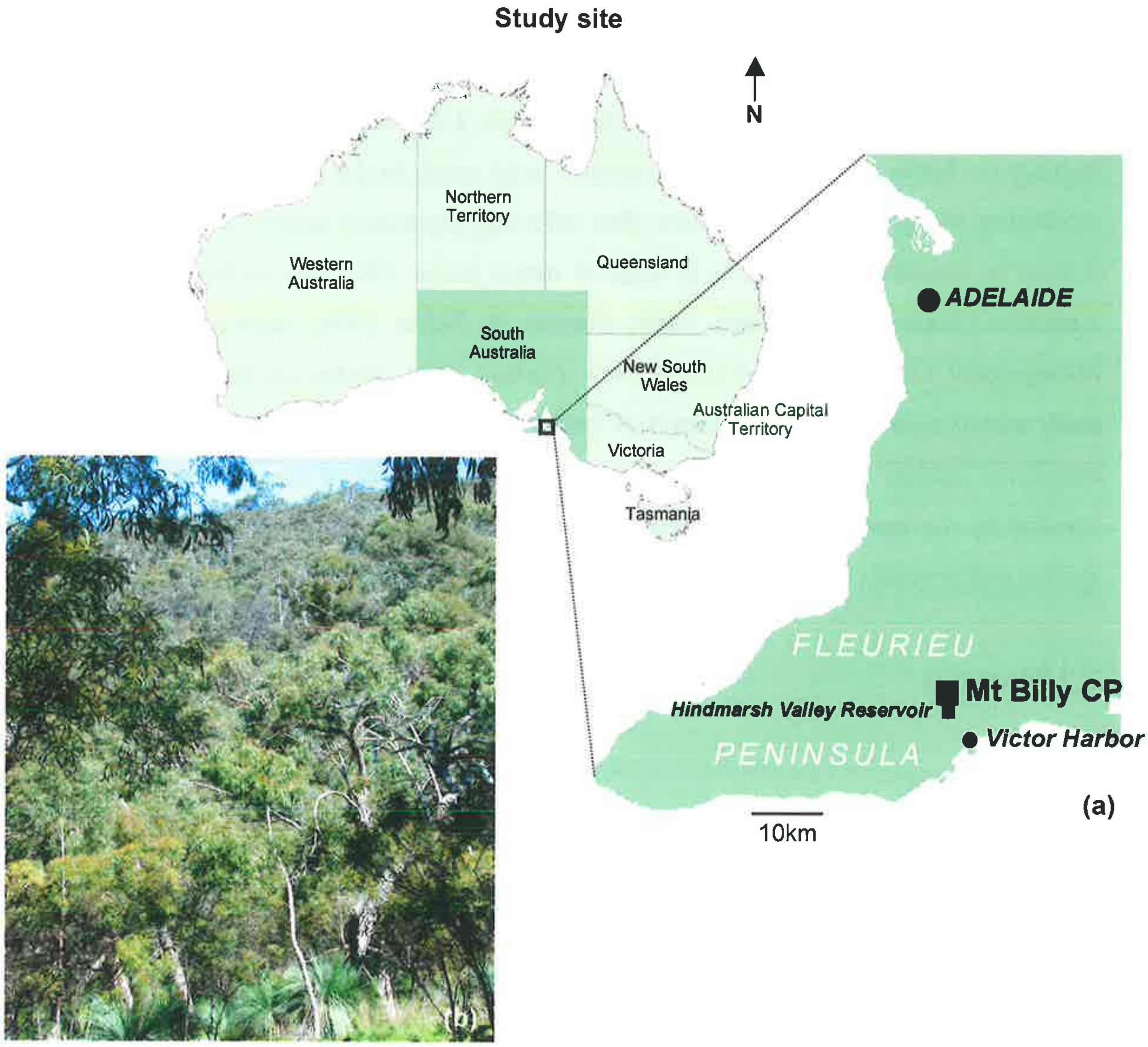


Figure 2.2 (a) Location map of the study site, Mount Billy Conservation Park (CP), on the Fleurieu Peninsula, South Australia (SA); and **(b)** study habitat, *Eucalyptus leucoxylon* and *E. fasciculosa* woodland at Mt Billy CP.

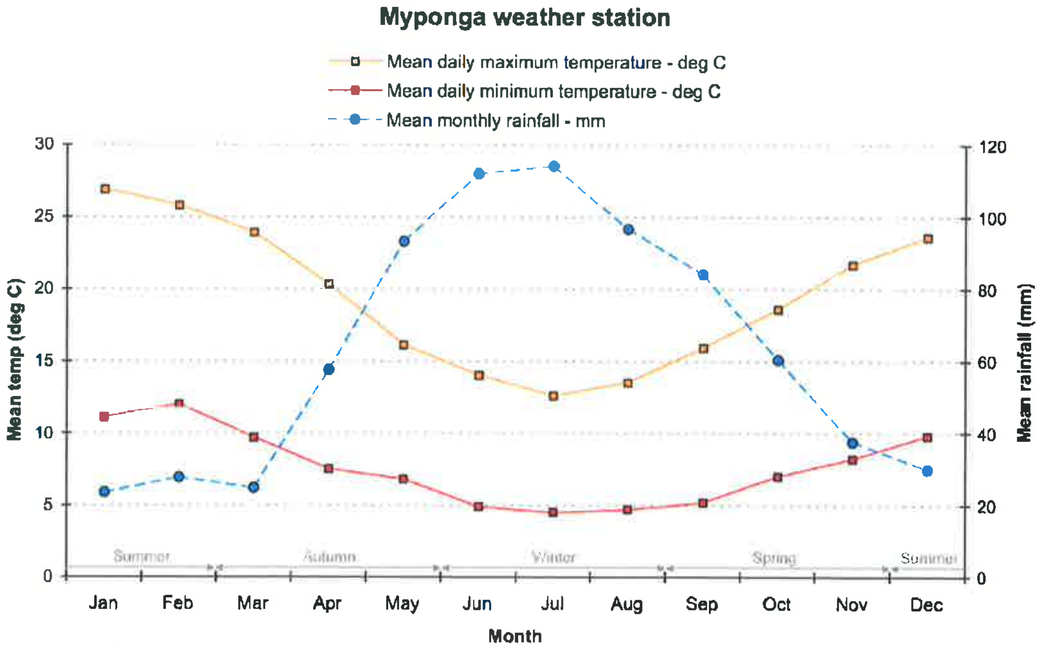


Figure 2.3 Mean (1914 - 2001) daily maximum and minimum temperatures, and mean monthly rainfall recorded from the Myponga weather station, Fleurieu Peninsula, SA (Bureau of Meteorology, Melbourne), 20km NE of the study site, Mt Billy CP.

2.2.2 Vegetation and habitat survey

As bridal creeper invades and covers the ground-cover habitat, the scope of this project was narrowed to focus on the ground-cover plant and associated arthropod communities. Thus, a survey of the ground-cover vegetation was undertaken at Mt Billy CP to determine the impact of bridal creeper on the native ground-cover community.

Adair & Groves (1998) outline four principal techniques to determine the impact of weed invasion on native biodiversity: (1) multi-site comparisons (a non-manipulative survey technique); (2) weed removal; (3) weed addition; and (4) time-sequence studies. They suggest that the multi-site comparison method, where species diversity is measured, is the most suitable for investigations into the effect of environmental weeds on faunal communities. In addition, manipulative studies such as weed removal or addition and time-sequence studies require long-term investigations to determine the effects of weed invasion (Adair & Groves 1998). As this study was relatively time-limited and the major focus were arthropod communities, the multi-site comparison technique was used throughout the research reported in this thesis. A manipulative method (weed removal or addition) may often be preferable, particularly to determine the underlying processes of observed effects of weed invasion. However, it was necessary to initially describe the effects of bridal creeper on plant and arthropod communities, particularly as nothing was known of its specific impacts on native flora and fauna. This was considered important, as without the observation and description of ecological patterns there is no basis for proposing explanatory models about processes to be tested via manipulations (Underwood, *et al.* 2000).

Eight pairs of native and bridal creeper-invaded transects (15m x 1m) were established in two locations in *E. leucoxylon* and *E. fasciculosa* woodland at Mt Billy CP (Figure 2.4). An underlying assumption when using a multi-site comparison technique is that the species composition of invaded areas is the same or similar to control areas prior to invasion. Thus, as pre-invasion states cannot be determined, care needs to be taken to match control and weed-invaded habitats (Adair & Groves 1998). As highlighted in Section 2.1, in contrast to many invasive plant species, bridal creeper can establish without prior habitat disturbance. As such, areas could be chosen at Mt Billy CP with the same history and no prior soil or fire disturbance in both invaded and native habitat. Transect locations in both native and invaded habitats were primarily selected based on the presence or absence of bridal creeper. However, effort was made to control for natural between-site microhabitat variability by locating transects in the same habitat type (open spaces among eucalypt trees), and away from the edge of native and invaded patches to limit the effect of changes in microhabitat and community structure that can occur at the edge of a habitat (Schowalter 2000). In addition, transect pairs were placed parallel along the hill to account for the sloping habitat and were established similar distances away from the base of large eucalypt trees that seasonally shed large amounts of bark that covered the ground-cover vegetation. The area beneath these trees also would have been the invasion points of the weed (Section 2.1) and may have originally had different microhabitats prior to invasion. Tree canopy cover was similar above each transect (around 70%) and each bridal creeper invaded transect was located within 10m of a native (control) transect.

Figure 2.4 Examples of native (control) and bridal creeper invaded habitat where transects were established and used for vegetation surveys and arthropod sweep-netting (Chapter 3). Native habitat in **(a)** July 2001 and **(b)** February 2002 and invaded habitat in **(c)** July 2001 and **(d)** February 2002.

Transects in native habitat were installed in areas with little or no bridal creeper (Figure 2.4a). Conversely weed-invaded transects were located in areas with high levels of bridal creeper cover (Figure 2.4c). Within each transect, using 24 randomly placed 10 x 10cm quadrats, the following measurements were recorded: percent cover of bridal creeper, leaf litter, moss (bryophytes), and bare ground (measured independently, thus do not total to 100%), and the identity of each plant species (recorded as presence/absence). As bridal creeper and native plants senesce over summer (Figure 2.4b,d), the plant survey was undertaken in spring (September 2000). This was when bridal creeper was at its maximum growth and coincided with the maximum growth and presence of flowers and seed heads of native species that allowed for their identification.

These transects were also used for sweep netting plant-associated arthropods over 14 months (April 2001 to May 2002) (Chapter 3). In addition to sampling arthropods over this time, the percent cover of bridal creeper and leaf litter was also recorded in 24 random quadrats (10cm x 10cm). An indication of vertical habitat structure was also recorded by measuring the maximum height of the vegetation (or litter or bare ground) at 60 random points within each transect.

2.2.3 Data analysis

The data was analysed using the number of species (counts) and species frequency, ie. the number of times a plant species was recorded in a transect divided by the number of quadrats used per transect. Bridal creeper was included in the analysis only as an explanatory variable, not as a plant species. As native and bridal creeper transects were paired, the differences in plant species richness and frequency and the percent cover of bridal creeper, litter, moss and bare ground between native and invaded transects were analysed using paired t-tests using GraphPad Prism (ver. 4.0 for Macintosh, GraphPad Software, San Diego California USA). The percent cover of bridal creeper, vegetation height and litter cover in invaded and non-invaded transects over time were compared using repeat measures analysis of variance (ANOVA) using GraphPad Prism with Bonferroni post-tests to determine which sample dates differed for invaded and non-invaded transects. The relationship between the level of bridal creeper invasion (percent cover) and plant species richness was examined using linear regression in GraphPad Prism.

Non-metric multi-dimensional scaling (NMDS) using PC-ORD (ver. 4.25) was used to examine plant community composition and habitat variables. Non-metric multi-dimensional scaling is generally considered to be the most effective ordination method for community data (McCune & Grace 2002). The NMDS was run using the Sørensen distance measure and the 'Auto-pilot: slow and through' option in PC-ORD and significant habitat variables were overlaid as correlation vectors to further investigate the arrangement of transects in the ordination. Native and exotic species in invaded and non-invaded transects were also examined by comparison of their ranked mean frequencies. Indicator species analysis (Dufrêne & Legendre 1997) was used to detect plant species that were indicators of native and invaded habitat using PC-ORD. This method combines information on the concentration of species abundance in a particular group or, in this case, habitat, and the faithfulness of occurrence of a species in a particular habitat. It produces an indicator value for each species in each habitat that range from zero (no indication) to 100 (perfect indication). Perfect indication means that presence of a species points to a particular habitat without error, thus the species is always present in that habitat and is exclusive to it. Indicator values were tested for statistical significance ($P<0.05$) using Monte Carlo random permutations.

2.3 Results

2.3.1 Plant species richness

A total of 73 ground-cover plant species from 29 families were recorded (excluding bridal creeper) (Appendix A). Of these, 47 species were native and 26 were exotic annual pasture grasses and weedy herbs, presumably from surrounding farmland. Many individuals of Poaceae (grass) could not be identified in the field during the survey due to lack of seed heads, thus were recorded as 'Poaceae sp.'. When separating plant species into native and exotic species for analysis, 'Poaceae sp.' were grouped with the native species, however it is likely that some were exotic.

Comparison of invaded and non-invaded habitats within Mt Billy CP found that areas invaded by bridal creeper had significantly lower plant species richness ($t=4.708$, $P=0.0022$) (Figure 2.5a) and species frequency ($t=5.618$, $P=0.0008$) (Figure 2.5b) than non-invaded habitat. When native and exotic species were examined separately, only the number ($t=5.267$, $P=0.0012$) (Figure 2.5a) and frequency ($t=7.664$ $P=0.0001$) (Figure 2.5b) of native species were significantly different. The number of exotic plant species recorded were not significantly different between invaded and non-invaded transects ($t=2.103$, $P=0.0736$) (Figure 2.5a), nor was species frequency ($t=0.7719$, $P=0.4654$) (Figure 2.5b).

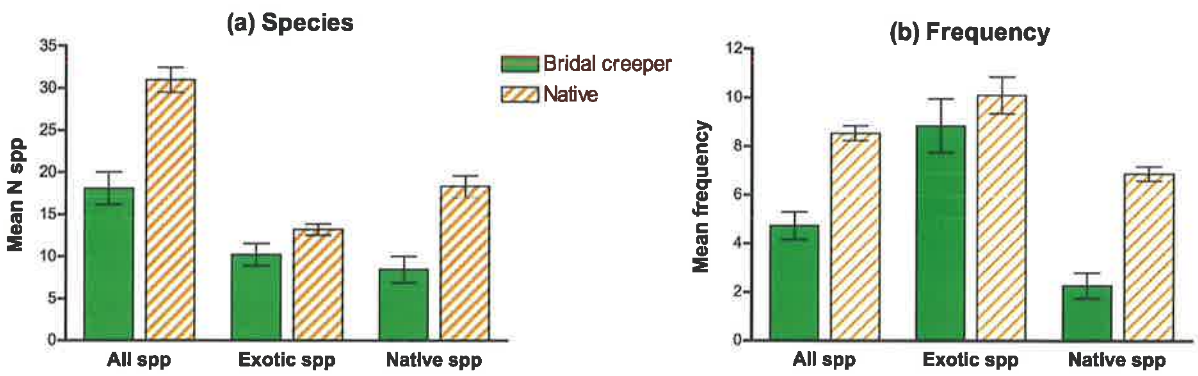


Figure 2.5 Mean (±SE) **(a)** number and **(b)** frequency of all, native, and exotic ground-cover plant species recorded from bridal creeper (n=8) and native (n=8) transects.

A strong negative relationship was found between the percent cover of bridal creeper and the total number of plant species (r^2=0.9037, P<0.0001), the number of native (r^2=0.8120, P<0.0001), and number of exotic species (r^2=0.9005, P<0.0001) (Figure 2.6).

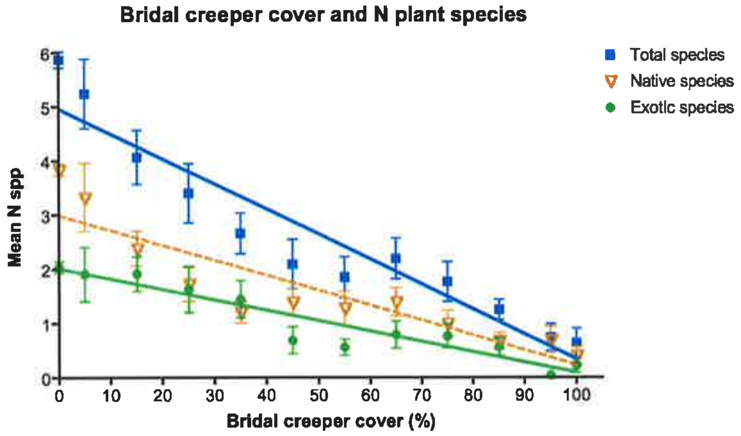


Figure 2.6 Relationship between the percent cover of bridal creeper and mean (±SE) number of ■ total (r^2=0.9037, P<0.0001), ▽ native (r^2=0.8120, P<0.0001), and ● exotic (r^2=0.9005, P<0.0001) plant species (n=384 quadrats).

2.3.2 Community composition

An ordination of transects showed that bridal creeper and native transects clearly separated based on plant frequency and species composition, particularly along Axis 1 where the bridal creeper transects cluster on the right with the native transects to the left (Figure 2.7).

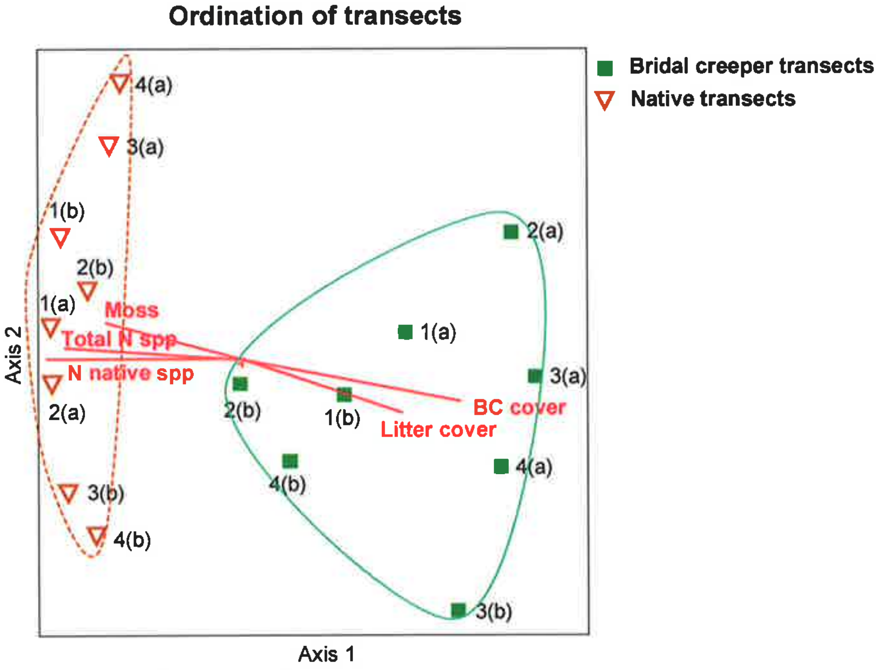
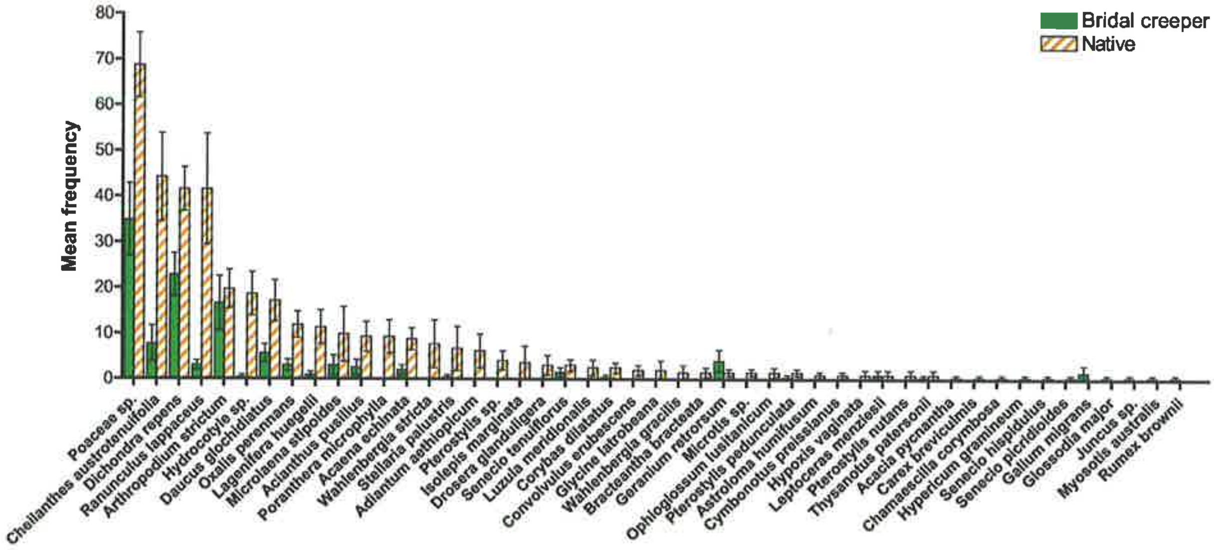


Figure 2.7 Two-dimensional ordination (NMDS) of plant frequency and species composition. The numbers next to each transect correspond to transect pairs and letters in brackets correspond to sites (a and b). The model explains 87.8% of the total variation (Axis 1= 85.1, Axis 2=2.7%) and the superimposed vectors (constrained to r^2=0.5) show the correlation between plant species and environmental variables. Vectors are the percent cover of moss, bridal creeper and litter, the total number of plant species and total number of native species. The length of each vector indicates the strength of the correlation and the orientation the direction of increase. Distance measure: Sørensen; final stress for the 2-dimensional solution=6.82649; final instability=0.00001; number of iterations=56.

This separation can be explained by an overlay of environmental variables showing that the percent cover of moss, the total number of plant species and the number of native plant species correlated with the plant community recorded from transects in native habitat, whereas increasing litter cover and percent cover of bridal creeper correlated with transects in invaded habitat (Figure 2.7).

The ranked frequency of native plant species (Figure 2.8a) revealed that most species found in invaded transects were also those more frequently recorded in native transects. Thus, the assemblage of native plants remaining in habitat invaded by bridal creeper is a subset of the ground-cover plant community. However, most exotic plant species (Figure 2.8b) are found in both native and invaded transects.

(a) Native species



(b) Exotic species

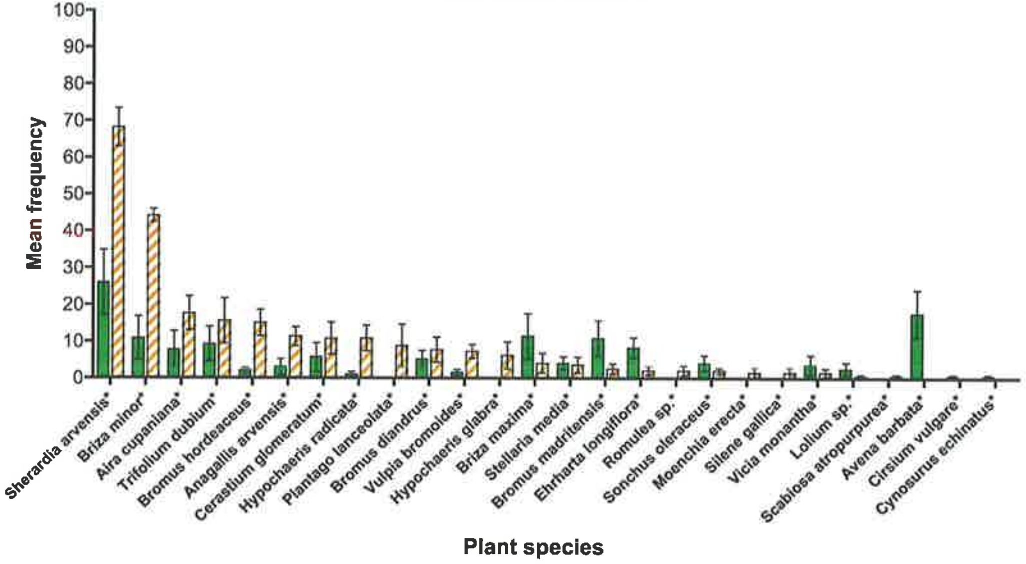


Figure 2.8 Mean (±SE) frequency of **(a)** native plant species and **(b)** exotic plant species (*) from bridal creeper and native transects. For comparison, plant species have been ranked by descending frequencies in native transects.

Not unexpectedly, bridal creeper was a significant indicator species of invaded habitat (Table 2.1). The only other indicator species for invaded habitat was an exotic grass species, *Avena barbata*, that was only recorded from invaded transects. However, there were 16 significant native and exotic indicator species for native habitat (Table 2.1). Some more abundant native species (Figure 2.8a) were significant indicators of native habitat: *Cheilanthes austrotenuifolia, Dichondra repens, Daucus glochidiatus Hydrocotyle* sp., *Lagenifera huegelii, Oxalis perennans*, and *Ranunculus lappaceus* (Table 2.1). Two less abundant native species, *Acaena echinata, Poranthera microphylla* also have relatively high indicator values for native habitat.

Table 2.1 Significant indicator plant species for native and bridal creeper invaded habitat and Monte Carlo significance of observed maximum indicator values for each species (1000 permutations). * exotic species. Frequency: species frequency from the indicated habitat.

Species	Habitat	Frequency (%)	Observed indicator value	P value
Acaena echinata	Native	8.85	70.8	0.0210
*Anagallis arvensis**	Native	11.46	68.7	0.0270
*Asparagus asparagoides**	Bridal creeper	97.40	91.2	0.0010
*Avena barbata**	Bridal creeper	17.71	87.5	0.0020
*Briza minor**	Native	44.27	80.2	0.0010
*Bromus hordeaceus**	Native	15.10	65.9	0.0520
Cheilanthes austrotenuifolia	Native	44.27	85.0	0.0050
Daucus glochidiatus	Native	17.19	65.6	0.0690
Dichondra repens	Native	41.67	64.5	0.0210
Hydrocotyle sp.	Native	18.75	85.1	0.0070
*Hypochaeris radicata**	Native	10.94	68.5	0.0240
Lagenifera huegelii	Native	11.46	68.7	0.0220
Oxalis perennans	Native	12.00	69.4	0.0310
Poaceae sp.	Native	68.75	66.3	0.0070
Poranthera microphylla	Native	9.38	75.0	0.0060
Ranunculus lappaceus	Native	41.67	81.4	0.0140
*Sherardia arvensis**	Native	68.23	72.4	0.0040
*Vulpia bromoides**	Native	7.30	72.1	0.0170

2.3.3 Bridal creeper and habitat variables

The percent cover of bridal creeper recorded from native transects ranged from 0-10 (mean 0.86%) and from invaded transects 0-100 (mean 58.69%) (t=18.41, P<0.0001). There was no difference in the small precent of bare ground (t=1.122, P=0.2987), however there was a higher percent cover of leaf litter recorded from bridal creeper transects (t=5.529, P=0.0009), and greater cover of moss in native transects (t=4.825, P=0.0019) (Figure 2.9).

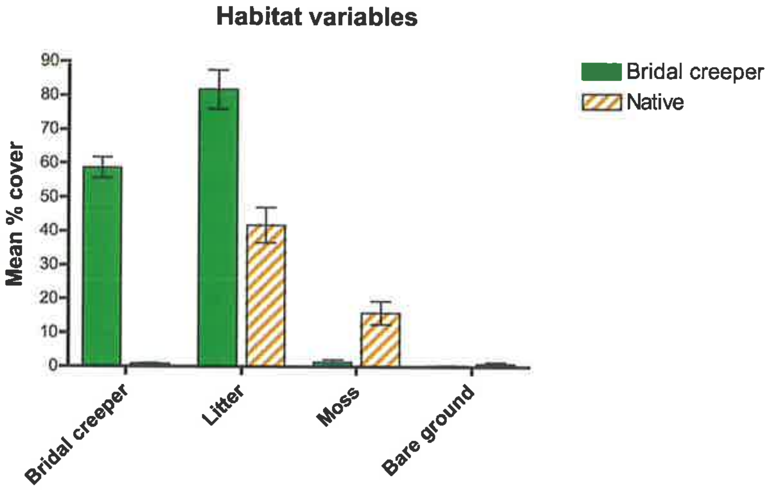


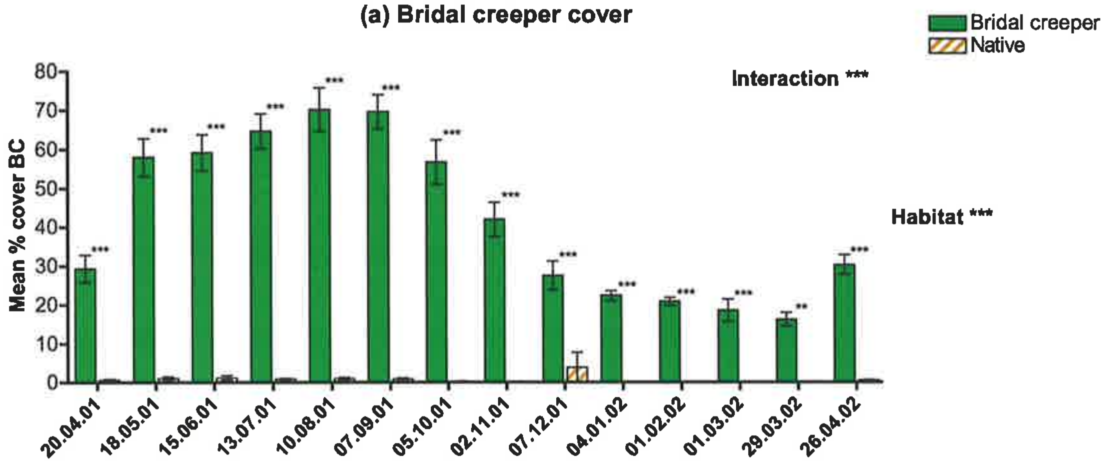
Figure 2.9 Mean (±SE) percent cover of bridal creeper, litter, moss, and bare ground from bridal creeper (n=8) and native (n=8) transects.

As previously reported from other Mediterranean climates in Australia (Raymond 1999; Agriculture & Resource Management Council of Australia & New Zealand 2001), the presence of bridal creeper's above-ground biomass was strongly influenced by sample date ($F_{1,98}$=1524.61, P<0.0001). The percent cover of bridal creeper peaks in the winter and spring months, decreases significantly over summer as the weed senesces, and rapidly increases again in autumn as it re-shoots (Figure 2.10a). There was a significant interaction effect between sample date and habitat ($F_{13,98}$=26.30, P<0.0001), indicating there were differences in the amount of bridal creeper between native and invaded transects over time. However, this was due to the large differences in the amount of bridal creeper cover in invaded transects between winter/spring and summer/autumn. Reflecting the choice of transect locations, bridal creeper cover was consistently greater in invaded transects ($F_{13,98}$=1.09, P=0.3341) (Figure 2.10a).

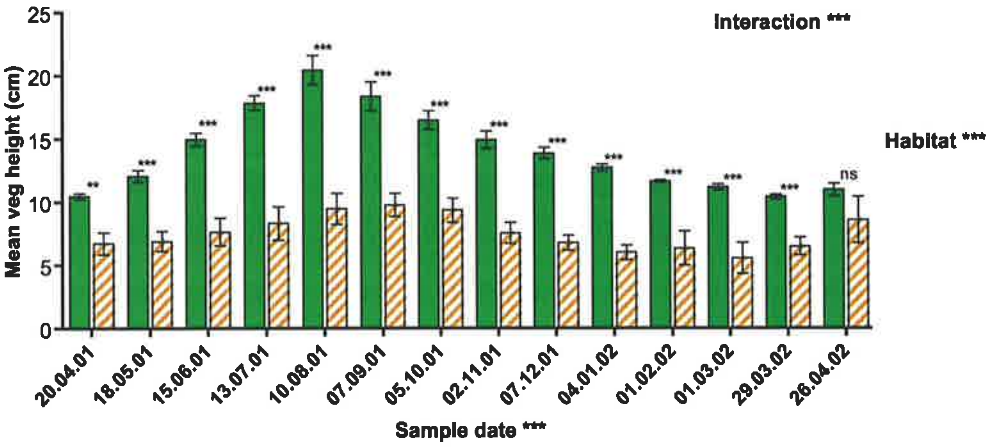
Vegetation height was significantly affected by sample date ($F_{1,98}$=692.30, P<0.0001) and habitat ($F_{13,98}$=8.75, P<0.0001), with taller vegetation in bridal creeper invaded transects. The maximum height of bridal creeper peaks over the same period as its percent cover. The vegetation in non-invaded areas also follows a similar pattern, although the difference between seasons is not as great (Figure 2.10b). There were significant interaction effects between habitat and time for vegetation height ($F_{13,98}$=26.41, P<0.0001), and post-tests show that there were significant differences in mean height for all sample dates, except for the last sample in April 2002 (Figure 2.10b).

Both sample date ($F_{1,98}$=306.35, P<0.0001) and habitat ($F_{13,98}$=5.44, P<0.0001) significantly influenced the amount of leaf litter recorded. There was also a significant interaction between sample date and habitat ($F_{13,98}$=2.30, P=0.0104). Post-tests revealed that during autumn and early winter, when there is the greatest litter cover in both habitats, there was no difference in leaf litter between invaded and non-invaded habitat. As the season progressed however, there was a decline in litter cover in native transects while remaining fairly constant in invaded transects, resulting in significant differences in cover between bridal creeper and native habitats (Figure 2.10c).

(a) Bridal creeper cover



(b) Vegetation height



(c) Leaf litter

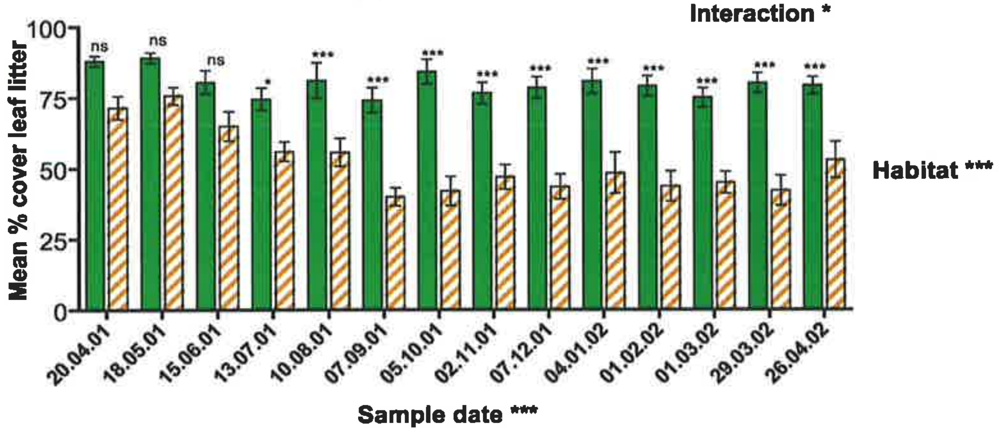


Figure 2.10 Mean (±SE) **(a)** percent cover of bridal creeper, **(b)** maximum vegetation height, and **(c)** percent cover of leaf litter over time from bridal creeper (n=8) and native (n=8) transects. ns: not significant, * P< 0.05, ** P< 0.01, ***P< 0.001

2.4 Discussion

2.4.1 Bridal creeper and native plant species

The results of this survey confirmed that the invasion of bridal creeper has a negative effect on native plant species by reducing both species richness and abundance (frequency) (Figure 2.5). There were still a number of native plant species growing in bridal creeper-invaded areas, however, in general their frequency was lower than in non-invaded native habitat. Those species remaining in invaded areas were the most abundant species from the control transects (Figure 2.8a), suggesting that rare species, with naturally low frequencies, were the first to be displaced by bridal creeper. This may have an impact on future invasions, or has possibly even facilitated the spread of bridal creeper, as it has been shown that a reduction in plant species richness at a local scale via the loss of rare species can increase the invasibility of a system (Lyons & Schwarta 2001).

There was also a negative relationship between increasing bridal creeper cover and decreasing number of native ground-cover species such that when bridal creeper cover was 90-100%, no other native ground-cover species were recorded (Figure 2.6). Herbaceous species richness and native tree seedling density were also negatively correlated with increasing cover of the introduced shrub *Mimosa pigra* in northern Australia (Braithwaite, *et al.* 1989). This response to weed invasion has been described by Adair & Groves (1998) ('Type II model'), where some measure of weed infestation (eg. percent cover of bridal creeper) increases uniformly in relation to a decrease in some biodiversity value (eg. native plant species richness). This model predicts that any level of weed reduction will result in an increase in biodiversity values. Thus, it may be predicted that a decrease in bridal creeper below 90-100% cover will lead to an increase in the number of native plant species present in the study area (Figure 2.6). Alternately, intervention such as herbicide use or biological control agents that prevent high levels of bridal creeper, will maintain higher numbers of plant species. The abundance of the native habitat indicator species, which also had lower frequencies in invaded areas (Figure 2.8a), could be used as indicators of habitat integrity if bridal creeper invasion is restricted, or habitat recovery as weed levels are reduced.

In Australia, bridal creeper is considered a threat to several endangered native plant species (Sorensen & Jusaitis 1995; Adair & Groves 1998; Groves & Willis 1999; Bickerton 2001), although the processes behind this are often not documented. Raymond (1999) summarises the key factors that make this species such a formidable and successful weed and highlights the possible competitive advantages bridal creeper has over native plant species. Bridal creeper's stem density can reach up to >90 stems/m^2 (around 80% cover), shading the soil and ground-cover habitat and reducing the amount of light reaching the soil by up to 94% (Raymond 1999). Increased light levels have been shown to increase under-story forb abundance and species richness (Carson & Root 2000). Thus, the shading effect of bridal creeper is a possible reason for its negative impact on native species. Although not directly measured at Mt Billy CP, bridal creeper's above-ground biomass was likely to be greater than that of native species as vegetation height was constantly greater in bridal creeper transects (Figure 2.10a). Furthermore, the greater percent cover of moss in native areas (Figure 2.9) indicates a more open habitat with less vegetation cover. This suggests that bridal creeper probably has increased resource use (such as water, light and nutrients) in invaded areas.

The majority of bridal creeper's biomass (over 80%) is in the root tubers which are huge storage reserves that allow it to stay dormant during hot dry conditions, shooting again when temperatures drop and moisture levels rise. Up to 6000 individual tubers per square metre (an average of over 800g dry mass/m^2), with an above ground biomass averaging between 70-80% cover, has been reported (Raymond 1999). Extrapolating to the current study, where the mean percent cover of bridal creeper was around 60% (Figure 2.9) and reached 100%, the below ground biomass is likely to be reaching similar levels at Mt Billy CP. This extensive root system is likely to reduce space for native seedling establishment and nutrient availability (Raymond 1999). Bridal creeper is considered to be the main weed threat to the shrub *Pimelea spicata* in remnant populations in eastern NSW where Groves & Willis (1999) suggest that bridal creeper's roots may be potentially competing for nutrients, water and 'space' below ground. It may be that continuous competition with bridal creeper's massive root system has more of an impact on native plants than the more ephemeral shading effect of its aboveground foliage (Groves & Willis 1999). Phenological and morphological similarities between bridal creeper and the endangered greenhood orchid *Pterostylis arenicola* in South Australia are considered to be the likely cause for the negative relationship between bridal creeper cover and orchid numbers, as both the orchid and weed grow from underground tubers over autumn and winter, and both fruit and senesce during spring and summer (Sorensen & Jusaitis 1995; Groves & Willis 1999). This may be an issue also at Mt Billy CP where there were many native geophytes and other annual and perennial species that senesce and shoot or re-shoot at the same time as bridal creeper (Appendix A).

Invasive plant species have also been shown to reduce fungal diversity and abundance, including mycorrhizae species (Goodwin 1992; Allen, *et al.* 1995). Thus, further investigation of the impacts of bridal creeper's underground root system is required to determine the impact on fungal communities. This has implications not only for decomposition processes, but also for the many orchid species in the habitat that have specific mycorrhizal symbiotionts (Jones 1988) (Appendix A).

The species-richness and frequency of the other exotic plants in the habitat (mostly pasture species) were not significantly reduced in bridal creeper invaded areas (Figure 2.5). It is possible that many of these species are more tolerant of bridal creeper invasion than many native species because they are also 'weedy', possessing many characteristics that have allowed them to be successful invaders. However, there was a negative relationship between bridal creeper cover and exotic plant species-richness (Figure 2.6). In addition, many of the exotic species recorded also had reduced frequencies in invaded habitat (Figure 2.8b), showing that bridal creeper has a detrimental effect on, and eventually displaces, both native and exotic species.

2.4.2 Bridal creeper invasion and leaf litter

At Mt Billy CP, the invasion of bridal creeper also modifies some of the physical characteristics of the ground level habitat, such as moss and leaf litter cover (Figure 2.9). It may be that increased litter is also contributing to the lower plant species richness (and moss cover) in invaded areas. Leaf litter generally has a negative effect on vegetation influencing factors such as germination rates, light levels and herbivory (Facelli 1994; Foster & Gross 1998), and is considered to be one of the fundamental factors controlling plant community structure (Xiong & Nilsson 1999). In particular, the higher levels of *Eucalyptus* leaf litter in bridal creeper invaded areas could be having a considerable impact on native plant species due to the leaching of allelopathic chemicals that inhibit seedling growth (May & Ash 1990; Florentine & Fox 2003).

Typically, leaf litter is not equally distributed across a habitat and litter patchiness is common in forests, woodlands and other habitats with plant canopies. Litter is frequently redistributed by wind and water, often accumulating beneath understory plants, thus having large impacts on resource distribution, plant productivity and animal activity (Boerner & Kooser 1989; Todd, *et al.* 2000; Boeken & Orenstein 2001). Dighton (2000) showed via surveys and experimentally that leaf litter accumulation was related to the density of shrub stems, ie. the more ground-cover shrubs (and hence stems), the greater amount of litter on the ground. Thus, a possible hypothesis emerging from this study is that the thick mat of bridal creeper stems and leaves are having a similar effect in invaded patches. At Mt Billy CP, leaf litter accumulation also occurred under the ground-level foliage of *X. semiplana* (grass-trees) (pers.

obser.). Further evidence for litter accumulation around bridal creeper is the temporal comparison that showed over autumn and early winter that there was little difference in leaf litter cover between habitats, but as the season progressed, litter cover in native areas was reduced while remaining constant across invaded sites (Figure 2.10c). As this coincides with bridal creeper's autumn re-growth, it may be that when wind and water redistribute leaf litter it becomes trapped by the weed's twinning stems and accumulates under the thick foliage. Another investigation of bridal creeper at Mt Billy CP also indicates greater litter accumulation in invaded habitat. Holt (2005) found that litter depth was also greater under bridal creeper due to a deeper, more broken-down, decomposed litter layer compared to that found in native areas, suggesting that bridal creeper does 'trap' and accumulate leaf litter under its thick foliage.

Determining the impacts of weed invasion by comparing locations differing in the presence or absence of weeds is often problematic because of confounding effects of other site factors (Adair & Groves 1998). Thus, an alternate hypothesis is that bridal creeper simply only grows where there is a greater cover of litter. For example, Raymond (1999) showed that litter cover enhanced the germination of bridal creeper seeds. However, this effect was complicated somewhat as sites with greater litter cover were also under tree canopies and, once established, canopy cover did not affect seedling survivorship. In addition, the invasion points of bridal creeper are typically under trees (Stansbury 1996), where more leaf litter may be expected. However, the age of invasion at Mt Billy CP (>20 years, R. Taylor 'Friends of Mt Billy CP' pers. comm. 2000) was such that the weed had spread out from the base of large trees so areas could be chosen where the canopy cover was the same above native and invaded transects. Therefore, the careful selection of sites with similar slope and canopy cover (Section 2.2.2), and the obvious 'open' type of habitat in non-invaded areas, does suggest that the extent of leaf litter was not as great prior to invasion.

If the presence of bridal creeper is resulting in greater litter accumulation in invaded areas, then the weed not only has a direct negative impact on native plant diversity, but is likely to be changing ecosystem processes such as decomposition, and nutrient and soil dynamics. Decomposition rates are influenced by litter quality and composition and site microclimate (Köchy & Wilson 1997). Invasive tamarisk trees (*Tamarix aphylla*) in northern Australia produce a densely packed litter layer with low cover compared to the loose litter with higher cover and more logs found in the native eucalypt woodland they displace (Griffin, *et al.* 1989). Because bridal creeper did not change the woodland canopy, the composition of leaf litter was the same between invaded and non-invaded habitats, consisting of *Eucalyptus* and

Acacia leaves, bark and twigs. However, there may be fine-scale changes in the litter produced by the monoculture of bridal creeper compared to that from a diverse community of native herbs and grasses. The invasive wetland species, purple loosestrife (*Lythrum salicaria*) in North America not only modifies the composition and decomposition rates of the leaf litter layer, but also changes the timing of decomposition and thus nutrient release as its leaves fall from the plant in autumn, compared to native species whose leaves decompose in late winter and spring (Blossey, *et al.* 2001). The dead plant material produced by bridal creeper and ground-cover native species would be introduced into the litter layer over similar periods as both senesce over summer. However, there is no information about the decomposition rates and nutrient content of the leaf litter produced by bridal creeper compared to that produced by the native species it replaces.

In an experimental comparison of forest and adjacent prairie habitats, litter decomposition rates were found to be the highest in un-shaded prairie suggesting that shade may limit decomposition in forests (Köchy & Wilson 1997). In contrast however, the tall, dense mats of the invasive perennial *Tradescantia fluminensis* in lowland podocarp forests in New Zealand produced a microclimate that increased litter decomposition rates and nutrient availability when compared to more the open native ground covers (Standish, *et al.* 2004). Accordingly, the significant shading effects of bridal creeper (Raymond 1999) may also be modifying the temperature and moisture of the litter microclimate and thus, decomposition rates. A more targeted study into bridal creeper growth and its effects on litter accumulation, and associated decomposition and nutrient cycles, is required. In particular, a comparison of stem density, litterfall, and litter depth, composition, and nitrogen content between native and invaded habitat would be valuable for investigating both community and ecosystem effects.

2.5 Conclusion

Invasive species that constitute a large proportion of an ecosystem's biomass at one trophic level can alter ecosystem structure and processes (Dukes & Mooney 2003). This study showed that bridal creeper is likely to be doing this. By transforming an open, species-rich ground-cover habitat into a closed, homogenous one, bridal creeper clearly has a deleterious effect on the native plant community. The invasion of bridal creeper has increased both the above- and below-ground biomass of vegetation in the ground-cover habitat, thus probably changing the use and flow of resources such as water, nutrients, and light. Undoubtedly the weed is excluding many native plant species and, in particular, could be regarded as a serious threat to the viability of some populations considering the small size and isolated nature of the conservation park. In addition to reducing native plant diversity, bridal creeper may also be changing ecosystem processes such as nutrient and soil dynamics and decomposition via litter accumulation that, in turn, may be impacting on factors such as seedling establishment and growth.

Invaders that modify ecosystems by changing the availability or quality of resources (eg. food, living space, water, heat or light) have been shown to cause cascading effects for associated plants and animals (Crooks 2002). Groves and Willis (1999) suggest that the negative impacts of an invader on the bottom of a food web may have significant consequences due to 'bottom-up' effects through the food chain. The plants within a habitat provide food, display and hunting areas, shelter from predators, and suitable microclimate for diverse range of arthropods (New 1988). Therefore, it may be predicted that the significant decrease in plant diversity and considerable habitat changes due to bridal creeper invasion found in this study will be causing comparable changes in the plant-associated arthropod community. The following chapter investigates this hypothesis.

Chapter 3

The impact of bridal creeper on arthropod and parasitic wasp communities

3.1 Introduction

Extreme diversity, abundance and ubiquity make arthropods a major contributor to the biodiversity and ecological functioning of terrestrial ecosystems. As herbivores, predators, parasitoids, decomposers, and pollinators, arthropods disperse seeds, control populations, cycle nutrients, maintain soil structure and fertility, pollinate plants, and provide a major prey source for other taxa (Seastedt & Crossley Jr. 1984; Schowalter 2000). Within a habitat, plants influence the distribution and abundance of many arthropods, providing resources such as food, shelter from predators, display and hunting areas, and suitable microclimate (New 1988). Almost every plant has its own guild of associated arthropods, mostly insects, that consume leaves, stems, roots, seeds, flowers and nectar (Miller 1993). Although monophagy and oligophagy are widespread across most orders, most herbivorous insects form complex communities where a variety of plant species are consumed (Pimm & Lawton 1980; Strong, *et al.* 1984). The food webs of plant-associated insect communities become larger and more complex when a third trophic level of associated natural enemies are included (Price, *et al.* 1980). Again, specialisation is widespread, but it is more common for a single prey or host species to be shared among more than one predator or parastioid (Askew 1980; Memmott, *et al.* 2000).

Increasing plant diversity can lead to an increase in herbivorous insects due to more available resources, more types of plants and an increase in structural complexity (Lawton 1983; Siemann 1998; Knops, *et al.* 1999). Increases in herbivore diversity can then cascade up to higher trophic levels resulting in greater diversity of predators and parasitoids (Siemann 1998). Arthropod predators and parasitoids are also strongly influenced by plant diversity that determines the number of floral food resources available (Jervis, *et al.* 1993; Tooker & Hanks 2000). They are also affected by plant structure that can influence movement and foraging efficiency and provide refuge from predation and access to alternative prey (Coll & Bottrell 1996; Langellotto & Denno 2004). Thus, from a 'trophic-level hypothesis', the simplification of a plant community is predicted to cause a decline in phytophagous insects as they are separated from their resource, and a corresponding decline of their natural enemies (Kruess & Tscharntke 2002, 2002).

Weeds can directly affect native fauna by providing new resources such as food or habitat. For example, native frugivorous birds often consume the berries produced by bridal creeper (Stansbury 1996; Raymond 1999). Many native phytophagous insects have been shown to expand their host range onto introduced plants (Strong 1974; Andow & Imura 1994; Fraser & Lawton 1994; Yela & Lawton 1997; Memmott, *et al.* 2000), and utilise pollen, nectar (Memmott & Wasner 2002) and seeds (French & Major 2001) of exotic species. Although bridal creeper's leaves, stems, pollen, fruit and seeds all potentially represent new food resources for herbivorous insects, it is unlikely these have been exploited. There were no native Asparagaceae within the study site at Mount Billy Conservation Park (CP) (Appendix A) or any native *Asparagus* in Southern Australia (Agriculture & Resource Management Council of Australia & New Zealand 2001). Therefore, it was unlikely there were any insect herbivores present at Mt Billy CP that could consume asparagus species. Although this study did not formally quantify feeding damage, there was no obvious evidence of insect herbivory on bridal creeper cladodes and exotic honeybees (*Apis mellifera*) were the only insect visitors to the open flowers in the study area (pers. obs.). An extensive invertebrate survey in Victoria also recorded very few insects feeding on bridal creeper (Raymond 1999). Honeybees were also the only insects recorded visiting bridal creeper flowers. Leaf and fruit damage by phytophagous insects was negligible with far less than 1% of the total surface of any cladodes being damaged. Only four individuals of a polyphagous weevil (*Phlyctinus callosus*) and the larvae of two unidentified Lepidoptera were recorded from foliage samples and three individuals of the polyphagous light brown apple moth (*Epiphyas postvittana*) from 500 fruit samples. Furthermore, there was no seed removal by insects such as ants (Raymond 1999).

The results from Chapter 2 showed that bridal creeper has a significantly detrimental effect on the species-richness and frequency of native ground-cover plant species. Ecological theory predicts that changes caused by loss of biodiversity at the base of an ecosystem can impact on the entire system (eg. Knops, *et al.* 1999). Furthermore, it has been widely demonstrated that compositional and structural changes to a habitat can have significant effects on associated fauna (eg. Hughes, *et al.* 2000; Kruess 2003; Langellotto & Denno 2004). Considering bridal creeper was unlikely to be providing an alternate food source, and the close relationships between arthropods and plants, it was predicted that arthropods that rely on the leaves, flowers, and seeds of native species as either food and/or habitat and their associated predators and parasitoids would also be adversely affected via interactions through the food web. In addition, higher trophic levels, such as parasitic Hymenoptera, are often more responsive to environmental changes than herbivores due to their close relationships with hosts, complex life cycles and high trophic level (LaSalle 1993; Polis, *et al.* 1996; Tscharntke, *et al.* 1998). Therefore, the aims of this study were to determine the effect of bridal creeper invasion on the arthropod communities associated with ground-cover vegetation and, in particular, parasitic wasp assemblages, whose abundance and species richness were placed in an ecological context by examining host associations.

3.2 Methods

3.2.1 Arthropod sampling

Transects established for the plant survey (Chapter 2) were also used for sampling arthropod communities associated with the ground-cover vegetation. Eight pairs of native and bridal creeper-invaded transects (15m x 1m) were established in two locations in *Eucalyptus leucoxylon* and *E. fasciculosa* woodland at Mt Billy CP (Chapter 2: Figure 2.4). The open mid-story and low ground-cover meant that sweep-netting was considered to be a suitable method for sampling arthropods directly associated with the ground-cover vegetation (New 1998). A 45cm diameter triangular net was used to take 15 sweeps in each transect, sweeping a 180° arc passing through the vegetation and just above the ground with each sweep. The net contents were emptied into a zip-lock plastic bag and returned to the laboratory for processing where samples were stored in 70% ethanol. To standardise sampling, arthropods were sweep-netted between 1000 and 1400 hours on rain-free days with minimum wind speed; all transects were sampled on the same day for each sampling period; and sweep-netting was limited to a single operator. As temperature, rainfall and ground-cover vegetation were extremely seasonal (Chapter 2), sampling was undertaken over an extended period of time (14 monthly samples from April 2001 to May 2002) to account for plant growth and senescence.

Using a stereo microscope, arthropods were sorted to order using Naumann (1991) and Harvey (1989) and the number of individuals in each order were recorded. The Hymenoptera were further identified to family using Naumann (1991), Goulet (1993) and Austin, *et al.* (2002). Due to the focus on wasp taxa in this study, the Formicidae (ants) were not processed any further. The wasps (and few bees present) were subsequently sorted to 'morphospecies'.

Morphospecies, or recognisable taxonomic units, are taxa that are readily identified by morphological differences distinct to individuals without extensive taxonomic training. The use of morphospecies results in faster processing as samples do not need to be identified by taxonomists (Oliver & Beattie 1993, 1996). This method is commonly used in arthropod biodiversity research as a surrogate for species richness and is particularly suited for such studies because of the large numbers of individuals collected and the fact that many species are undescribed. For ants and some families of beetles, morphospecies counts have been shown to correlate with actual species numbers (Oliver & Beattie 1996). However, due to non-specialist sorting this method does have a major limitation; as morphospecies are determined, species may be 'lumped', where one morphospecies may contain one or more species, or alternately, 'split', where one species has been identified as several morphospecies (Oliver & Beattie 1993, 1996). This is particularly important for arthropod taxa as: (1) without detailed knowledge of specific taxonomic characters many closely related species may appear identical; (2) species may have sexually dimorphic males and females, or display other polymorphisms, for example, seasonal developmental changes in cuticle colour and wing length; and (3) larval (and often nymphal) stages are morphologically very different to the adult (Austin 1999). For these reasons, wasps were useful taxa to use due to access to hymenopteran taxonomists who verified the morphospecies (for most families) as separate species (see Appendix B). In addition, male and female morphospecies were matched where possible and only adult wasps could be utilised as larval stages are rarely encounted.

For each family every new morphospecies was labelled with an individual number and stored in a separate vial. These specimens formed a voucher collection to which each subsequent sample was compared. In addition, a habitus digital photograph of each morphospecies was taken to create a digital voucher collection that was used to facilitate ongoing sorting. The identity and number of each morphospecies in each sample was recorded. The voucher collection has been deposited in the Waite Insect and Nematode Collection (WINC), University of Adelaide, South Australia. The wasp morphospecies are referred to as 'species' for the remainder this chapter.

3.2.2 Wasp functional groups

Parasitoid species attack a wide spectrum of host arthropods (insects and spiders) that are found in most terrestrial niches, including all parts of living plants, leaf litter, soil, bark, wood, and fungi. The evolution of specific host-parasitoid associations and a parasitoid's ability to regulate the abundance of their hosts within a habitat (LaSalle 1993) allow for indirect investigation of other arthropod groups, their associated habitats, and trophic levels. As such, all wasp species were further identified to at least subfamily, and in most cases, tribe and/or genus using various published taxonomic keys and assistance from hymenopteran taxonomists (Appendix B). Using this level of identification allowed each species to be assigned a functional group based on host or prey association and/or biology using available information sourced from the literature (Appendices C & D). Functional group or guild analysis, based on the common utilisation of particular environmental resources, such as food or habitat types, allows for an ecological interpretation of species richness and abundance (Simberloff & Dayan 1991; Andersen 1995; Lockwood, *et al.* 1996; Fisher 1998; Hövemeyer 1999; Andersen, *et al.* 2001; Davies 2002). It also provided a qualitative measurement of host-parasitoid interactions.

Eight functional groups were determined for wasps recorded in this study (Table 3.1; Appendix E). Four groups parasitise hosts in plant-associated niches, with varying degrees of specialisation (Groups 1-4); two are associated with hosts in dead plant material, fungi and soil (Groups 5 & 6); one group within wasp and bee nests (Group 7); and a group that covers taxa with a wide spectrum of plant, and some litter, associated host niches (Group 8).

Table 3.1 Functional groups allocated to wasp taxa recorded from Mt Billy CP. Functional groups are based on larval niche/habitat associations sourced from available host and general biology records (Appendices C & D). Taxa belonging to each group are presented in Appendix E.

Group		Description
1	Plant-sucking	Parasitoids (or hyperparasitoids) of plant-sucking insects (herbivores) or insects associated with plant-sucking insects (predators)
2	Plant tissue	Parasitoids (or hyperparasitoids) of insects feeding inside plant tissue, eg leaf or stem mines, fruit or seeds (herbivores)
3	Plant	Parasitoids (or hyperparasitoids) of free-living plant-associated insects (herbivores or predators)
4	Gall	Plant gall-associated (parasitoids or phytophagous inquelines or gall-formers)
5	Wood	Parasitoids of wood-boring insects (detritivores, predators)
6	Litter	Parasitoids of detritvores and other soil- and litter-associated arthropods (detritivores, predators)
7	Vespid	Parasitoids of solitary, and more rarely social, Vespoidea and Apidae in nests
8	Plant/litter	Parasitoids (or hyperparasitoids) of arthropods found in a wide spectrum of plant-associated niches, but also some litter-associated arthropods (herbivores, predators or detritivores)

3.2.3 Data analysis

The total arthropod order-level abundance (all 14 sample periods combined), number of wasp species (species-richness) and species abundance were used for analyses to gain a more comprehensive understanding of community and assemblage responses. As native and bridal creeper transects were paired, the differences in abundance and richness in arthropod orders, wasp families and functional groups between native and invaded transects were analysed using paired t-tests undertaken in GraphPad Prism (ver. 4.0 for Macintosh, GraphPad Software, San Diego California USA). The abundances of individual orders from invaded and non-invaded transects over time (sample periods) were compared using repeat measures analysis of variance (ANOVA) using GraphPad Prism with Bonferroni post tests to determine which sample dates invaded and non-invaded transects differed. To investigate the temporal habitat use of individual species, the temporal abundance patterns of the most abundant wasp species recorded from both native and invaded habitat were compared.

Arthropod orders, wasp families and functional groups from native and bridal creeper transects were also examined by comparison of their ranked mean frequencies. The number of species and the mean number of individuals were graphed against the number of native or bridal creeper transects from which they were recorded ('incidence data' (Magurran 2004) to investigate the distribution (or density) of species across the two habitat types. To further investigate wasp diversity, the evenness (species relative abundances) (Magurran 2004) of native and bridal creeper assemblages were compared using rank abundance curves for each functional group. The most common rank abundance model for stable, species-rich ecological communities, the log-normal model (Schowalter 2000; Magurran 2004), was fitted and tested using the method described by Wilson (1991) using the Rank-Abundance or Dominance/Diversity Models in R: A language and environment for statistical computing (R Development Core Team, R Foundation for Statistical Computing) to compare assemblages from native and invaded habitat. The 'veiled' log-normal function, which assumes that only a proportion of the assemblage was sampled, was used to account for species that may have been missed. Non-metric multi-dimensional scaling (NMDS) using PC-ORD (ver. 4.25) was used to examine wasp assemblage composition and habitat variables. Indicator species analysis (Dufrêne & Legendre 1997) was used to detect wasp species that were indicators of native and invaded habitats using PC-ORD (refer to Chapter 2 for full descriptions of NMDS and indicator species analysis).

3.3 Results

3.3.1 Arthropod community

A total of 26,462 individual arthropods were collected over the 14 monthly samples. The most numerically abundant taxa, accounting for around 82% of all individuals, were (in descending order): flies (Diptera) (by far the dominant taxa), mites (Acarina), springtails (Collembola), and wasps (Hymenoptera).

The total number of arthropods was slightly greater in native habitat, however this difference was only marginally significant (P=0.0552) (Table 3.2). There was also no difference in the total number of individuals recorded from the majority of orders, however there were significantly more Lepidoptera (P=0.0002), Coleoptera (P=0.0057), Thysanoptera, and Hemiptera (P=0.0366) recorded from native transects (Table 3.2) (Figure 3.1).

Table 3.2 Arthropod orders recorded in sweep-net samples from Mt Billy CP; and the total and difference (paired t-test) in number of individuals from bridal creeper (BC) and native habitat. nt: not tested, ns: not significant, * P< 0.05, ** P< 0.01, ***P< 0.001.

Taxa	BC	Native	t-test
Arachnida			
Acarina (mites)	1731	1898	ns (t=0.4420 P=0.6718)
Araneae (spiders)	412	434	ns (t=0.3842 P=0.7123)
Malacostraca			
Isopoda (slaters)	13	0	nt
Diplopoda			
Julida (julid millipedes)	1	0	nt
Polyxenida (pin-cushion millipedes)	20	3	ns (t=1.726 P=0.1280)
Collembola			
Collembola (springtails)	1729	1368	ns (t=1.681 P=0.1366)
Insecta (insects)			
Blattodea (cockroaches)	1	0	nt
Coleoptera (beetles)	325	566	** (t=3.930 P=0.0057)
Diptera (flies)	6141	7378	ns (t=1.689 P=0.1351)
Hemiptera (aphids, scale insects, true bugs, & whiteflies)	486	691	* (t=2.557 P=0.0366)
Hymenoptera (ants)	132	89	ns (t=0.9076 P=0.3942)
(bees)	30	22	ns (t=2.014 P=0.0788)
(wasps)	794	984	ns (t=2.165 P=0.0671)
Lepidoptera (butterflies & moths)	26	147	*** (t=6.955 P=0.0002)
Neuroptera (lacewings)	8	31	ns (t=2.232 P=0.0608)
Orthoptera (crickets & grasshoppers)	5	14	ns (t=1.938 P=0.0938)
Phasmatodea (stick insects)	0	1	nt
Psocoptera (booklice)	26	32	ns (t=0.5363 P=0.6083)
Thysanoptera (thrips)	229	747	* (t=2.797 P=0.0266)
Total	12079	14383	ns (t=2.298 P=0.0552)

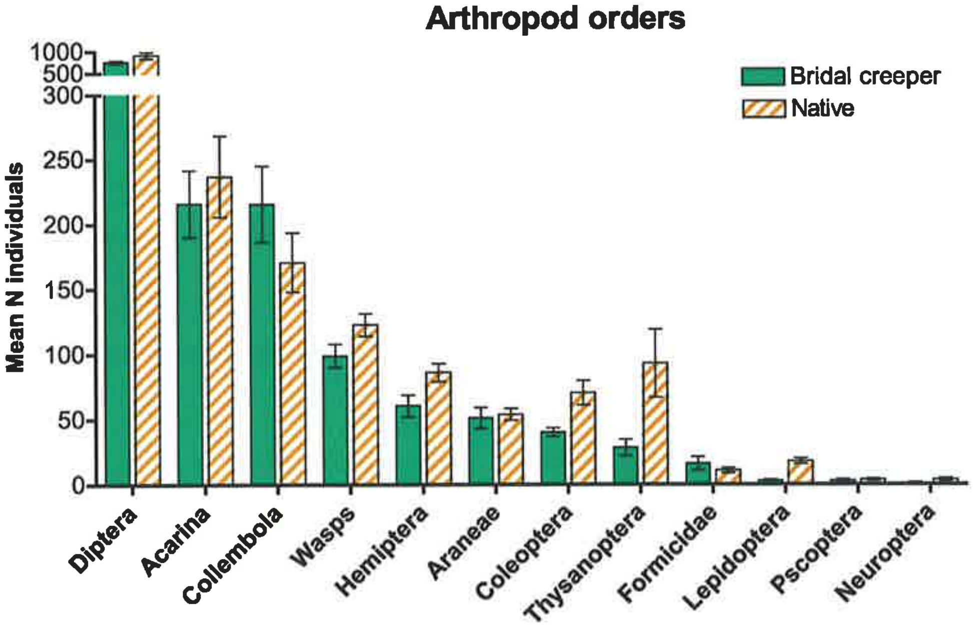


Figure 3.1 Mean (±SE) number of individuals in the most abundant orders from bridal creeper (n=8) and native (n=8) transects (all sample dates combined). For comparison, orders have been ranked by descending number of species and individuals from bridal creeper traps.

3.3.2 Arthropod temporal abundance patterns

In addition to differences in the total abundance of several orders (Table 3.2), many of the more abundant groups had strong temporal differences in abundance between native and bridal-creeper invaded vegetation (Table 3.3):

(a) The number of flies (Diptera) collected was significantly influenced by habitat type (P=0.0198) and by sample date (P<0.0001), with numbers peaking over spring and dropping considerably over summer and early autumn (Table 3.3; Figure 3.2a). There was also a significant interaction between date and habitat type (P<0.0001), with post-tests showing that there were more flies in bridal creeper in May (P<0.01), but more in native habitat in November (P<0.05) and December (P<0.001);

(b) The number of mites (Acarina) collected was significantly affected by sample date (P<0.0001) peaking in numbers in autumn but there was no effect of habitat, or any interaction between date and habitat (Table 3.3; Figure3.2b);

(c) Sample date significantly influenced the number of Collembola (P<0.0001) with the highest numbers collected in winter with none or very few collected over summer and early autumn (Table 3.3; Figure 3.2c). Habitat also had a significant effect (P=0.0354), and there was a significant interaction between date and habitat (P=0.0011), with significantly more Collembola collected in native transects in May (P<0.001);

(d) The number of wasps was significantly affected by sample date (P=<0.0001). There was no effect of habitat, however there was an interaction between habitat and date (P<0.0001) with more wasps recorded from bridal creeper in May (P<0.001) and from native transects in October (P<0.001), November (P<0.001), and December (P<0.01) (Table 3.3; Figure 3.2d);

(e) The number of bugs (Hemiptera) collected was significantly influenced by season (P<0.0001), with a peak in numbers in spring (Table 3.3; Figure 3.2e). Habitat also had significant effect on the number of bugs recorded (P=0.0003), and there was an interaction between habitat and date (P<0.0001), and post tests showed that there were significantly more bugs in native transects over November (P<0.01) and December (P<0.001);

(f) The number of spiders (Araneae) recorded was significantly influenced by sample date (P<0.0001), with an increase in numbers over spring and summers compared to autumn and winter (Table 3.3; Figure 3.2f). However, there was no effect of habitat and no interaction between date and habitat;

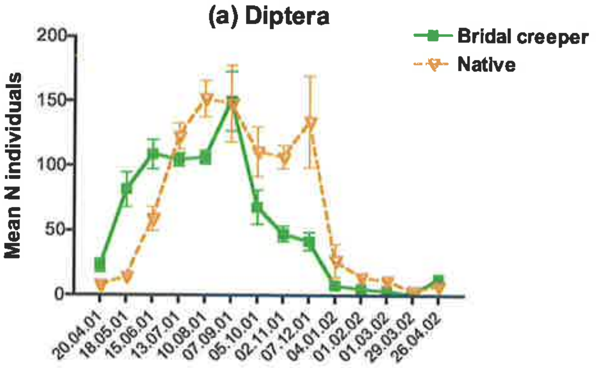
(g) Season (P<0.0001) and habitat (P<0.0001) both had significant effects on the number of beetles (Coleoptera) recorded, and there was a significant interaction between date and habitat (P=0.0057) with more beetles in native vegetation in February (P<0.05), March (P<0.001), and April (P<0.01) (Table 3.3; Figure 3.2g);

(h) The number of thrips (Thysanoptera) collected was significantly influenced by sample date (P<0.0001) and habitat (P<0.0001), and there was a significant interaction between date and habitat (P<0.0001) with more thrips in native vegetation in October (P<0.001) and November (P<0.001) (Table 3.3; Figure 3.2h); and

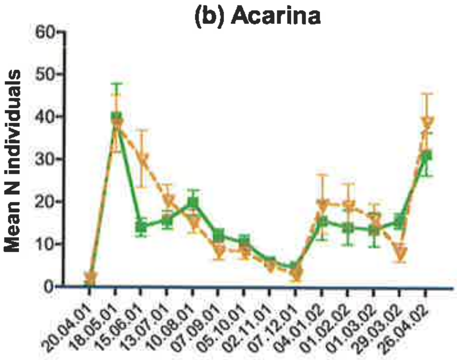
(g) Although their abundances were low numbers, the number of moths and butterflies (Lepidoptera) was also significantly affected by season (P<0.0001) and habitat (P<0.0001), and there was a significant interaction between date and habitat (P<0.0001) with more Lepidoptera in native vegetation in October (P<0.001), November (P<0.001), and December (P<0.001) (Table 3.3; Figure 3.2i).

Table 3.3 Results of the repeat measures ANOVA examining the effects of sample date and habitat on the abundance of the most abundant arthropod orders collected in sweep-net samples from Mt Billy CP. nt: not tested, ns: not significant, * P< 0.05, ** P< 0.01, ***P< 0.001.

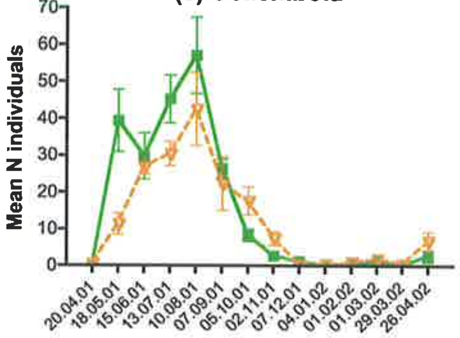
	Df	Sum-of-squares	Mean square	F		P
Diptera (flies)						
Interaction	13	89290	6868	5.644	***	(P< 0.0001)
Sample date	13	534500	41120	32.18	***	(P< 0.0001)
Habitat	1	6831	6831	5.614	*	(P=0.0198)
Subjects	98	125200	1278	1.050	ns	(P=0.4045)
Residual	98	119200	1217			
Acarina (mites)						
Interaction	13	1841	141.6	1.249	ns	(P=0.2574)
Sample date	13	24360	1874	14.12	***	(P< 0.0001)
Habitat	1	124.5	124.5	1.099	ns	(P=0.2972)
Subjects	98	13013	132.7	1.171	ns	(P=0.2179)
Residual	98	11110	113.3			
Collembola (springtails)						
Interaction	13	4932	379.4	2.966	**	(P=0.00111)
Sample date	13	56520	4348	30.02	***	(P< 0.0001)
Habitat	1	581.8	581.8	4.549	*	(P=0.354)
Subjects	98	14200	144.9	1.133	ns	(P=0.2696)
Residual	98	12530	127.9			
Wasps (Hymenoptera)						
Interaction	13	1420	109.2	7.211	***	(P< 0.0001)
Sample date	13	1174	90.34	4.825	***	(P< 0.0001)
Habitat	1	40.29	40.29	2.660	ns	(P=0.1061)
Subjects	98	1835	18.72	1.236	ns	(P=0.1479)
Residual	98	1484	15.15			
Hemiptera (bugs)						
Interaction	13	909.6	69.97	5.310	***	(P< 0.0001)
Sample date	13	5609	431.5	20.70	***	(P< 0.0001)
Habitat	1	187.6	187.6	14.24	***	(P=0.0003)
Subjects	98	2043	20.85	1.582	*	(P=0.0121)
Residual	98	1291	13.18			
Araneae (spiders)						
Interaction	13	88.30	6.793	0.7919	ns	(P=0.6670)
Sample date	13	923.3	71.02	7.257	***	(P< 0.0001)
Habitat	1	0.07143	0.07143	0.008327	ns	(P=0.9275)
Subjects	98	959.1	9.787	1.141	ns	(P=0.2576)
Residual	98	840.6	8.578			
Coleoptera (beetles)						
Interaction	13	258.9	19.92	2.485	**	(P=0.0057)
Sample date	13	853.3	65.64	6.420	***	(P< 0.0001)
Habitat	1	259.3	259.3	32.36	***	(P< 0.0001)
Subjects	98	1002	10.23	1.276	ns	(P=0.1147)
Residual	98	785.3	8.013			
Thysanoptera (thrips)						
Interaction	13	2070	159.2	3.820	***	(P< 0.0001)
Sample date	13	5700	438.5	8.763	***	(P< 0.0001)
Habitat	1	1198	1198	28.74	***	(P< 0.0001)
Subjects	98	4903	50.03	1.201	ns	(P=0.1836)
Residual	98	4084	41.68			
Lepidoptera (moths & butterflies)						
Interaction	13	112.8	8.679	10.86	***	(P< 0.0001)
Sample date	13	120.1	9.237	12.43	***	(P< 0.0001)
Habitat	1	65.36	65.36	81.79	***	(P< 0.0001)
Subjects	98	72.81	0.7430	0.9298	ns	(P=0.6404)
Residual	98	78.31	0.7991			



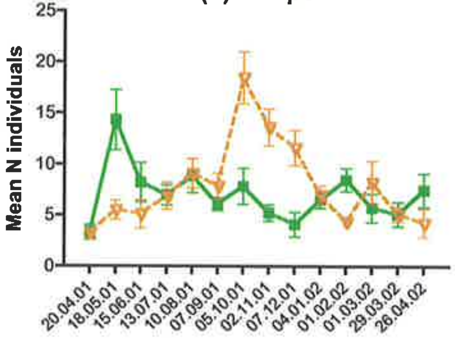
(a) Diptera



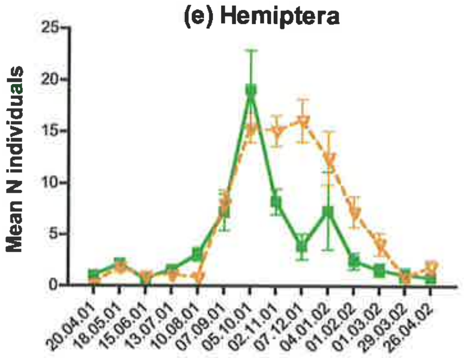
(b) Acarina



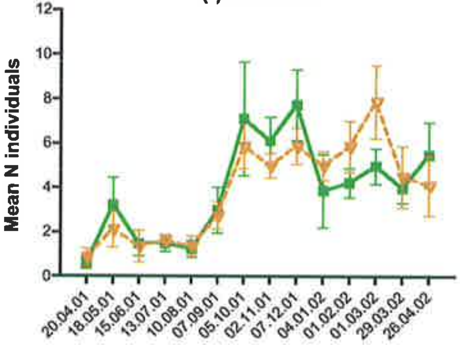
(c) Collembola



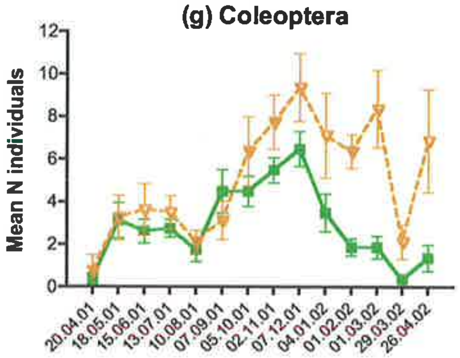
(d) Wasps



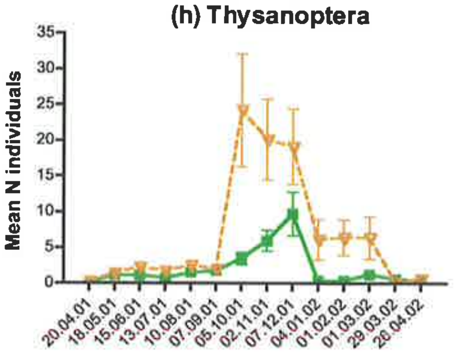
(e) Hemiptera



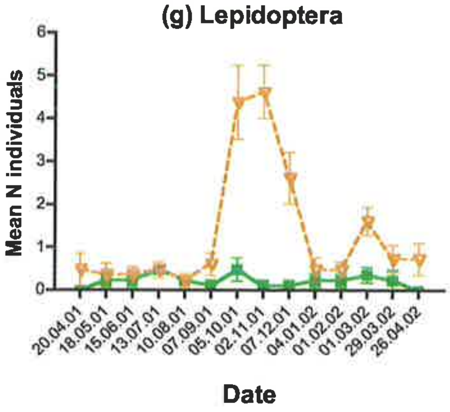
(f) Araneae



(g) Coleoptera



(h) Thysanoptera



(g) Lepidoptera

Figure 3.2 Mean (±SE) number of **(a)** Diptera (flies), **(b)** Acarina (mites), **(c)** Collembola (springtails), **(d)** wasps (Hymenoptera), **(e)** Hemiptera (bugs), **(f)** Araneae (spiders), **(g)** Coleoptera (beetles), **(h)** Thysanoptera (thrips) and **(i)** Lepidoptera (moths and butterflies) over time from bridal creeper (n=8) and native (n=8) transects.

3.3.3 Wasp species richness and abundance

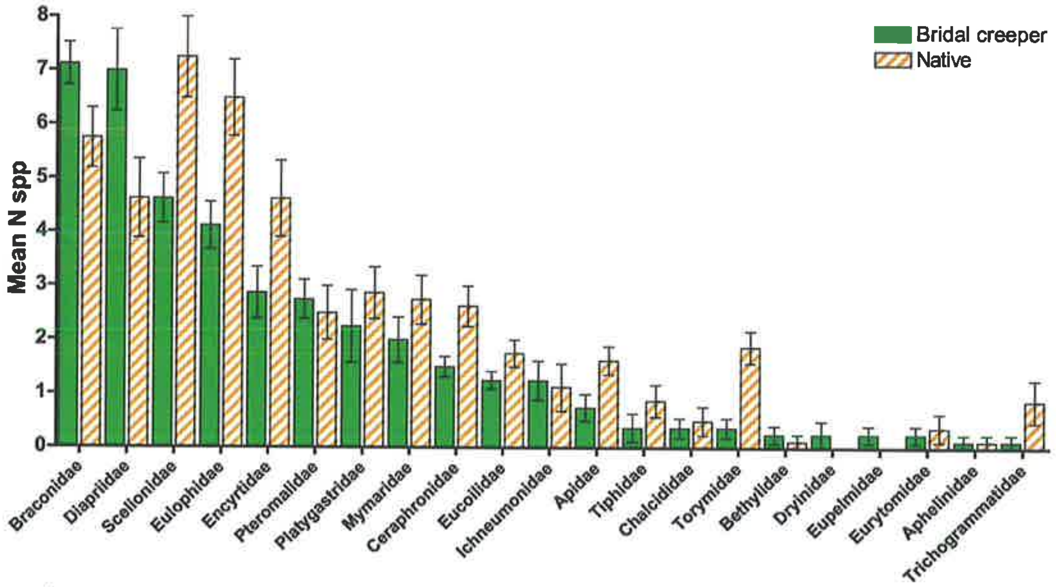
A total of 1597 wasps and bees from 25 families in 10 superfamilies were collected (Table 3.4). The majority were parasitoids (Appendix C) and the family Diapriidae was the most abundant group collected (22.8%), followed by Braconidae (17.2%), Scelionidae (14.8%) and Eulophidae (8.8%). A total of 301 species were identified. Braconidae was the most species-rich family with 42 species, followed by Scelionidae (41), Eulophidae, (34), Encyrtidae (28), Diapriidae (28), Pteromalidae (24) and Platygastridae (22). The species accumulation curves are beginning to plateau (Appendix F) suggesting that both native and invaded habitat were sampled sufficiently over the 14 months to allow for a meaningful comparison of abundance and species richness between habitats (Gotelli & Colwell 2001).

Table 3.4 Hymenopteran families (excluding Formicidae) recorded in sweep-net samples from Mt Billy CP; and the total and difference (paired t-test) in the number of (a) species and (b) individuals for each family from bridal creeper (BC) and native transects. nt: not tested, ns: not significant, * P< 0.05, ** P< 0.01, ***P< 0.001

	(a) total N species			**(b) total N individuals**		
Family	**BC**	**Native**	**t-test**	**BC**	**Native**	**t-test**
APOIDEA						
Apidae (bees)	2	3	nt	30	22	nt
CERAPHRONOIDEA						
Ceraphronidae	5	5	* (t=2.826 P=0.0256)	22	45	ns (t=2.186 P=0.0651)
Megaspilidae	0	1	nt	0	4	nt
CHALCIDOIDEA						
Aphelinidae	1	1	nt	1	1	nt
Chalcididae	2	2	nt	3	4	nt
Encyrtidae	20	20	ns (t=2.139 P=0.0698)	31	52	ns (t=1.535 P=0.1688)
Eulophidae	19	29	* (t=2.517 P=0.0400)	46	101	ns (t=2.341 P=0.0517)
Eupelmidae	2	0	nt	2	0	nt
Eurytomidae	1	1	nt	2	3	nt
Mymaridae	8	10	ns (t=1.158 P=0.2849)	20	35	ns (t=1.622 P=0.1489)
Pteromalidae	14	15	ns (t=0.3859 P=0.7110)	33	33	ns (t=0.0000 P=1.0000)
Torymidae	3	3	*** (t=5.612 P=0.0008)	4	48	* (t=3.383 P=0.0117)
Trichogrammatidae	1	3	nt	1	11	nt
CHRYSIDOIDEA						
Bethylidae	2	1	nt	3	2	nt
Dryinidae	1	0	nt	2	0	nt
CYNIPOIDEA						
Eucoilidae	5	5	ns (t=1.528 P=0.1705)	14	21	ns (t=1.433, P=0.1949)
EVANOIDEA						
Evaniidae	0	1	nt	0	1	nt
Gasterupiidae	1	0	nt	1	0	nt
ICHNEUMONOIDEA						
Braconidae	20	19	ns (t=1.519 P=0.1725)	142	129	ns (t=0.3144 P=0.7624)
Ichneumonidae	4	5	ns (t=0.5517 P=0.5983)	23	16	ns (t=1.507 P=0.1755)
PLATYGASTROIDEA						
Platygastridae	8	9	ns (t=0.7061 P=0.5029)	30	39	ns (t=0.8553 P=0.4207)
Scelionidae	15	19	** (t=3.721 P=0.0074)	95	134	ns (t=1.948 P=0.0925)
PROCTOTRUPOIDEA						
Diapriidae	19	14	ns (t=2.096 P=0.0743)	209	166	ns (t=0.9424 P=0.3774)
Monomachidae	1	0	nt	1	0	nt
VESPOIDEA						
Tiphiidae	2	3	ns (t=1.323 P=0.2275)	3	12	ns (t=2.183 P=0.0654)
TOTAL	156	170	* (t=2.568 P=0.0371)	718	879	ns (t=1.962 P=0.0906)

Overall, there was no difference in the number of wasps collected, but there were slightly more species recorded from native habitat (t=2.568 P=0.0371) (Table 3.4). The abundances of wasp families recorded from native and bridal creeper transects were similar. Torymids were the only family that was collected in significantly different numbers between habitats, being more abundant in native areas. However, Ceraphronidae, Eulophidae, Torymidae and Scelionidae were all significantly more species-rich in native habitat (Table 3.4). In general, the ranked abundance and species-richness of families was similar for both habitats with the same families the most abundant and species-rich (Figure 3.3).

(a) Species



(b) Individuals

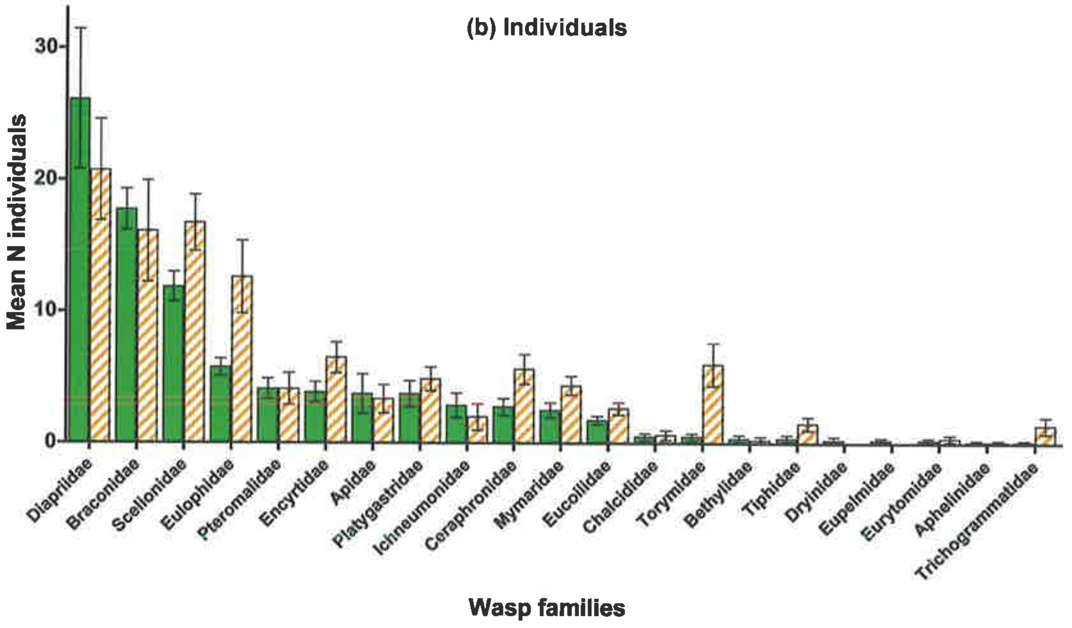


Figure 3.3 Mean (±SE) number of **(a)** wasp species and **(b)** individuals in each family recorded from bridal creeper (n=8) and native (n=8) habitat (all sample dates combined). For comparison, families are ranked by descending number of species and individuals from bridal creeper transects.

Functional groups

Parasitoids of litter- and soil-associated arthropods were the most abundant and species-rich group across both habitats, followed by parasitoids of free-living plant-associated insects (Table 3.5, Figure 3.4). However, wasps associated with plant galls were the only functional group that had significantly different numbers of individuals and species between native and bridal creeper habitats, being more numerous and speciose in native habitat (Table 3.5, Figure 3.4). The higher numbers of gall-associated wasps from native transects was due to the greater number of torymid genera that all had host records associated with plant galls (Table 3.4; Appendix C).

Table 3.5 Total and difference (paired t-test) in the number of **(a)** species and **(b)** individuals for each functional group from bridal creeper (BC) and native habitats. nt: not tested, ns: not significant, * P< 0.05, ** P< 0.01, ***P< 0.001

	(a) total N species			**(b) total N Individuals**		
Functional group	**BC**	**Native**	**t-test**	**BC**	**Native**	**t-test**
1 Plant sucking	26	26	ns (t=1.488 P=0.1805)	42	71	ns (t=1.813 P=0.1127)
2 Plant tissue	7	8	ns (t=0.6831 P=0.516)	12	51	ns (t=1.855 P=0.1060)
3 Plant	34	46	ns (t=1.997 P=0.0859)	172	200	ns (t=1.146 P=0.2893)
4 Gall	25	37	** (t=3.674 P=0.0079)	57	160	*** (t=10.46 P<0.0001)
5 Wood	6	2	nt	7	2	nt
6 Litter	56	54	ns (t=1.321 P=0.2281)	355	303	ns (t=0.9701 P=0.3643)
7 Vespid	2	0	nt	2	0	nt
8 Plant/litter	25	29	ns (t=1.722 P=0.1288)	63	89	ns (t=1.182 P=0.2759)

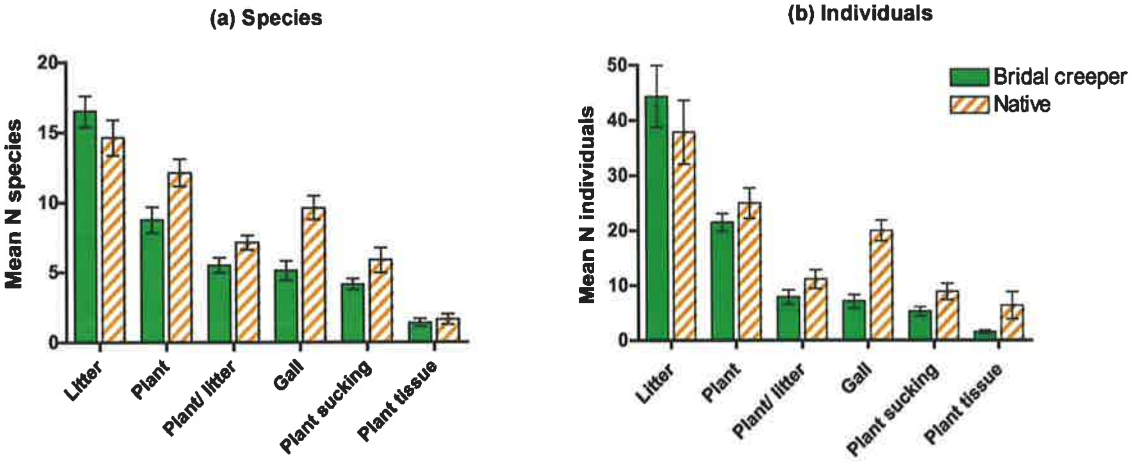


Figure 3.4 Mean (±SE) number of **(a)** species and **(b)** individuals in each functional group collected from bridal creeper (n=8) and native (n=8) transects. For comparison, functional groups have been ranked by descending number of species and individuals from bridal creeper. Parasitoids of wood-boring insects (Group 5) and those associated with Vespoidea and Apidae nests (Group 7) were not included due to the very low numbers collected (Table 3.5).

3.3.4 Wasp assemblage structure and composition

Habitat distribution

The incidence of species, or their spatial distribution across the habitat, was the same for both bridal creeper and native transects. There was a negative relationship between the number of species and the number of transects in which a species was present, where the majority of species were recorded only from one location (ie. only one transect) (Figure 3.5a). Conversely, there was a strong positive relationship between the mean abundance of a species and the number of transects it was recorded from, which was also the same for both bridal creeper and native habitat (Figure 3.5b). Therefore, the most abundant species were also the most widespread taxa, whereas the least abundant species were those that were less widely distributed.

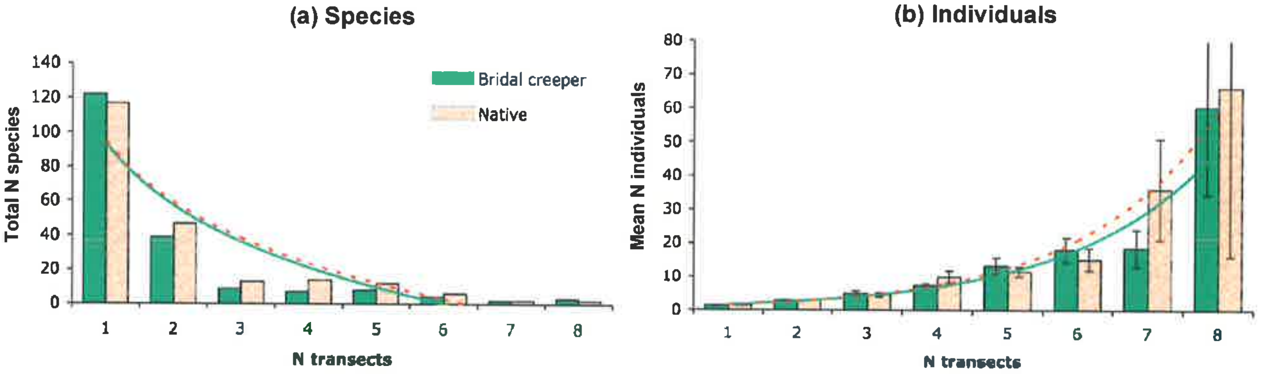


Figure 3.5 (a) Number of wasp species recorded across different numbers of bridal creeper and native transects (fitted line (logarithmic): BC: r^2=0.7878, N: r^2=0.8483; and **(b)** mean (±SE) number of individuals from species recorded across different numbers of bridal creeper and native transects (fitted line (exponential): BC: r^2=0.9629, N: r^2=0.9796).

Rank abundance distributions

The relative proportion of species represented by less than 10 individuals was the same for both habitats (91%). The proportion with less than 5 individuals was also similar (bridal creeper: 85%; native: 79%), as was the proportion of species recorded as a single specimen (bridal creeper; 49%, native: 42%). As such, the rank abundance distributions of species from both bridal creeper and native wasp assemblages, across all functional groups, were very similar. Distributions were left-skewed, generally with a relatively long tail of rare species following a lognormal distribution model (Figure 3.6). Parasitoids of insects feeding inside plant tissue (Figure 3.6b) were collected in low numbers, thus the shape of the curves, however all the other functional groups had a very similar slope, and hence evenness, between invaded and native habitat. Thus, similar evenness (Figure 3.6) and species richness (Tables 3.3-4), indicate there is very little difference in wasp diversity between invaded and non-invaded habitat for a range of biologically diverse taxa.

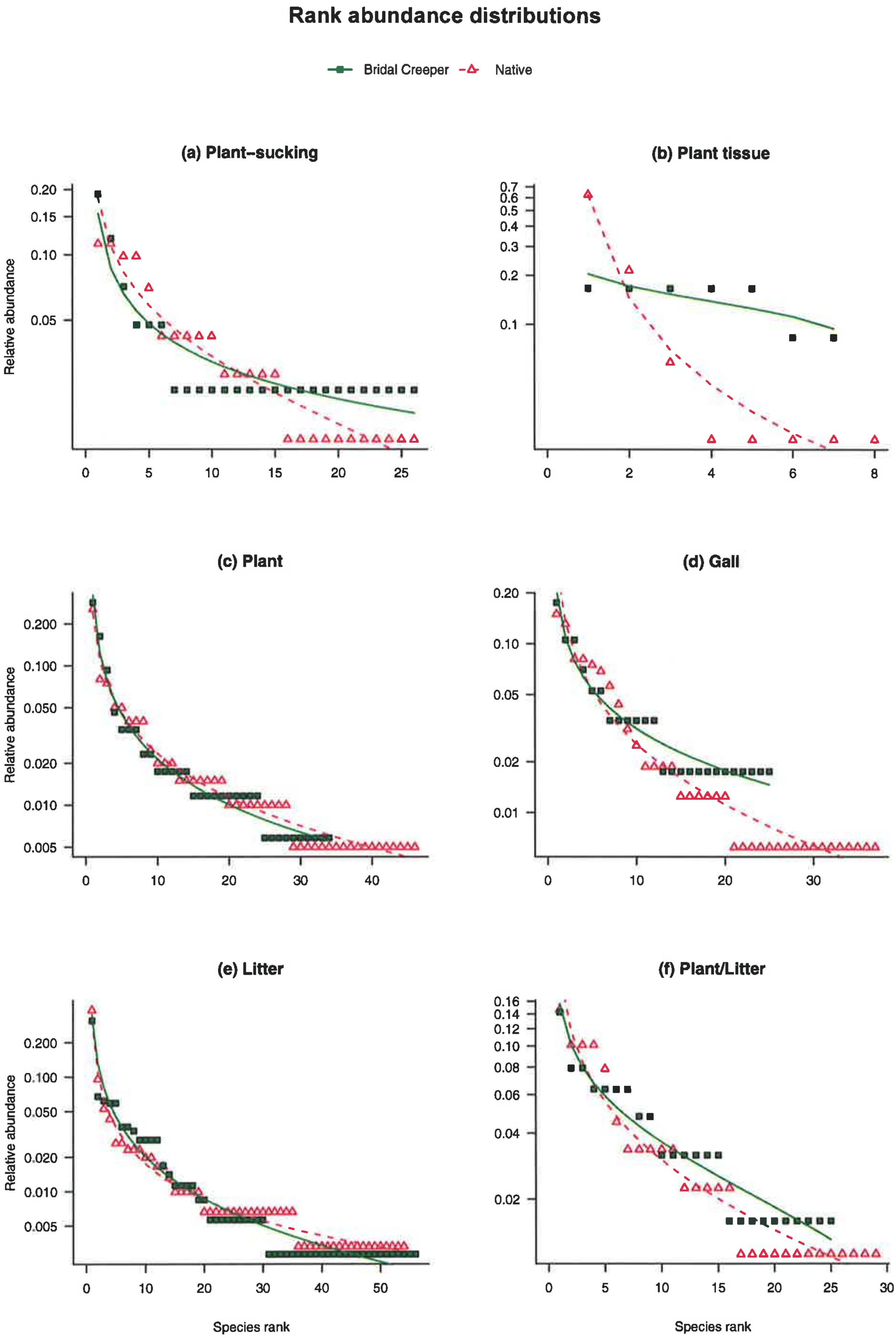


Figure 3.6 Rank abundance distributions (RADs) of wasp species from bridal creeper and native transects for **(a)** plant sucking- associated parasitoids, **(b)** plant tissue-associated parasitoids, **(c)** plant-associated parasitoids, **(d)** gall-associated parasitoids and wasps, **(e)** litter and soil-associated parasitoids, and **(f)** plant/ litter associated parasitoids. When the fit for a (veiled) lognormal was significant the curve was drawn (solid line: bridal creeper; broken line: native).

Furthermore, the two most abundant species were the same from both habitats and contributed to a similar proportion of the assemblage: Diapriidae sp. 04 (Belytinae, *Stylaclista* sp.), a litter and soil-associated parasitoid, and Scelionidae sp. 17 (Telenominae, *Telenomus* sp.), a plant-associated parasitoid (Figure 3.7).

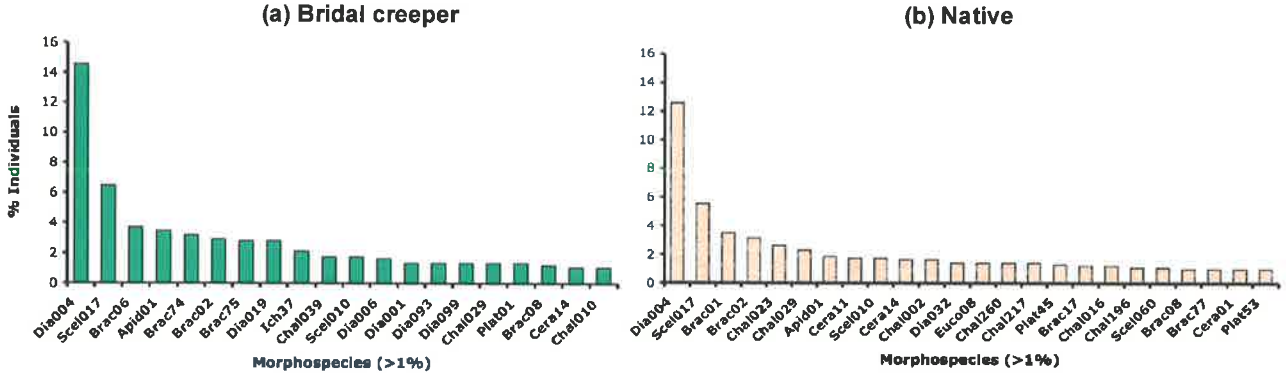


Figure 3.7 Frequency distributions of species that contributed to 1% or greater of the total assemblage from **(a)** bridal creeper and **(b)** native transects.

Assemblage composition

Around 35% of species (105 spp.) were 'common' to both bridal creeper invaded and native habitats. An almost equal number (107 spp.) were recorded exclusively from native transects with 89 species recorded only from bridal creeper (Figure 3.8a). Species 'unique' to only one habitat were collected in much lower numbers than those recorded from both habitats (Figure 3.8b).

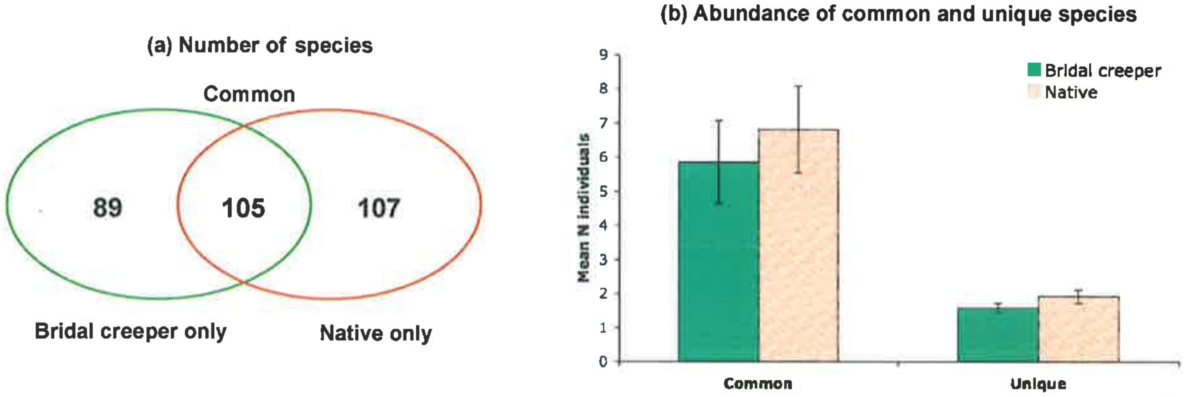


Figure 3.8 (a) Venn diagram illustrating the total number of 'common' (overlapping circles) and 'unique' species and **(b)** mean (±SE) number of individuals from 'common' and 'unique' species from bridal creeper and native transects.

An ordination (NMDS) of transects did not show a clear separation of bridal creeper and native transects based on wasp abundance and species composition (Figure 3.9). However, the bridal creeper transects clustered more closely than the native transects, suggesting more similar wasp assemblages occurred across invaded areas compared to those in native habitat. An overlay of environmental variables showed that the percent cover of moss correlated with the wasp assemblages recorded from some of the native transects, whereas the percent cover of bridal creeper and litter correlated with the cluster of transects in bridal creeper (Figure 3.9).

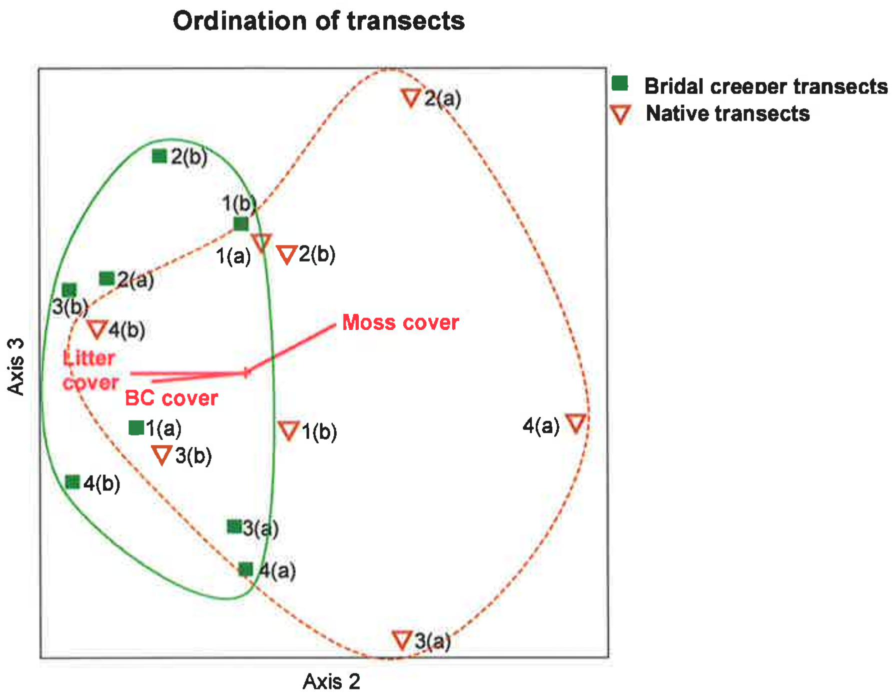


Figure 3.9 Three-dimensional ordination (NMDS) of wasp abundance and species composition from sweep-netting. Numbers next to each transect correspond to transect pairs and letters in brackets correspond to sites (a and b). The model explains 83.7% of the total variation (Axis 1=15.7%, Axis 2=47.9%, Axis 3=20.0%) and the superimposed vectors (constrained to r^2=0.5) show the correlation between wasp species and environmental variables. The length of each vector indicates the strength of the correlation and the orientation the direction of increase. Distance measure: Sørensen; final stress for the 3-dimensional solution=9.63314; final instability=0.00001; number of iterations= 67.

Four species were significant indicator species of bridal creeper-invaded habitat: three braconids and a diapriid, three of which were litter and soil-associated, and one plant-associated (Table 3.6). Five species were indicators of native habitat: a eulophid, three torymids and a platygastrid. The eulophid (*Parasecodella*) could not be assigned a functional group as there was no host information available for this genus, however the other native indicator species are all gall-associated wasps (Table 3.6).

Table 3.6 Significant indicator species (spp.) for bridal creeper (BC) and native (N) habitats and Monte Carlo significance of observed maximum indicator values for each species (1000 permutations). N: number of individuals from the indicated habitat.

Spp.	Taxa	Fun. group	Habitat	N	Observed indicator value	P value
Brac06	Rogadinae	Plant	BC	28	70.0	0.0270
Chal16	Torymidae, Megastigminae, *Megastigmus*	Gall	N	11	57.3	0.0500
Chal23	Torymidae, Monodontomerinae, *Torymoides*	Gall	N	23	57.7	0.0530
Chal217	Torymidae, Monodontomerinae, *Torymoides*	Gall	N	13	62.5	0.0330
Platy53	Platygastrinae, *Platygaster* sp	Gall	N	9	75.0	0.0070
Diap093	Diapriinae, *Entomacis*	Litter/ soil	BC	10	62.5	0.0240
Brac74	Alysiinae, Alysiini	Litter/ soil	BC	24	80.8	0.0070
Brac75	Alysiinae, Alysiini	Litter/ soil	BC	21	65.6	0.0340
Chal02	Eulophidae, Euderinae, *Parasecodella*	no host records	N	15	55.1	0.0560

3.3.5 Species temporal abundance patterns

The temporal abundance patterns of the most abundant wasps recorded from both habitats were compared to investigate seasonal habitat use. Despite differences in abundances, some species were present over the same dates in both native and bridal creeper. For example, Diapriidae sp. 04 (Figure 3.10a), Scelionidae sp. 10 (Figure 3.10b), Ichneumonidae sp. 37 (Figure 3.10c), Eucoilidae sp. 08 (Figure 3.10d), and Scelionidae sp. 17 (Figure 3.10e) have very similar temporal abundance patterns in both habitats. Other species with less specific temporal patterns (ie. those that occurred across a range of sample dates throughout the sample period) were recorded in varying numbers in bridal creeper and native habitat at different times; for example Braconidae sp. 02 (Figure 3.10f), Chalcidoidea sp. 29 (Figure 3.10g) and Ceraphronidae sp. 14 (Figure 3.10h).

3.4 Discussion

3.4.1 Bridal creeper and native arthropod and parasitoid communities

The significantly adverse effects of bridal creeper on native flora led to the prediction that reduced native plant diversity should have a flow-on affect to associated arthropods. However, the arthropod community was clearly not depleted in the invaded habitat. Arthropod and wasp abundance, wasp species richness, assemblage composition and structure, and host associations all indicate that there were few obviously negative effects of bridal creeper invasion on the arthropod community associated with the ground-cover plant community at Mt Billy CP. Accordingly, this study also revealed that bridal creeper provides some degree of habitat for a functionally diverse arthropod community and wasp assemblage. Recent studies investigating the impact of weed invasion on arthropods have also had difficulty in demonstrating a clear impact on species abundance and richness, with taxa in the same community responding differently to weed invasion and many highly modified, (plant) species-poor, weed-invaded habitats supporting abundant and diverse arthropod communities (Samways, *et al.* 1996; French & Eardley 1997; Toft, *et al.* 2001; Costello, *et al.* 2003; Harris, *et al.* 2004; Standish 2004).

Community composition

The invasion of bridal creeper appears to have had little effect on such standard measurements of biodiversity as species richness, abundance and evenness. The same arthropod orders and wasp families were collected from both native and invaded transects. There were also very few differences overall in the abundance and order-, family- and species-level richness between habitats (Tables 3.2 & 3.4). Furthermore, the rank abundance

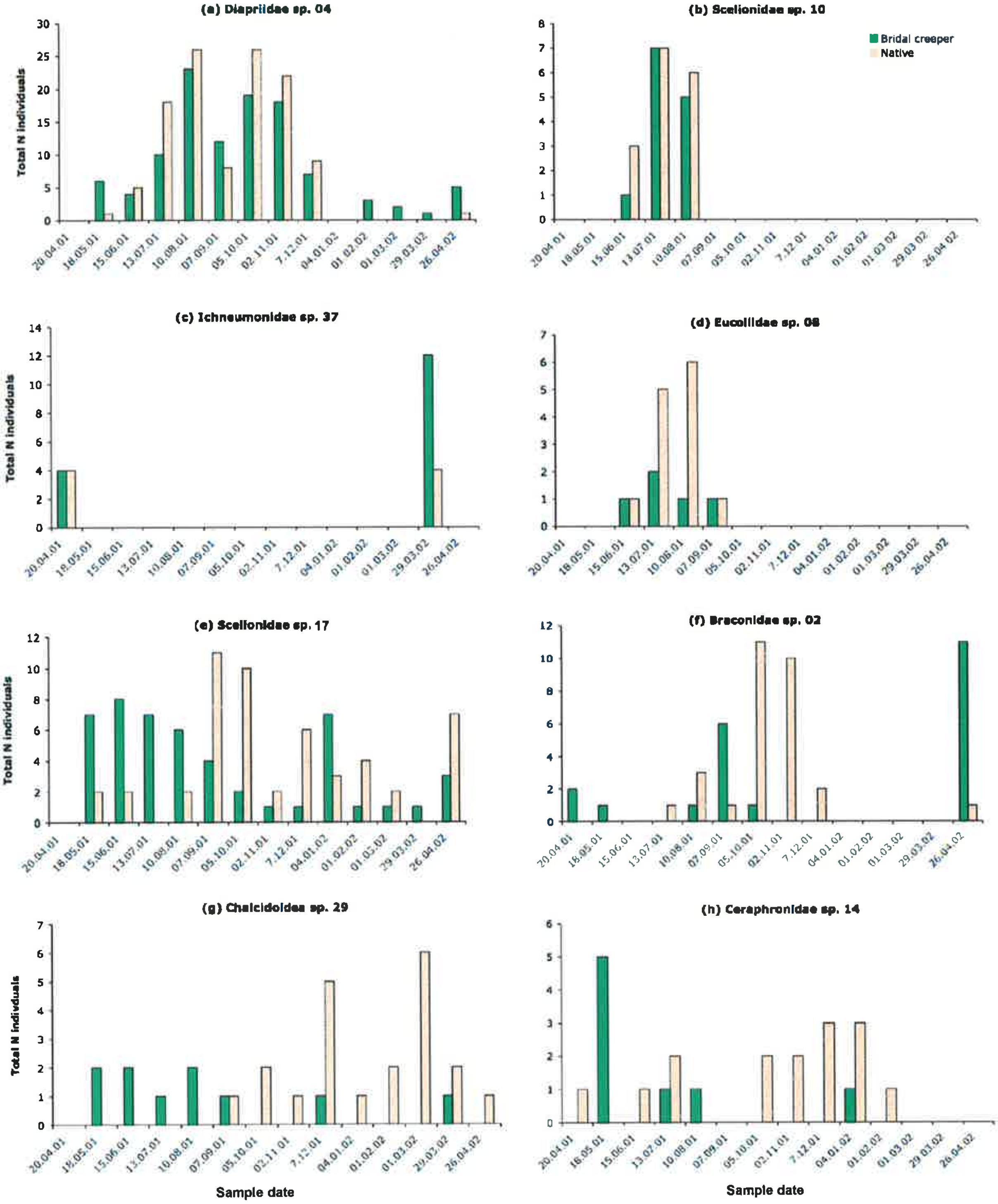


Figure 3.10 Temporal abundance patterns in bridal creeper and native habitat of **(a)** Diapriidae sp. 04 (*Stylaclista* sp.), litter-associated; **(b)** Scelionidae sp. 10 (*Trimorus* sp.), litter-associated; **(c)** Ichneumonidae sp. 37 (*Lissonata* sp.), plant associated; **(d)** Eucoilidae sp. 08, plant/litter; **(e)** Scelionidae sp. 17 (*Telenomus* sp.), plant-associated; **(f)** Braconidae sp. 02 (Alysiinae), litter-associated; **(g)** Chalcidoidea sp. 29 (*Epichrysocharis* sp.), gall-associated; and **(h)** Ceraphronidae sp. 14 (*Aphanogmus* sp.), plant-associated.

curves showed that the evenness (similar slope) of the two wasp assemblages was also very similar between habitats, indicating there was little overall difference in wasp diversity between native and invaded habitat (Figure 3.6). The two most abundant species (contributing to approximately 20% of all individuals) were the same for both habitat types (Figure 3.7) and the two wasp assemblages could not be distinguished as different based on species composition and abundance (Figure 3.9). This was despite a relatively high proportion of species unique to either invaded or native habitat (Figure 3.8). However, these unique species were recorded in low numbers (on average >2 individuals) (Figure 3.8). Such a pattern of abundant species being shared across adjacent habitat types, and rarer species found in only one, is commonly reported in arthropod biodiversity studies (eg. Toft, *et al.* 2001; Sax 2002). It is possible that these species may have simply been missed when sampling and longer and/or more intense sampling may have yielded these species from both native and invaded areas. Thus, little can be concluded about their habitat preferences and further investigation is required to determine if their rarity is due to sampling regime, or if these species really are restricted to bridal creeper and native habitats. However, rare species are a regular occurrence and are important in structuring arthropod assemblages (Magurran 2004) (see below). In addition, these 'unique' species occurred across all functional groups, representing a range of taxa and host associations, suggesting there were perhaps no ecological or habitat-associated differences influencing the abundances of these species between native and invaded habitat.

Despite the fact that the ordination did not separate bridal creeper and native transects, it did however reveal that the bridal creeper transects cluster much more closely together than the more widely dispersed native transects (Figure 3.9). This shows that the composition of wasp assemblages occurring across invaded areas were more homogenous than those in native areas. The more uniform habitat produced by bridal creeper compared to that of native habitat (Chapter 2) might explain these patterns of wasp assemblage composition and suggests that a significant impact of bridal creeper invasion is the homogenization of both the plant and wasp communities (discussed further in Chapter 4).

Community structure

The structure of the arthropod communities and wasp assemblages recorded from native and bridal creeper invaded habitat was unexpectedly similar. The same arthropod orders (Figure 3.1), wasp families (Figure 3.3) and functional groups (Figure 3.4) were collected in similar proportions and rank abundances from both habitats. The pattern of habitat distribution for wasp species, where the majority were collected from only one or two transects in low numbers (Figure 3.5a), and the strong positive relationship between the mean abundance of a species and the number of transects it was recorded from (Figure 3.5b), were identical for both bridal creeper and native habitat. Such species and abundance-distribution relationships, where spatial distribution (ie. the number of sites occupied) is either positively correlated with mean site abundance, or negatively with species richness, is a ubiquitous, well-documented ecological attribute of populations and communities of closely related, ecologically similar species (such as parasitoids) that holds across local to regional spatial scales (Brown 1984; Kemp & Harvey 1990; Niemelä & Spence 1994; Adair & Groves 1998; Hughes, *et al.* 2000; Ulrich 2004). These similar patterns across invaded and weed-free habitats indicate there was little effect of bridal creeper on the structure and organisation of arthropod and wasp communities.

Another common feature of large ecological assemblages is a log-normal type species rank abundance distribution (RAD) (Schowalter 2000; Magurran 2004) that could be fitted to the wasp assemblages from native and invaded across all functional groups (Figure 3.6). Several alternative and contrasting mechanisms can produce similar RAD models, and accordingly, a good-fit does not imply a specific mechanism (Wilson 1991). However, rank abundance models are considered extremely useful for the comparison of communities (Wilson 1991; Magurran 2004). Environmental impacts have been shown to alter RAD patterns when there are small numbers of species able to adapt to the changes, often resulting in the dominance of a few species (Schowalter 2000; Castillo & Lobo 2004; Magurran 2004). Therefore, the same rank abundance distributions of wasp functional groups from both invaded and native areas also suggests that the presence of bridal creeper has not significantly changed wasp assemblage structure in invaded areas. The log-normal model is often widely applicable because mathematically it results from random variation among a large number of factors producing a normal distribution. Thus, although the biological meaning of such models is often debated (Wilson 1991), in natural communities it has been suggested that the log-normal RAD is generally considered to characterise stable complex communities that are regulated by a large range of environmental factors (Schowalter 2000; Magurran 2004). This may explain why the habitat changes caused by bridal creeper invasion are having little effect on the wasp diversity; it is likely that other habitat factors other than the presence of ground-level native plant species are governing wasp assemblages (discussed below).

Ecological processes

The parasitic wasp assemblages recorded in this study are indicators of diverse host groups and indirectly provide insight into species trophic-level interactions and hence, underlying ecological processes. In a comparison of sites in burnt and un-burnt mature pine forest, burnt habitat had a greater abundance and diversity of parasitoids of non-woody herbivores and nectar feeders due to the post-fire flush of herb and forb growth, but an absence of parasitoids fungivores and detritivores due to the loss of leaf litter (Lockwood, *et al.* 1996). In the current study there were no functional groups absent from invaded habitat, particularly the plant-associated groups that may have been predicted to be the most significantly affected. The diverse range of arthropod orders collected (Table 3.2) also undoubtedly represents taxa from many trophic levels (for example, spiders are significant predators; Hemiptera are important herbivores, etc.). At a finer scale, the results from the parasitoid functional group analysis revealed that invaded habitat contains parasitoids that are potentially attacking an extremely diverse range of herbivores, detritivores and predators (Appendices C and D). As such, when compared to the native habitat, a 'complete' ecological community could be considered to also exist in bridal creeper invaded areas. Parasitoids were also predicted to be particularly responsive to the effects of weed invasion as they are often more sensitive to changes caused by habitat modification due to their close relationship with their hosts, complex life cycles and high trophic level (Naumann 1991; LaSalle 1993; Polis, *et al.* 1996; Tscharntke, *et al.* 1998; Cronin & Haynes 2004). As such, the functionally diverse parasitoid assemblage recorded suggests that bridal creeper has not significantly disrupted the arthropod community. A number of possible explanations can be proposed as to why there was little apparent effect of bridal creeper invasion on arthropods associated with the ground-cover vegetation and these are discussed below.

3.4.2 Minimal impact on arthropods: possible explanations

Number of herbivores

The impact of weed invasion on arthropods varies with the extent of the resulting habitat change and the associations various species have with the parts of the habitat that are modified (Samways, *et al.* 1996; French & Eardley 1997; Anthelme, *et al.* 2001; Toft, *et al.* 2001; Greenwood, *et al.* 2004). For example, specialist herbivores will be absent if their host plant is not present (Harris, *et al.* 2004). The negligible effect of bridal creeper on native arthropods may have been because there were few herbivorous species that directly relied on the native ground-cover plant species, and thus be affected by their decline. Parasitoid functional group analysis revealed that leaf litter and soil-associated parasitoids were by far the most abundant and species-rich group recorded from both habitat types (Table 3.4). Furthermore, plant-associated parasitoids are unlikely to be directly associated with bridal creeper as it is improbable there are herbivores feeding on the weed (Section 3.1). Indeed, many of the other plant-associated parasitoids (plant, plant-tissue, plant-sucking and in particular, gall-associated wasps) have host and biological records that suggest these species are parasitising hosts from the tree canopy (Appendix C). Consequently, the ground-cover plant community that was significantly altered by bridal creeper may not be as important as other components of the woodland habitat, such as the soil, leaf litter and canopy microhabitats, for the reproduction and development of the majority of taxa recorded.

Further evidence for an impoverished herbivore community comes from studies that have shown that perennial and annual herbs and grasses, such as those in the studied native habitat (Chapter 2; Appendix A), support a much lower diversity of insects, including herbivores, compared to trees and woody shrubs. It has been suggested this is because the availability of niches increases with plant size and complexity (Lawton 1978; Askew 1980; Lawton 1983). For example, in an Indonesian rainforest Stork and Brendell (1993) measured the abundance of arthropods from the tree canopy, tree trunks, ground-cover herb layer, leaf litter and soil. Overall, 32,000 individuals were collected, with the soil (56%) and litter (14%) habitats combined containing over twice as many arthropods per m^2 of ground as the canopy (28%). The numbers recorded from tree trunks (just over 1%), and especially the ground-cover herb layer (less than 1%), were negligible (Stork & Brendell 1993). The extremely seasonal nature of the native under-story comprised of annuals, geophytes and deciduous perennials at Mt Billy CP (Chapter 2: Figure 2.4) also points to a naturally depauperate herbivore community, with the tree canopy providing a more continuous source of plant tissue. Stireman (2003) suggested that lepidopteran parasitoid (Diptera: Tachinidae) richness did not vary between trees, shrubs or herbs because the mesquite-oak savannah habitat sampled had a stable, non-deciduous herbaceous plant community. At Mt Billy CP, geophytes, and annual and deciduous perennial herbaceous species build-up their above-ground biomass from nothing each season. This is in contrast to the canopy trees and mid-story shrubs that remain relatively unchanged in terms of their structure throughout the year, thus providing a more continuous variety of feeding, resting, hiding and over-wintering sites for resident arthropods (see Lawton 1983).

Habitat provided by bridal creeper

This study distinguished bridal creeper and native habitat based on plant diversity (Chapter 2). However, this distinction may be an artificial concept from an arthropod perspective. At both local and regional scales, habitat 'type' is a strong determining factor for the composition of arthropod communities, influencing both species presence and abundance (Kemp & Harvey 1990; Kemp, *et al.* 1990; Johnson & Bond 1992; Hughes, *et al.* 2000; Haslett 2001; Lassau & Hochuli 2005). Therefore, the overall similarity between arthropod communities and wasp assemblages collected from the two habitats suggests that the native and invaded ground-cover areas are not significantly different arthropod habitat. It is possible that bridal creeper simply has not caused a significant enough change to the habitat to bring about a corresponding change in the arthropod community.

The structural complexity or architecture of a plant community, rather than simply the number of plant species (or whether the plant is native or exotic), is often more important in determining the range of microhabitats available to arthropod herbivores, predators and parasitoids (Joern 1982; Lawton 1983; Samways & Moore 1991; Marino & Landis 1996; Sanchez & Parmenter 2002; Sax 2002; Kruess 2003; Langellotto & Denno 2004). In the studied habitat, bridal creeper had not created a new under- or mid-story like an invasive woody weed might have done, such as *Mimosa pigra*, that changes the structure of the invaded habitat from sedgeland to tall shrubland (Braithwaite, *et al.* 1989). Indeed, significant changes in arthropod communities due to weed invasion only seem to occur when the weed considerably changes the physical state of the habitat. For example, significantly reduced arthropod diversity was found in habitat dominated by willow (*Salix* x *rubens*) with no under-story compared with native habitat composed of a range of native trees with a shrub and herb understory (Greenwood, *et al.* 2004). Arthropod diversity was also reduced in shrubland of exotic shrubs and trees that was transformed from open grasslands (Samways, *et al.* 1996; Anthelme, *et al.* 2001). A study investigating the use of ants as indicator taxa in Western Australia found that weed invasion into native habitat resulted in little measurable change in community composition and species richness and no change in the number of genera or functional groups. However, the complete replacement of native vegetation by gardens or plantations resulted in a significant reduction in the number of species and functional groups, and altered species composition (Burbidge, *et al.* 1992).

If there were few herbivores present, the structure of native ground-cover plant community would be more important than plant diversity per se, providing resting and hunting areas with a suitable microclimate, rather than a direct food resource for arthropods. Therefore, although there appeared to be considerable changes to the structure of the habitat (loss of open, mossy areas: Chapter 2), the invasion of bridal creeper may not have resulted in a loss of habitat for the majority of the arthropod community. Furthermore, the diversity of groups collected from bridal creeper suggests that its foliage provides additional resting, hiding and hunting spaces in the habitat. Weeds, like all plant species, provide shelter for a range of non-herbivorous taxa and other studies of invasive plant species have recorded many arthropod species from a weed's foliage. For example, a survey of the invasive tree *Melaleuca quinquenervia* in Florida found that, of the most commonly occurring insect species, 67% were predators or detritivores and only 20% were herbivores, and of the 328 arthropod species recorded, only eight were observed feeding on the tree (Costello, *et al.* 2003).

The phenological similarities of bridal creeper and native flora (Chapter 2) also suggests that bridal creeper had not caused a significant temporal change in the habitat provided by the ground-cover vegetation. Its above-ground biomass is providing similar habitat structure as the native flora throughout the year (however, see Section 3.4.3). There were also no major differences in leaf litter composition between invaded and native areas, with *Acacia* and *Eucalyptus* leaves and bark being the major components of leaf litter in both habitats (Chapter 2). Thus, in comparison to an invader that considerably changes leaf litter composition by contributing large amounts of new plant material to the litter layer (eg. Griffin, *et al.* 1989; Clouse 1999; Blossey, *et al.* 2001), it is unlikely there has been considerable changes in litter chemical composition, suggesting that litter-feeding detritivores, and their parasitoids and predators are unlikely to be affected.

Patchy habitat

In addition to not causing considerable structural changes to the ground-cover habitat, bridal creeper also had not yet dominated the entire woodland habitat. From a landscape perspective, the woodland was still a botanically and structurally diverse system with the canopy trees and mid-story shrubs remaining intact and a ground-cover made up of a mosaic of bridal creeper patches inter-dispersed among native areas. Adult and juveniles life stages, particularly in holometabolous groups, can also have very different habitat requirements and many insects move between habitats depending on life stage (Delettre, *et al.* 1998; Cane & Tepedino 2001; Hunter 2002). As discussed above, parasitoids of plant-associated insects and gall wasps were found in both native and invaded habitat and, as bridal creeper does not provide herbivores with a food source, it is likely these wasps are moving between the canopy and the ground-cover vegetation that may be used as resting or hiding places. Furthermore, the collection from foliage of litter-associated parasitoids, along with the presence of plant-associated parasitoids on bridal creeper, shows that many species are developing elsewhere and are using both native and invaded ground-cover vegetation as adults.

In addition to multi-habitat use for adults and juveniles, a well-known fundamental process in arthropod population and community dynamics is that individuals frequently move between patches of suitable habitat for a range of biological reasons (Stinner, *et al.* 1983; Langellotto & Denno 2001; Denys & Tscharntke 2002; Hunter 2002). The degree to which this occurs depends largely on the biology of the species, but in general is also influenced by factors such as patch size, connectivity, distance between patches and suitability of habitat between patches (Hunter 2002; Cronin & Haynes 2004). Parasitoids, for example, have been shown to move relatively large distances following their hosts from 100m per season to 100's kms over several years (Hastings 2000; Schellhorn & Silberbauer 2003). Considering the limited flowering season of bridal creeper and the lack of insect visitors (Raymond 1999), the current patchiness of the habitat may be extremely important as most adult parasitoids need to feed on nectar from flowers or extra-floral nectaries (Jervis, *et al.* 1993; Tooker & Hanks 2000). Thus, it is possible that non-invaded areas contain flowering plant species used as a food source for highly mobile adult parasitoids and other nectar and pollen-feeding groups such as Lepidoptera and Diptera (see below). It is likely therefore, that arthropods in the studied system still had ready access to non-invaded areas and may simply move between the adjacent, relatively small, highly connected patches (from invaded to native areas) for food and other habitat requirements that may not have been provided by bridal creeper. Movement of parasitoids between native and invaded patches may also explain the lack of distinction between the two wasp assemblages recorded (Figure 3.9). Insect parasitoids have been shown to be influenced by habitat mosaic structure at different spatial scales, responding to habitat patches of different sizes (Roland & Taylor 1997). Considering the diversity of taxa recorded in this study, it is likely that different species would be responding differently to habitat patchiness caused by bridal creeper. To determine this, the movement of individual species would need to be investigated (eg. Coll & Bottrell 1996; Jones, *et al.* 1996). Such a study may also identify those species that could, or could not, move between invaded and non-invaded areas, which would have implications for the further spread of bridal creeper.

3.4.3 Temporal effects

Despite the similarities between the arthropod communities and wasp assemblages associated with invaded and native habitat, differences in temporal abundance for several groups suggest a more subtle effect of bridal creeper invasion. Significant seasonal influences, in addition to (or instead of) habitat effects, are usually found when temporal measurements are incorporated into arthropod studies (eg. Newell 1997; Barbosa & Marquet 2002; Greenwood, *et al.* 2004). Considering the strong seasonal influence of rainfall and temperature on plant growth and senescence (Chapter 2), and thus available resources and habitat structure, corresponding differences in arthropod abundance is not unexpected. In general, the population dynamics of arthropods follow the seasonality of a Mediterranean climate (Stamou, *et al.* 2004). The significant interactions between sample date, habitat and abundance also suggest that the habitat provided by bridal creeper varies temporally and that, for some taxa, non-invaded areas are providing important habitat for some parts of the year, particularly in spring and summer (Figure 3.2). At Mt Billy CP, there were significantly fewer Lepidoptera, Coleoptera, Hemiptera and Thysanoptera overall recorded from bridal creeper transects (Table 3.1; Figure 3.1). These are all orders that include major specialist herbivores that, as both juveniles and adults, feed on leaves, seeds, fruits, pollen and nectar (Naumann, *et al.* 1991). The significant differences in abundance for these groups were in spring and summer (except for Coleoptera, whose numbers were different over autumn) (Figure 3.2e, g, h, i) which corresponds to the presence of maximum native plant growth and the availability of nectar, pollen and seeds. It may be that over spring and summer, bridal creeper does not provide resources equivalent to those from native plants for these, and other plant-feeding groups such as nectar-feeding flies and wasps that also had significant temporal differences in their abundances between native and invaded habitat (Figure 3.2a, d). However, these groups certainly were not absent from bridal creeper transects and the level of identification used could not determine if particular species were present in native areas only, or at certain times (except for wasps, see below). Considering the original trophic-level hypothesis of this study, and that species of specialist herbivorous Lepidoptera and Coleoptera have been found to be adversely affected when their specific food plants are displaced by weed invasion (Harris, *et al.* 2004), further work is needed to determine if any of the ground-cover species at Mt Billy CP are important food plants for herbivorous taxa. Detailed knowledge of food-plant associations is usually only available for well-known, specific taxa or systems (eg. Joern & Lawlor 1981; Dubbert, *et al.* 1998; Corff, *et al.* 2000; Memmott, *et al.* 2000), and this type of data are rarely available for entire assemblages, let alone communities (but see Memmott, *et al.* 1993; Memmott, *et al.* 1994; Valladares & Salvo 1999). As such, a more targeted study on single, or small groups of, species and native plants would be useful.

The effect of sample date was also considered for the most abundant wasps common to both habitats to investigate, at a species level, if invaded and native areas were providing habitat for individual species throughout the year (Figure 3.10). The total numbers of these species are quite low and cannot be tested statistically, but these patterns show that for a range of biologically diverse species (Figure 3.10a-d), their temporal occurrence and abundance in native habitats were similar to that in invaded areas. This suggests that bridal creeper provides these species with seasonally equivalent habitat and supports the hypothesis that, overall, their habitat has not been significantly altered by bridal creeper. Several other species, which occurred almost throughout the entire sampling period (Figure 3.10e-h), showed some temporal differences in their occurrence and abundance, perhaps indicating that bridal creeper and native ground-cover vegetation provides habitat for these species at different times of the year. The data could not isolate what specifically it is about the two habitats that is providing resources for some species and not others at different times of the year, as adult parasitoids are influenced by a range of habitat factors such as habitat type, structure, shelter, food plants, temperature and rainfall (Jervis, *et al.* 1993; Shapiro & Pickering 2000; Tooker & Hanks

2000; Whitfield & Lewis 2001). Host abundance and distribution also determine the presence of a parasitoid species (Dubbert, *et al.* 1998; Ulrich 1998; Doak 2000; Ulrich 2004). However, as discussed above, mobility and the patchiness of the habitat would allow adult wasps to move between patches to suitable habitat and resources, and thus from the collection of adults it is difficult to determine if individual species are responding to the presence of available hosts.

Finally, three orders did not have significant interactions between sample date and habitat. Mites (Acarina), springtails (Collembola) and spiders (Araneae) all had highly variable temporal abundance patterns that were not significantly different between native and invaded habitat (except for Collembola in just one of the 14 months) (Figure 3.2b, c, f). Mites and Collembola are very common in soil and leaf litter, favouring moist habitats (Harvey & Yen 1989; Naumann, *et al.* 1991), while spiders and predacious mites are strongly influenced by habitat structure provided by both plants and litter (Langellotto & Denno 2004). It is likely therefore, that for these groups that are less reliant on the presence of specific types of plants, the habitat structure provided by bridal creeper is equivalent to the native habitat it replaces in terms of factors such as structure and moisture.

3.5 Conclusion

The predicted hypothesis that the decline of the basal trophic level would have flow-on effects to higher trophic levels was not found in this study. The lack of difference between arthropod and wasp abundance, wasp species richness and assemblage structure and composition suggests that overall, the arthropod community in bridal creeper was very similar to that found in non-invaded native areas. As such, bridal creeper appears to have had very little impact on the ground-cover plant-associated arthropod community. Possible explanations include the natural absence of insect herbivores that would otherwise be directly affected by the loss of native plant species; the limited change to the arthropod habitat, particularly its structure; and the patchy invasion of the weed that was still allowing mobile species access to native habitat if required.

The lack of impact on arthropod diversity also revealed that bridal creeper's foliage provided habitat for a wide range of arthropods and parasitoids. However, despite the presence of these typically mobile adult insects, it cannot be assumed that bridal creeper provides a complete range of arthropod habitat requirements. There were strong temporal effects for several plant-dependent groups that suggested bridal creeper might not be providing habitat all year round.

This was in contrast to taxa that would respond more to structure and microclimate, and thus were unaffected by plant diversity per se. Adult and juveniles life stages, particularly in holometabolous groups, can also have very different habitat requirements and many insects move between habitats depending on life stage (Delettre, *et al.* 1998; Cane & Tepedino 2001; Hunter 2002). For example, parasitoids are largely immobile as parasitic larvae, but as adults move about to consume nectar and pollen, and search for mates and hosts. Parasitoid host records revealed that this was indeed occurring in the studied habitat. Gall and other plant-associated wasps associated with the canopy were collected in the ground-cover vegetation. The collection from foliage of litter-associated parasitoids and, in the absence of herbivores, the presence of parasitoids of plant-associated hosts on bridal creeper, showed that many species develop elsewhere and move into both native and invaded ground-cover vegetation as adults.

Despite a comparable wasp assemblage being collected from bridal creeper's foliage, it is not known if ecological processes (such as parasitism of hosts) are actually taking place within invaded habitat or if taxa collected from bridal creeper are simply 'tourist fauna', occupying secondary habitat at the edge of native habitat as resting and hunting spaces (French & Eardley 1997). To more fully determine the effects of bridal creeper on arthropod diversity, and in turn predict the consequences of its further spread, the habitat used for arthropod reproduction and development needs to be considered. This was investigated by examining the effect of bridal creeper on parasitic wasp larval habitat and host associations, and is presented in the following chapter.

Chapter 4

The impact of bridal creeper on parasitic wasp developmental habitat and host associations

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4.1 Introduction

The impact of habitat change, including that caused by weed invasion, is usually measured as an increase or decrease in species abundance and richness of a single group or a variation in community composition. However, the interpretation of such modifications is more meaningful when the functional component of biodiversity is considered. The functioning of ecological systems is largely determined by interactions among species that structure communities and facilitate energy and material flow (Chapin, *et al.* 2000). In the context of conserving insect biodiversity, Fisher (1998) suggests that it is not the presence or absence of a species that is important, but whether or not insect-driven interactions and ecological processes are occurring. The same approach can be taken when considering the effects of habitat modification. Consequently, the impact of weed invasion on an invaded community may not only directly affect the abundance and distribution of native species, but also the interactions these species are involved in, that will in turn influence ecological processes and functioning. The disruption of species interactions involving insects due to habitat alterations such as grazing and habitat fragmentation have been reported to impact on pollination systems, seed dispersal, decomposition, and host-parasitoid relationships (LaSalle & Gauld 1993; Dubbert, *et al.* 1998; Kearns, *et al.* 1998; Knops, *et al.* 2001; Steffan-Dewenter 2002). However, there is there is little research on the impact of weed invasion on such interactions (Blossey, *et al.* 2001; French & Major 2001), particularly those among parasitoids and their hosts.

Parasitic Hymenoptera are a major contributor to the functioning and stability of terrestrial ecosystems via the regulation of their arthropod host populations (LaSalle 1993). Across most terrestrial niches, parasitic wasps are involved in interactions with arthropod herbivores, detritivores and predators. The evolution of host-parasitoid associations has resulted in specialised relationships with both host taxa and host habitat. The specific type(s) of host attacked are determined by both host taxonomy and ecology, for example, host habitat or feeding niche (Godfray 1994). Hymenoptera are holometabolous insects whose larvae differ fundamentally in morphology, diet and lifestyle from adults, and undergo complete metamorphosis via a pupal stage (Gullan & Cranston 2004). As such, larval and adult parasitic wasps have very different mobilities and habitat requirements. Parasitic larvae and pupae are relatively immobile and rarely free-living, whereas adult wasps move about to consume nectar and pollen, and search for mates and hosts. Apart from the mutualistic association adult wasps have as pollinators of flowering plants, it is the larval stage that is more ecologically significant due to the intimate interaction with their hosts and the diversity of taxa attacked. Specific habitat requirements, complex life-cycles and often naturally small populations make parasitic Hymenoptera prone to changes caused by habitat modification (LaSalle 1993; Polis, *et al.* 1996; Tscharntke, *et al.* 1998). In particular, parasitic larvae may be predicted to be better at detecting the effects of habitat change due to their habitat and host specificity and relative immobility. Their specific relationships with both host taxa and host niche also allow parasitoids to be used for the indirect investigation of other arthropod groups, their associated habitats, and trophic levels.

The results presented in Chapter 2 revealed that bridal creeper has a clear negative effect on native plant species and is changing habitat characteristics such as the amount of leaf litter. However, as reported in Chapter 3, there was little effect of removal of native ground-cover plant species on adult plant-dwelling arthropods. Indeed, it appears that bridal creeper's foliage is providing habitat for a wide range of arthropods, including parasitic wasps. However, the arthropod community associated with bridal creeper's foliage may simply be 'tourist fauna', occupying secondary habitat at the edge of native vegetation as resting and hunting spaces, not consuming bridal creeper or the leaf litter under it (eg. French & Eardley 1997). Thus, it may be that bridal creeper is not providing habitat for the development of parasitoids and their hosts. The results from Chapter 3 also prompted the question: was there no effect of bridal creeper invasion because the ground-cover habitat was not important for the reproduction and development of parasitoids and their hosts, ie. did the arthropods collected from bridal creeper and native ground-cover foliage come from elsewhere (Figure 4.1)? The collection from foliage of litter-associated parasitoids and, in the absence of herbivores, the presence of plant-associated parasitoids on bridal creeper, showed that many species developed elsewhere and moved into both native and invaded ground-cover vegetation as adults (Figure 4.1).

As the specific locations of parasitoid and host development are unknown, it is difficult therefore to clearly determine the effects of bridal creeper invasion on arthropod biodiversity. However, if hosts are occurring in invaded areas, the searching efficiency of parasitoids, and hence parasitism of hosts, could be predicted to be impacted upon by bridal creeper's thick

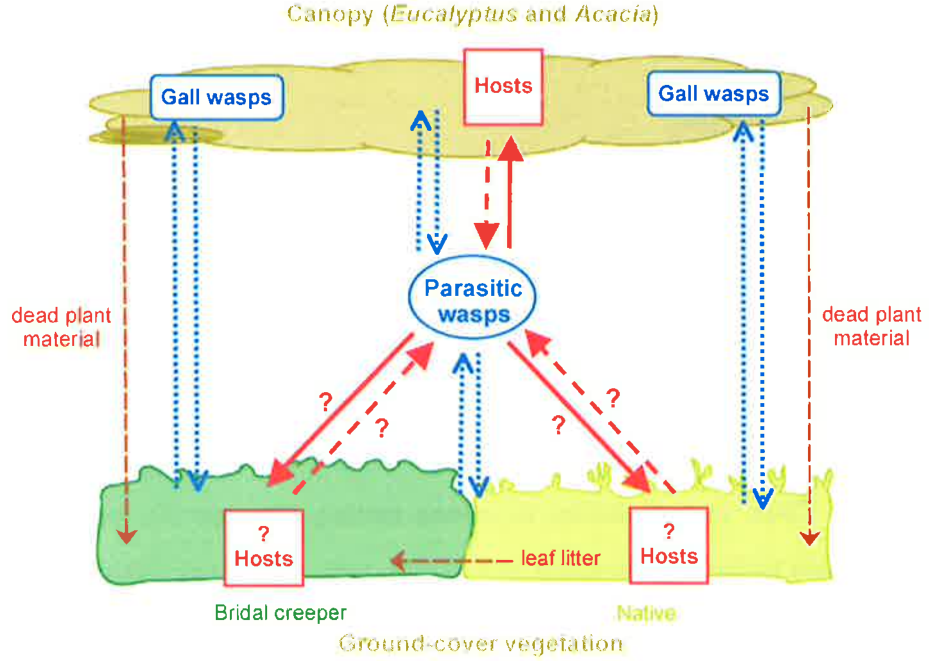


Figure 4.1 Descriptive model of parasitic wasp movement at Mt Billy CP. Adult parasitic wasps and gall wasps move between the canopy and ground level vegetation ⇠⇢. Host arthropods are parasitised in the canopy ⟶ and adult wasps emerge - - -▶ from hosts then move about to find food (nectar and pollen), mates and hosts. From the sweep net study it cannot be determined if the ground-cover habitat (vegetation and litter) is the location of the development of parasitoids and their hosts, and thus the possible impacts of bridal creeper on arthropod biodiversity have not been fully investigated and explained. In particular, considering the dominance of litter-associated parasitoids (and thus hosts), the accumulation of leaf litter ◀- - - in bridal creeper invaded areas (Chapter 2) requires further investigation as it might be predicted to be influencing soil and leaf litter-associated arthropods and their parasitoids.

growth or increased litter layer beneath the plant. It has been suggested that one of the impacts of invasive plants with thick, impenetrable growth is to impede the movement and activity of insects (Samways, *et al.* 1996; Steenkamp & Chown 1996), potentially influencing interactions such as those between predators and prey, or hosts and parasitoids. Furthermore, parasitoids usually show a preference for host-searching, for example at specific heights above ground, in areas of shade or sunlight, or high or low humidity (Sato & Ohsaki 1987; Gauld & Bolton 1996), and as such may be significantly influenced by changes to habitat structure (Langellotto & Denno 2004).

To more fully determine the effects of bridal creeper on arthropod biodiversity and in turn predict the consequences of further spread, the habitat used for parasitoid (and indirectly, host) reproduction and development needs to be considered (Figure 4.1). The high numbers of soil- and leaf litter-associated parasitoids reported in Chapter 3 also revealed the importance of dead plant material in this woodland system. As such, the accumulation of leaf litter under bridal creeper (Figure 4.1) may also have implications for the development of these parasitoids. Therefore, the aim of this study was to determine the impacts of bridal creeper invasion on arthropod diversity and community composition by examining the developmental habitat associations of parasitoids and their hosts.

4.2 Methods

4.2.1 Parasitic wasp sampling

The developmental habitat of holometabolus insects can be indirectly investigated by using emerging adults that are more readily identified than larvae (Hövemeyer 1999). As such, to quantitatively sample parasitoids and their hosts directly associated with the ground-cover microhabitat (plants, litter and soil), emergence traps that covered a fixed area of ground were used. Such traps are also particularly useful as they are selective, yield only resident taxa, and reflect the breeding success of individuals in the ground area covered by the traps (New 1998; Hövemeyer 1999). Thus, in comparison to sweep-netting (Chapter 3), individuals collected can be directly related to their (potentially more important) larval environments. Furthermore, the sampling intensity for both habitats was identical, being unaffected by sampling bias or differences sometimes caused by habitat structure and other sampling conditions (Melbourne 1999; Gotelli & Colwell 2001).

The emergence trap designed for this study was a triangular 80cm high, white, densely woven fabric tent with an open base (50cm x 50cm) firmly pegged to the ground to prevent surface arthropod movement in and out of the trap (Figure 4.2). In addition, the edges of the trap were buried approximately 5cm into the ground to further prevent arthropod movement. The top of the trap was connected to a removable collection bottle containing preserving fluid (70% ethanol). Arthropods that emerged within the trap were attracted upwards towards the light and collected in the bottle. The fabric allowed air, light and rainfall into the trap so that the microhabitat covered by the trap was not altered. Throughout the sampling period, both native plants and bridal creeper continued to grow, flower, senesce and re-shoot inside the traps identically to those immediately outside the traps (pers. obs.). Thus, it can be assumed that the soil and litter microhabitat also remained largely unchanged.

Three sites, each approximately 150m apart and consisting of an invaded (≈ 70m x 70m) and adjacent native (control) habitat patch, were selected within *Eucalyptus leucoxylon* and *E. fasciculosa* woodland at Mount Billy Conservation Park (CP) (refer to Chapter 2 for a full habitat description). Within each site, three pairs of traps were established: three in invaded and three in native habitat, giving a total of 18 traps. Those traps placed in the native areas were established over habitat free of bridal creeper (Figure 4.3a). Conversely, weed-invaded traps were installed over habitat with 90-100% cover of bridal creeper (Figure 4.3b).

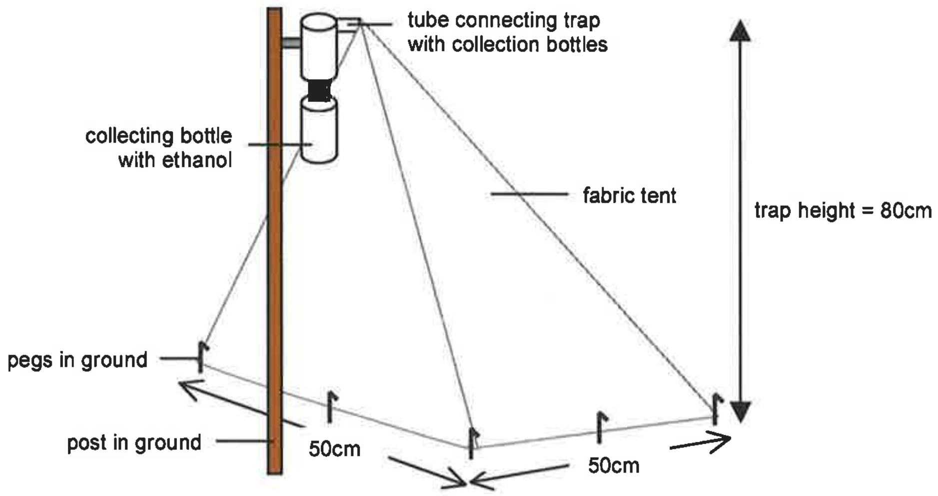


Figure 4.2 Emergence trap designed for this study. Arthropods that hatched and emerged from plants, litter and soil within the trap were attracted upwards towards the light and collected in the attached ethanol bottle.

Traps in both native and invaded habitats were placed away from the edge of patches to limit the effect of changes in habitat and community structure that can occur at the edge of a habitat (Schowalter 2000). In addition, it was considered that soil and litter dwelling larvae could have potentially moved under the edge of the trap and been collected. Having the traps situated well into the sampled habitat meant that if this was occurring, arthropods were likely to be only moving from the same habitat and not confounding results (refer to Chapter 2, Section 2.2 for an outline of multi-site comparisons and experimental site selection at Mt Billy CP). Where each trap was to be positioned, the following microhabitat measurements were recorded (5 random replicates (10 x 10cm quadrats) of each measurement in a 50cm x 50cm area): vegetation height and leaf litter depth, and the percent cover of bridal creeper, leaf litter, moss (bryophytes), and bare ground.

As temperature, rainfall and ground-cover vegetation in both the invaded and native habitats were extremely seasonal (Chapter 2), the emergence traps remained in the field from September 2001 to July 2002 to account for plant growth and senescence and changes in soil and litter moisture. The collection bottles were replaced weekly and samples returned to the laboratory for processing. The enclosed nature of the emergence traps allowed potential parasitoid host availability to be inferred by examining the arthropods that also emerged from the habitat covered by the traps. Collected arthropods were identified to order, and the wasps further identified to family, tribe and/or genus and then 'morphospecies'. Each morphospecies was assigned a functional group (Appendix E) based on host or prey association and/or biology (refer to Chapter 3, Section 3.2 for a full description of arthropod and wasp processing and functional group analysis). The wasp morphospecies are referred to as 'species' for the remainder of this chapter.

Figure 4.3 Emergence traps situated in **(a)** native and **(b)** bridal creeper-invaded habitat (September 2001).

4.2.2 Data analysis

The total arthropod order-level abundance, wasp species richness and abundance for all 43 weekly sample periods combined were used for analyses to gain more comprehensive understanding of community and assemblage responses. Initial investigation of the data revealed no difference between the three sampled sites (eg. Figure 4.9), thus all nine bridal creeper and nine native traps were used for analysis, ignoring patch distinction. As native and bridal creeper traps were paired, the differences in habitat variables and abundance and species richness of wasp families, functional groups and potential host taxa between native and invaded transects were analysed using paired t-tests utilising GraphPad Prism (ver. 4.0 for Macintosh, GraphPad Software, San Diego California USA).

The number of species and mean number of individuals were graphed against the number of native or bridal creeper traps from which they were recorded ('incidence data' (Magurran 2004) to investigate the distribution (or density) of species across the two habitat types. To further investigate wasp diversity, the evenness (species relative abundances) (Magurran 2004)) of native and bridal creeper assemblages were examined using rank abundance curves for each functional group. The log-normal model, which is the most common rank abundance model for stable, species-rich ecological communities (Schowalter 2000; Magurran 2004), was fitted and tested using the Rank-Abundance or Dominance/ Diversity Models in R: A language and environment for statistical computing (R Development Core Team, R Foundation for Statistical Computing) to compare assemblages from native and invaded habitat. The 'veiled' log-normal function, which assumes that only a proportion of the assemblage was sampled, was used to account for species that may have been missed. Non-metric multi-dimensional scaling (NMDS) using PC-ORD (ver. 4.25) was used to examine wasp assemblage composition and habitat variables for all wasp species and each functional group. Indicator species analysis (Dufrêne & Legendre 1997) was used to detect wasp species that were indicators of native and invaded habitat using PC-ORD (refer Chapter 2 for full descriptions of NMDS and indicator species analysis).

To investigate differences in wasp emergence, host use and development between bridal creeper and native habitat, the proportional weekly emergence patterns of the most abundant species common to both habitats were compared. To investigate the effect of leaf litter on wasp abundance and diversity, the relationship between litter depth and percent cover, and the number of individuals and mophospecies in each functional group, was analysed using the linear regression function in GraphPad Prism.

4.3 Results

4.3.1 Habitat covered by emergence traps

Reflecting the selection of trap sites, the percent cover of bridal creeper ranged from 90-100% under invaded traps and was absent (0% cover) from native traps (Figure 4.4). The dominant vegetation under invaded traps was bridal creeper, plus occasionally a small amount of grass (Poaceae sp.). The dominant plant species under native traps were maiden-hair fern (*Adiantum aethiopicum*), green rock fern (*Cheilanthes austrotenuifolia*), grass (Graminae sp.), native carrot (*Daucus glochidiatus*), kidney weed (*Dichondra repens*), coarse bottle-daisy (*Lagenifera huegelii*), native buttercup (*Ranunculus lappaceus*), and moss. These species varied considerably in their abundance and composition among native traps.

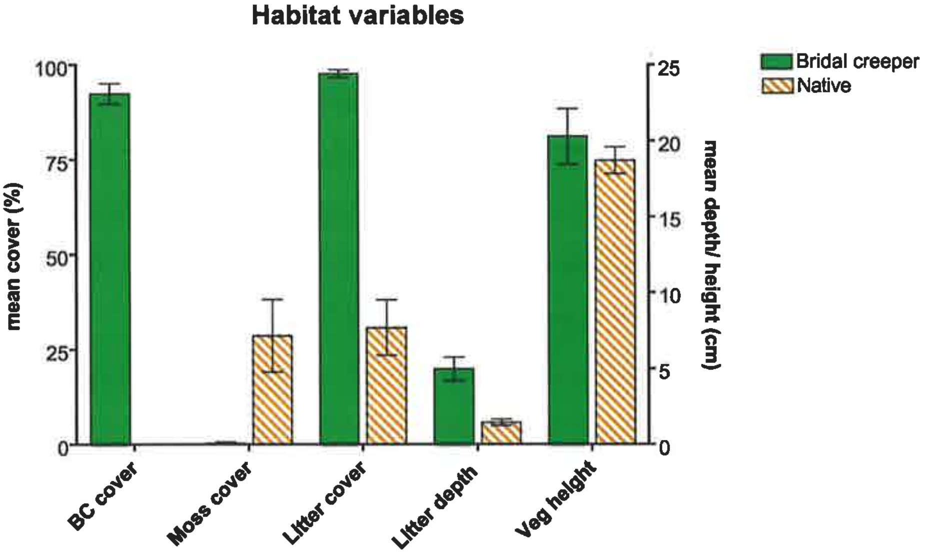


Figure 4.4 Mean (±SE) percent cover of bridal creeper, litter, moss, and litter depth and vegetation height from under bridal creeper (n=9) and native (n=9) emergence traps, September 2001.

As in the previous habitat survey (Chapter 2), the percent cover of moss was greater in native habitats, being almost absent from invaded habitat (t=2.977, P=0.0177) (Figure 4.4). However, moss cover varied considerably among native traps ranging from 0-90% cover. Also, as reported in Chapter 2, leaf litter consisted of *Eucalyptus* and *Acacia* leaves, bark, and twigs, and the percent cover of litter was greater in bridal creeper invaded habitat (t=11.33, P<0.0001), as was litter depth (t=3.917, P=0.0044) (Figure 4.4). As with the dominant plant species and moss cover, the percent cover of litter varied among native traps, ranging from 7-58%. Vegetation height was not significantly different between habitats (t=0.8006, P=0.4465) (Figure 4.4). No bare ground was recorded.

4.3.2 Wasp species richness and abundance

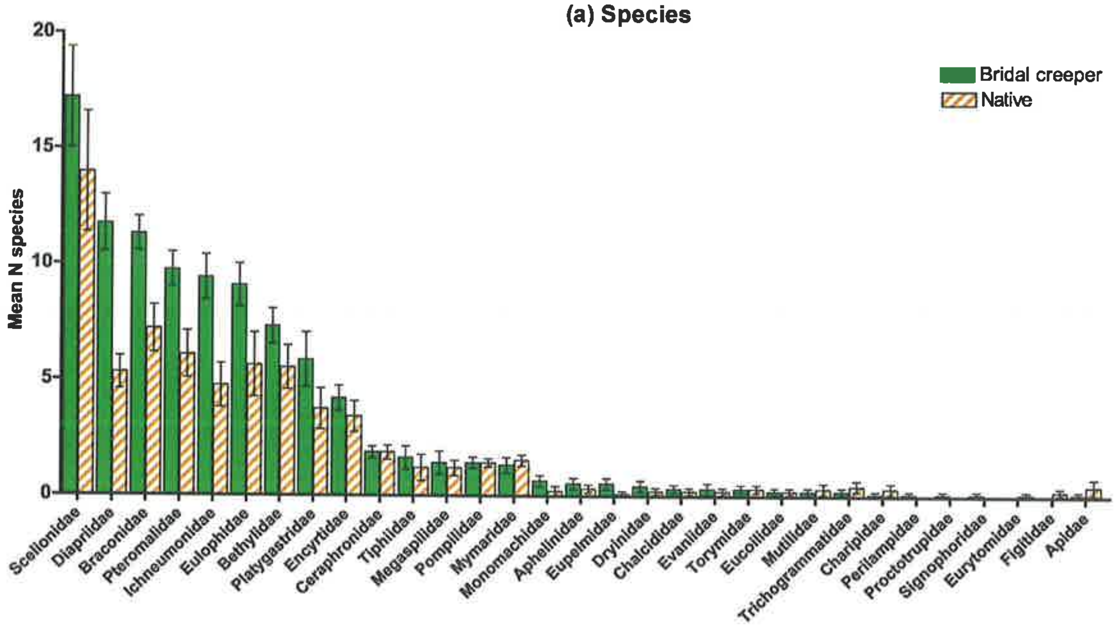
A total of 6316 Hymenoptera from 31 families in 10 superfamilies emerged over the 43 weeks from the emergence traps at Mt Billy CP (Table 4.1). The family Diapriidae was the most abundant (32.8% of all individuals collected), followed by Pteromalidae (11.7%), Braconidae (10.9%), Eulophidae (9.8%) and Scelionidae (9.3%). A total of 461 species were identified. Scelionidae was the most species-rich family with 75 species, followed by Braconidae (53), Platygastridae (41), Eulophidae (38), Diapriidae (36), Pteromalidae (34), Encyrtidae (33). The number of scelionid species may be slightly over estimated because of the difficulty in matching some male and female species (Appendix B). Both native and invaded habitat were sufficiently well sampled over the 43 weeks as indicated by the plateauing of species accumulation curves (Appendix F) that allowed for meaningful comparison of abundance and species richness between native and invaded habitats (Gotelli & Colwell 2001).

In distinct contrast to the results of Chapter 3, there were considerably more wasps collected from invaded than native habitat. Almost three times as many individuals emerged from bridal creeper-invaded habitat than from native habitat (Table 4.1). There were also more species collected in bridal creeper traps (Table 4.1). Although the majority of wasp families were recorded from both native and bridal creeper traps, several families were significantly more abundant (Eulophidae, Pteromalidae, Bethylidae, Braconidae, Ichneumonidae, Diapriidae), and more speciose (Encyrtidae, Eulophidae, Pteromalidae, Bethylidae, Braconidae, Ichneumonidae, Scelionidae, and Diapriidae) in invaded habitat (Table 4.1). The most noticeable difference was the abundance of Diapriidae. On average, native traps collected around 30 diapriid individuals over the sample period, whereas an average of 200 individuals emerged from traps in invaded habitat (Figure 4.5). The abundance of Diapriidae was dominated by one species, Diapriidae sp. 01 (Diapriinae: *Rostropria inopicida*), which made up 76% of all diapriids collected (BC: total=1487 (82.8% of all diapriids), mean±SE=165.2±46.4; Native: total=99 (35.9%), mean±SE=11±4.2). Despite the large differences in numbers, the same families were the most abundant and diverse within both invaded and native habitats (Figure 4.5).

Table 4.1 Hymenopteran families (excluding Formicidae) recorded in emergence trap samples from Mt Billy CP; and the total and difference (paired t-test) in the number of (a) species and (b) individuals for each family from bridal creeper (BC) and native habitat. nt: not tested, ns: not significant, * P< 0.05, ** P< 0.01, ***P< 0.001

	(a) total N species			(b) total N individuals		
Family	**BC**	**Native**	**t-test**	**BC**	**Native**	**t-test**
APOIDEA						
Apidae (bees)	1	2	nt	1	4	nt
CERAPHRONOIDEA						
Ceraphronidae	7	9	ns (t=0.000 P=1.000)	35	33	ns (t=0.273 P=0.791)
Megaspilidae	7	8	ns (t=0.3730 P=0.7188)	35	17	ns (t=0.9487 P=0.3706)
CHALCIDOIDEA						
Aphelinidae	3	3	nt	6	6	nt
Chalcididae	2	2	nt	6	2	nt
Encyrtidae	25	15	ns (t=1.421 P=0.1930)	232	99	* (t=3.183 P=0.0129)
Eulophidae	32	23	* (t=2.601 P=0.0315)	490	128	** (t=4.356 P=0.0024)
Eupelmidae	2	1	nt	7	0	nt
Eurytomidae	0	1	nt	0	1	nt
Mymaridae	5	5	ns (t=0.4264 P=0.6811)	18	35	ns (t=1.522 P=0.1665)
Perilampidae	1	0	nt	1	0	nt
Pteromalidae	28	20	* (t=3.317 P=0.0106)	549	191	* (t=3.104 P=0.0146)
Signophoridae	1	0	nt	1	0	nt
Torymidae	3	1	nt	3	4	nt
Trichogrammatidae	2	2	nt	2	5	nt
CHRYSIDOIDEA						
Bethylidae	24	21	** (t=4.438 P=0.002)	125	71	* (t=3.157 P=0.0134)
Dryinidae	2	2	nt	6	2	
CYNIPOIDEA						
Charipidae	1	2	nt	1	3	nt
Eucoilidae	2	1	nt	2	2	nt
Figitidae	0	1	nt	0	2	nt
EVANOIDEA						
Evaniidae	3	1	nt	3	2	nt
ICHNEUMONOIDEA						
Braconidae	39	34	** (t=3.406 P=0.009)	490	200	** (t=3.357 P=0.010)
Ichneumonidae	26	16	** (t=3.810 P=0.0052)	303	118	* (t=2.852 P=0.0214)
PLATYGASTROIDEA						
Platygastridae	30	19	ns (t=2.296 P=0.0508)	133	182	ns (t=1.068 P=0.3168)
Scelionidae	57	57	ns (t=1.262 P=0.2426)	357	231	* (t=2.881 P=0.0205)
PROCTOTRUPOIDEA						
Diapriidae	32	20	*** (t=5.575 P=0.0005)	1796	276	** (t=3.745 P=0.0057)
Monomachidae	1	1	nt	6	2	nt
Proctotrupidae	1	0	nt	1	0	nt
VESPOIDEA						
Mutilidae	2	3	nt	2	3	nt
Pompilidae	8	8	ns (t=0.000 P=1.0000)	16	17	ns (t=0.1890 P=0.8548)
Tiphiidae	6	7	ns (t=1.180 P=0.2721)	31	23	ns (t=1.037 P=0.3300)
TOTAL	353	285	** (t=4.050 P=0.0037)	4659	1657	*** (t=5.225 P=0.0008)

(a) Species



(b) Individuals

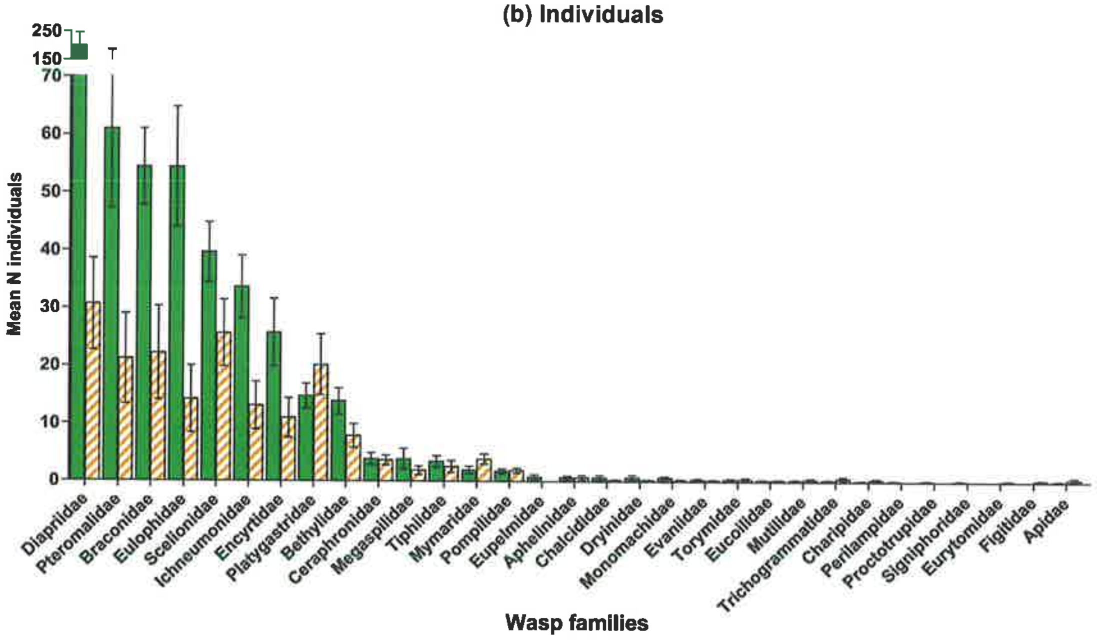


Figure 4.5 (a) Mean (±SE) number of wasp **(a)** species and **(b)** individuals for each hymenopteran family recorded from emergence traps in bridal creeper) (n=9) and native (n=9) habitat. For comparison, families have been ranked by descending number of species and individuals from bridal creeper traps.

Functional groups

No functional group was absent from either habitat type; all eight groups had members recorded from both bridal creeper and native habitats. As reported in Chapter 3, parasitoids of litter and soil dwelling arthropods were the most abundant and species-rich group across both habitats, followed by parasitoids of free-living plant-associated insects (Figure 4.6). However, four groups were significantly more abundant and speciose in bridal creeper: parasitoids of litter- and soil-associated arthropods, plant-associated insects, plant- and litter-associated arthropods, and insects feeding inside plant tissue (Table 4.2). The most notable difference was parasitoids of litter and soil arthropods. This group were considerably more species-rich, and particularly more numerous, in bridal creeper invaded habitat (Figure 4.6). This was largely due to the high numbers of Diapriidae and, in particular, Diapriidae sp. 01. The ranked order of both the number of individuals and species in each functional group were very similar across both habitats (Figure 4.6).

Table 4.2 Total and difference (paired t-test) in the number of (a) species and (b) individuals for each functional group collected in emergence traps from bridal creeper and native habitat. nt: not tested, ns: not significant, * P< 0.05, ** P< 0.01, ***P< 0.001. For details of each functional group see Chapter 3, Section 3.3.2 and Appendix E.

	(a) Species N			**(b) Individuals N**		
Functional group	**BC**	**Native**	**t-test**	**BC**	**Native**	**t-test**
1 Plant sucking-associated parasitoids	29	26	ns (t=2.014 P=0.0788)	85	100	ns (t=0.4291 P=0.6791)
2 Plant tissue- associated parasitoids	19	14	** (t=4.105 P=0.0034)	415	84	** (t=4.135 P=0.0033)
3 Plant-associated parasitoids	81	61	*** (t=7.272 P<0.0001)	903	410	*** (t=5.685 P=0.0005)
4 Plant gall-associated wasps	44	28	ns (t=1.755 P=0.1174)	161	176	ns (0.2684 P=0.7952)
5 Wood-boring associated parasitoids	2	2	nt	3	2	nt
6 Litter-associated parasitoids	109	89	*** (t=6.027 P=0.0003)	2545	615	** (t=3.895 P=0.0046)
7 Vespoidea and Apidae parasitoids	3	4	nt	6	6	nt
8 Litter/plant-associated parasitoids	51	50	** (t=2.422 P=0.0417)	522	251	* (t=3.105 P=0.00146)

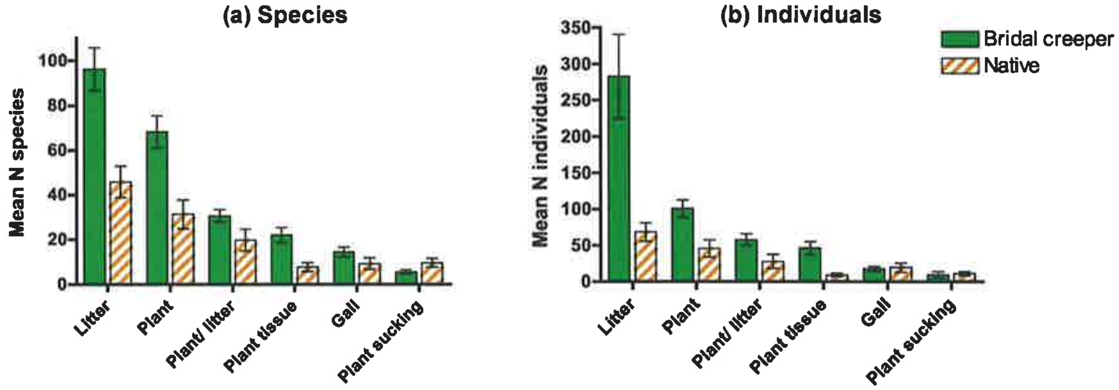
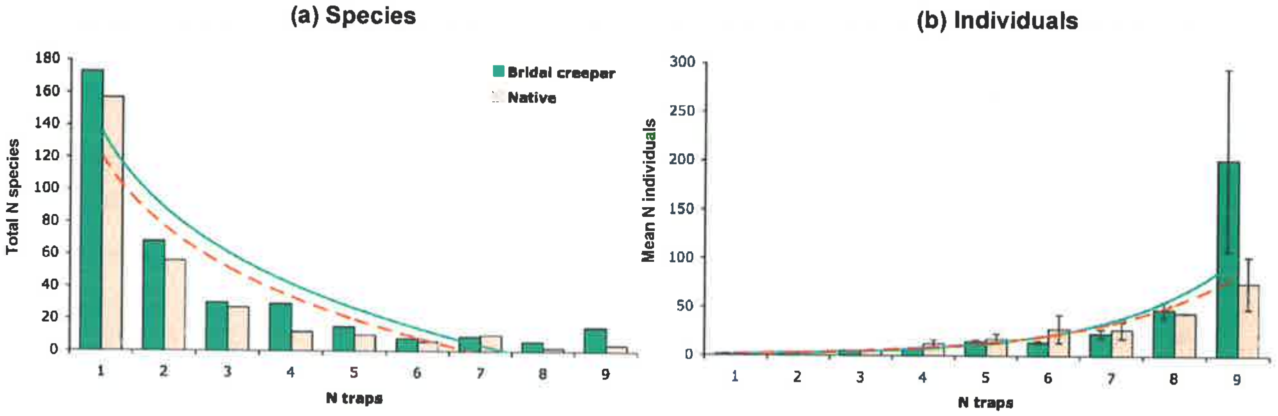


Figure 4.6 (a) Mean (±SE) number of **(a)** wasp species and **(b)** individuals in each functional group recorded from emergence traps in bridal creeper (n=9) and native (n=9) habitats. For comparison, functional groups have been ranked by descending number of species and individuals from bridal creeper traps. Parasitoids of wood-boring insects (Group 5) and those associated with Vespoidea and Apidae nests (Group 7) were not included due to the very low numbers collected.

4.3.3 Wasp assemblage structure and composition

Habitat distribution

As reported in Chapter 3, incidences of species, or their spatial distribution across the habitat, was almost identical for both bridal creeper and native habitat. There was a negative relationship between the number of species and the number of traps in which a species was present, where the majority of species were recorded only from one location (ie. only one trap) (Figure 4.7a). Conversely, there was a positive relationship between the mean abundance of a species and the number of traps it was recorded from, which was also the same for both bridal creeper and native habitat (Figure 4.7b). There was one noticeable difference in wasp abundance between habitats, with a comparatively high mean number of individuals recorded from all nine bridal creeper traps (Figure 4.7b). This was due to Diapriidae sp. 01, which emerged in high numbers from all nine traps across the invaded sites.


(a) Species

(b) Individuals

Figure 4.7 **(a)** Number of wasp species recorded across different numbers of traps (fitted line (logarithmic): BC: r^2=0.8231, N: r^2=0.8161); **(b)** Mean (±SE) number of individuals from species recorded across different numbers of traps (fitted line (exponential): BC: r^2=0.9456, N: r^2=0.9589).

Rank abundance distributions

The relative proportion of species represented by 10 or less individuals was 84% for bridal creeper and 89% for native habitat. The proportion with less than 5 individuals was also similar (bridal creeper: 75%, native: 80%) and the proportion of singletons (species recorded as a single specimen) was the same from both bridal creeper and native traps (35%). Accordingly, as with the assemblages reported in Chapter 3, the frequency distributions of species from both habitats are similarly left-skewed, with a long tail of rare species (Figures 4.8-9).

The ranked abundance distributions of each functional group mostly fitted a log-normal distribution (Figure 4.8a-d, f). The exception was soil and litter-associated parasitoids recorded from invaded habitat, where a log-normal curve could not be fitted (Figure 4.8e). This may be due to Diapriidae sp. 01 which dominated the bridal creeper assemblage. This species contributed to over 30% of all wasp individuals emerging from bridal creeper traps (Figure 4.9a). In contrast, the assemblage recorded from native traps was not dominated by one species. The species frequency distributions from native traps had a much shallower slope of suggesting greater species evenness in this assemblage (Figure 4.9b).

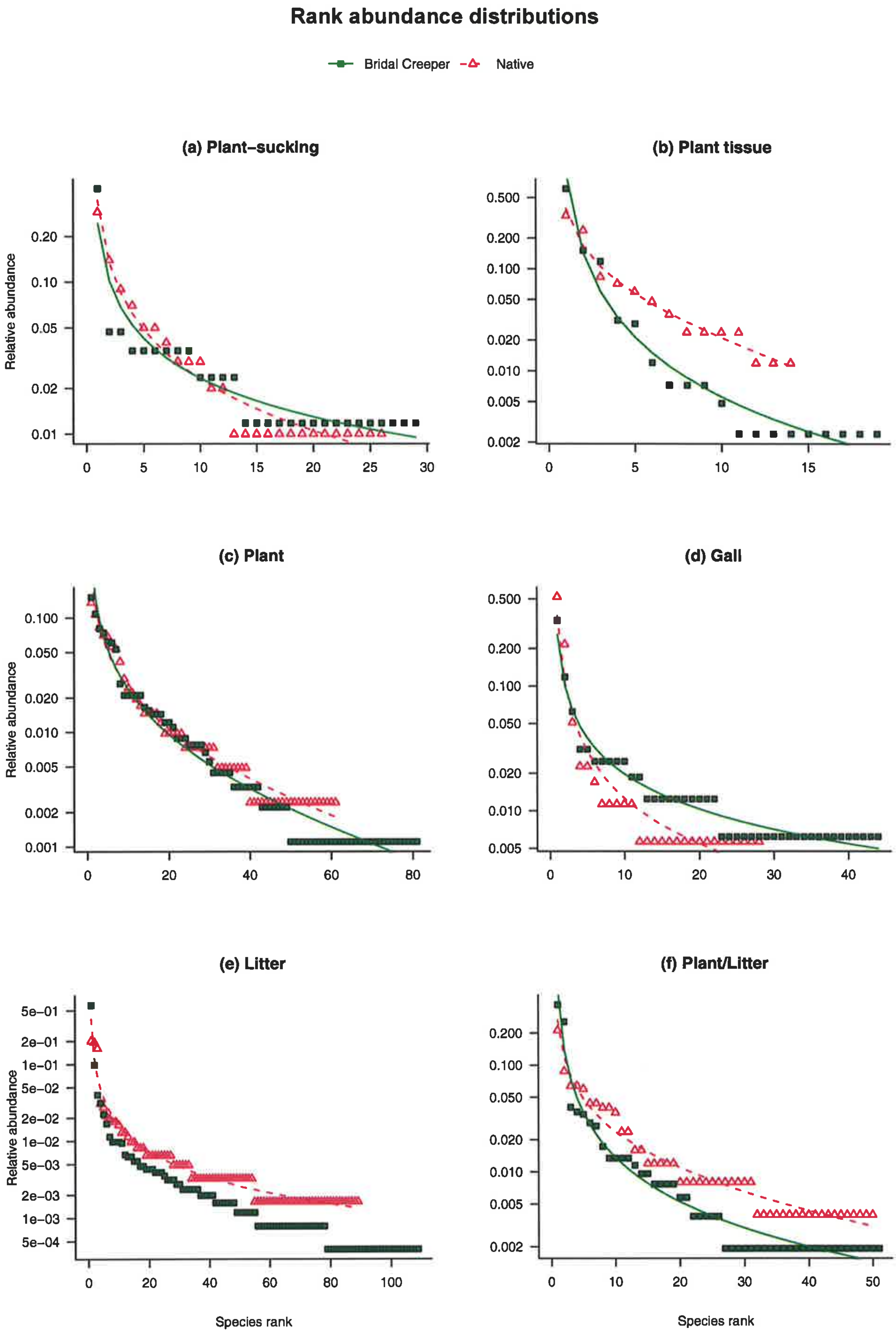


Figure 4.8 Rank abundance distributions (RADs) of wasp species from bridal creeper and native traps for **(a)** plant sucking-associated parasitoids, **(b)** plant tissue-associated parasitoids, **(c)** plant-associated parasitoids, **(d)** gall-associated parasitoids and wasps, **(e)** litter and soil-associated parasitoids, and **(f)** plant/ litter associated parasitoids. When the fit for a (veiled) log-normal distribution was significant the curve was drawn (solid line: bridal creeper; broken line: native).

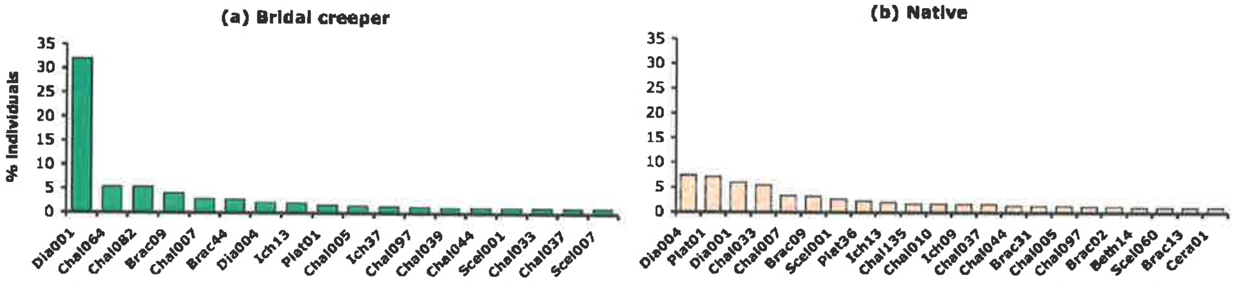


Figure 4.9 Frequency distributions of species that contributed to 1% or greater of the total assemblage from **(a)** bridal creeper and **(b)** native traps.

Assemblage composition

About 37% (176 species) of species were recorded from both invaded and native habitat. An almost equal number were recorded exclusively from bridal creeper traps with 110 recorded only from native traps (Figure 4.10a). The 'unique' species, ie. those only recorded from either native or bridal creeper, were recorded in much lower numbers than those recorded from both habitats. It was those species 'common' to both native and invaded traps that had significantly different abundances between habitat types (Figure 4.10b).

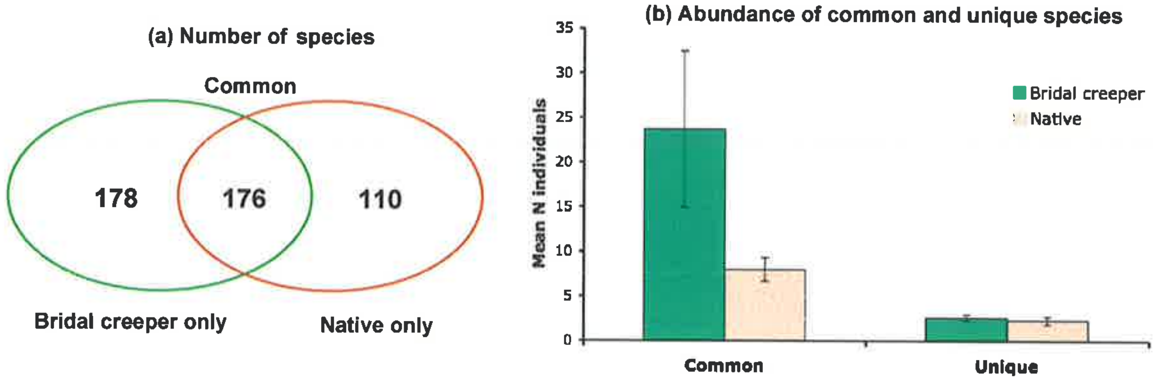
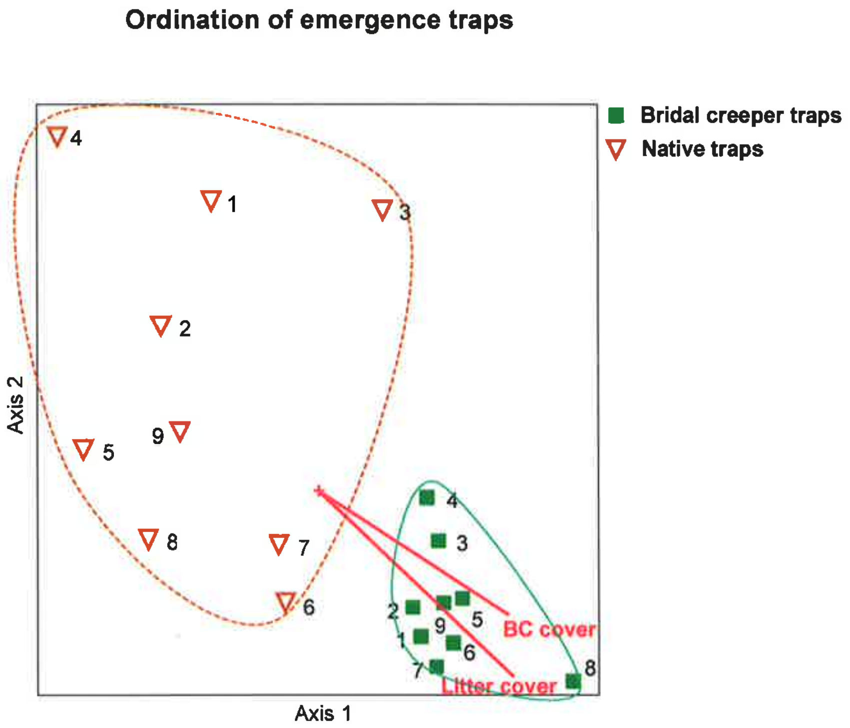


Figure 4.10 (a) Venn diagram illustrating the total number of 'common' (overlapping circles) and 'unique' species and **(b)** mean number of individuals from 'common' and 'unique' species from bridal creeper and native habitat.

An ordination (NMDS) of traps showed bridal creeper and native traps clearly separated based on wasp abundance and species composition (Figure 4.11). Not only are the traps in different habitat types (bridal creeper or native) clearly separated in the ordination, but individual trap pairs were also split apart, with no corresponding trap pair occurring together. Traps from the three sites (Section 4.2.1) also do not show any clear associations (Site 1 = Traps 1, 2 & 3; Site 2 = Traps 4, 5, 6; Site 3 = Traps 7, 8, 9). An overlay of environmental variables showed that increasing litter cover (and percent cover of bridal creeper) was correlated with traps in bridal creeper invaded habitat (Figure 4.11).

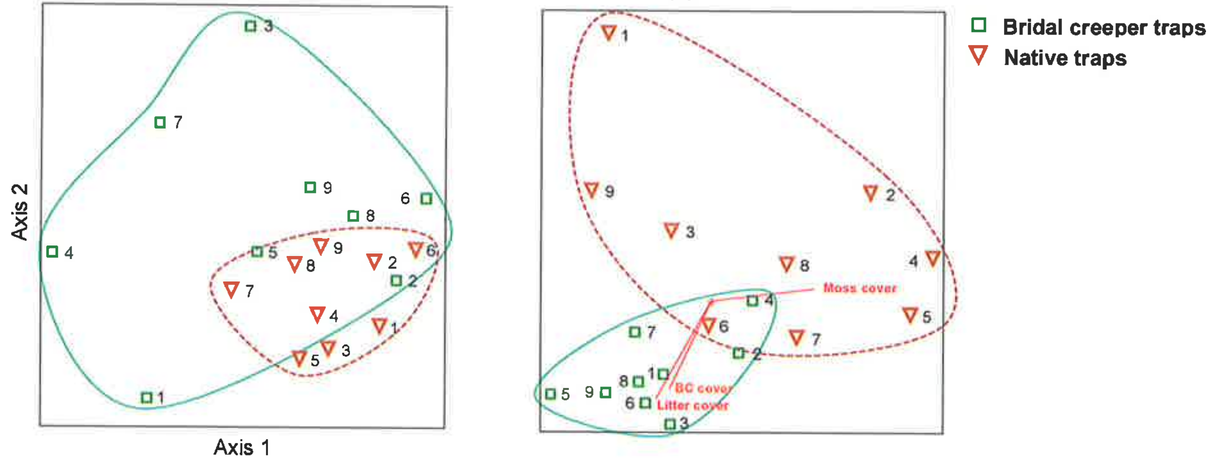


Ordination of emergence traps

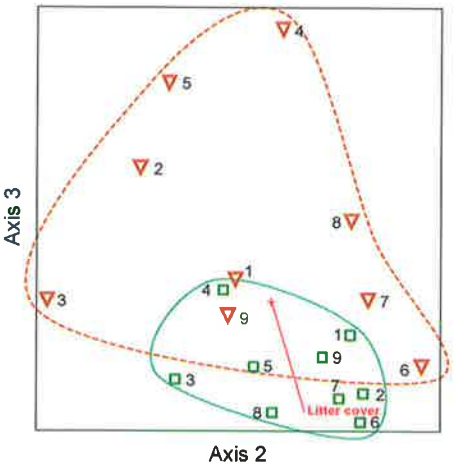
Figure 4.11 Two-dimensional ordination (NMDS) of wasp abundance and species composition from emergence traps. Numbers next to each trap correspond to trap pairs. The model explains 86.1% of the total variation (Axis 1=73.7, Axis 2=12.4) and the superimposed vectors (constrained to r^2=0.5) show the correlation between wasp species and environmental variables. The length of each vector indicates the strength of the correlation and the orientation the direction of increase. Distance measure: Sørensen; final stress for the 2-dimensional solution=9.44517; final instability=0.00001; number of iterations= 96.

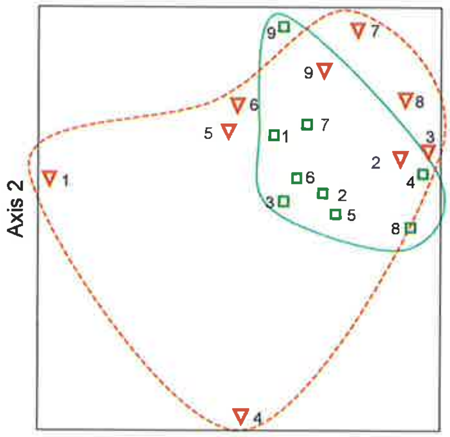
However, when wasp abundance and species composition from each functional group (Figure 4.12) were analysed separately, only parasitoids of soil and leaf litter arthropods showed the same clear separation of native and bridal creeper traps (Figure 4.12e). The other functional groups displayed considerable overlap in assemblage composition across native and bridal creeper habitat, particularly parasitoids of plant-associated arthropods and gall-associated wasps (Figure 4.12 c, d). Clearly, the overall assemblage composition of parasitoids emerging from the ground-cover habitat (Figure 4.11) was determined by the litter-associated functional group. This is perhaps not surprising given this group's numerical dominance and the sampled habitat covered by the emergence traps. An overlay of environmental variables showed that increasing litter cover was correlated with traps in invaded habitat for parasitoids of hosts feeding inside plant tissue (Figure 4.12b), plant-associated (Figure 4.12c), litter- (Figure 4.12e) and plant/litter- (Figure 4.12f) associated arthropods. The percent cover of moss was correlated with a cluster of native traps for parasitoids of plant-tissue feeding insects (Figure 4.12b). Of particular interest is the distinct close clustering of the bridal creeper traps in all the ordinations (except for parasitoids of plant-sucking insects; Figure 4.12a). This indicates that the assemblages emerging from invaded areas were similar, particularly parasitoids of soil and leaf litter arthropods (Figure 4.12e). In contrast, the native traps are more widely distributed indicating that more dissimilar assemblages emerged across the native habitat patches (Figures 4.11 and 4.12).

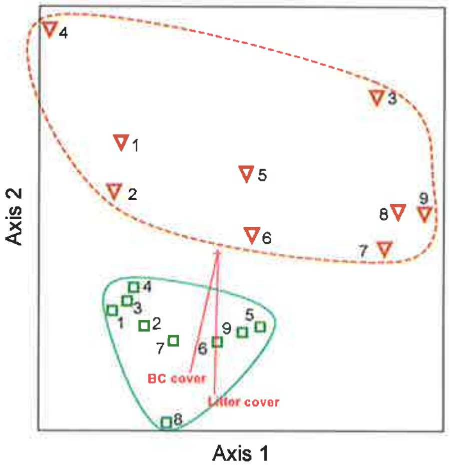
Ordinations of functional groups


(a) Plant sucking

(b) Plant tissue


(c) Plant


(d) Gall


(e) Litter

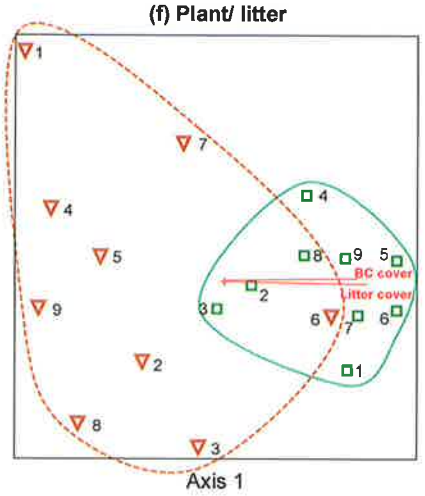

(f) Plant/ litter

Figure 4.12 Ordinations (NMDS) of wasp abundance and species composition for each functional group. **(a)** Two-dimensional NMDS of **plant sucking-associated parasitoids**. The model explains 55.9% of the total variation (Axis 1=25.9, Axis 2=30.0). Final stress for the 2-dimensional solution=24.59208; final instability=0.00393; number of iterations 88; **(b)** two-dimensional NMDS of **plant tissue-associated parasitoids**. The model explains 82.0% of the total variation (Axis 1=31.6, Axis 2=50.4). Final stress=16.91259; final instability=0.00070; number of iterations=33; **(c)** three-dimensional NMDS of **plant-associated parasitoids**. The model explains 90.0% of the total variation (Axis 1=12.9, Axis 2=44.9, Axis 3=32.2). Final stress=9.16594; final instability=0.00001; number of iterations= 85; **(d)** two-dimensional NMDS of **gall-associated wasps**. The model explains 65.9% of the total variation (Axis 1=37.3, Axis 2=65.9). Final stress=18.64963; final instability=0.00452; number of iterations=32; **(e)** two-dimensional NMDS of **litter and soil-associated parasitoids**. The model explains 79.7% of the total variation (Axis 1=12.3, Axis 2=67.4). Final stress=9.05378; final instability=0.00001; number of iterations=75; and **(f)** two-dimensional NMDS of **plant/litter associated parasitoids**. The model explains 72.4% of the total variation (Axis 1=46.5, Axis 2=25.9). Final stress=16.72665; final instability=0.00344; number of iterations=24. Numbers next to each trap correspond to trap pairs. Distance measure: Sørensen. The superimposed vectors (constrained to r^2=0.5) show the correlation between wasp species and environmental variables. The length of each vector indicates the strength of the correlation and the orientation the direction of increase.

The arrangement of traps in the ordinations indicating a more distinct range of assemblages occurring across native areas also explains why only one species was found to be a significant indicator of native habitat (Table 4.3). This species was Chalcidoidea sp. 10 (Mymaridae: *Mymar* sp.), which is likely to be a parasitoid of plant-sucking leafhoppers (Hemiptera: Delphacidae) (Appendix C). Chalcidoidea sp. 10 belongs to the only functional group where the native traps cluster relatively close together (Figure 4.10a). In comparison, the similarity of the assemblages emerging from bridal creeper traps (as indicated by the clustering of bridal creeper traps) meant that a wide range of species representing a variety of functional groups that attack a range of host taxa (Appendix C) were identified as indicator species of invaded habitat (Table 4.3).

Table 4.3 Significant indicator species (spp.) for bridal creeper (BC) and native (N) habitat, and Monte Carlo significance of observed maximum indicator values for each species (1000 permutations). N: number of individuals from the indicated habitat.

Spp.	Taxa	Fun. group	Habitat	N	Observed indicator value	P value
Chal10	Myrmaridae, *Mymar*	Plant-sucking	N	29	87.9	0.0020
Chal64	Eulophidae, Tetrastichinae, ?*Neotrichoporoides*	Plant tissue	BC	253	97.3	0.0010
Brac06	Rogadinae	Plant	BC	24	77.8	0.0300
Ichn13	Cryptinae, *Paraphylax*	Plant	BC	98	74.2	0.0330
Ichn17	Metopiinae	Plant	BC	13	61.9	0.0270
Ichn37	Banchinae, *Lissonata*	Plant	BC	67	90.5	0.0010
Scel07	Telenominae, *Telenomus*	Plant	BC	48	71.1	0.0200
Scel16	Scelioninae, *Gryon*	Plant	BC	19	67.2	0.0210
Chal72	Eulophidae, Tetrastichinae, *Quadrastichodella*	Gall	BC	19	52.8	0.0320
Beth10	Bethylinae, *Sierola*	Plant/ litter	BC	14	71.7	0.0300
Brac09	Microgastrinae, *Cotesia*	Plant/ litter	BC	192	78.4	0.0150
Brac44	Cheloninae, *Ascogaster*	Plant/ litter	BC	133	92.4	0.0010
Chal35	Pteromalidae, Diparinae, ?*Dipareta*	Litter/ soil	BC	25	67.3	0.0530
Chal39	Pteromalidae, Diparinae, ?*Dipareta*	Litter/ soil	BC	57	93.4	0.0010
Chal82	Pteromalidae, Diparinae, ?*Australolaelaps*	Litter/ soil	BC	250	99.6	0.0010
Diap01	Diapriinae, *Rostropria inopicida*	Litter/ soil	BC	1487	93.8	0.0010
Diap06	Belytinae, nr. *Aclista*	Litter/ soil	BC	16	59.3	0.0260
Diap07	Diapriinae, *Neurogalesus*	Litter/ soil	BC	16	66.7	0.0080
Diap20	Diapriinae, *Spilomicrus*	Litter/ soil	BC	25	53.4	0.0390
Diap25	Diapriinae, *Entomacis*	Litter/ soil	BC	29	55.6	0.0210

4.3.4 Potential host availability

From the arthropods collected, ten orders (18,021 individuals) are known to be attacked by the parasitoid taxa recorded from Mt Billy CP: Araneae (spiders), Blattodea (cockroaches), Coleoptera (beetles), Diptera (flies), Hemiptera (bugs), Lepidoptera (moths and butterflies), Neuroptera (lacewings), Pscoptera (booklice), Orthoptera (crickets and grasshoppers), and Thysanoptera (thrips) (Table 4.4). As with the wasps, there were significantly more arthropod individuals collected from bridal creeper (Table 4.4) and most host taxa were more abundant in invaded than native habitat (Figure 4.13). As reported in Chapter 3, Diptera were by far the most numerous taxon collected from both habitats and were significantly more abundant from bridal creeper traps. Araneae, Coleoptera, Lepidoptera and Psocoptera also emerged in significantly greater numbers from bridal creeper invaded habitat (Table 4.4, Figure 4.13).

Table 4.4 Arthropod orders recorded in emergence trap samples from Mt Billy CP, and the total and difference (paired t-test) in number of individuals from bridal creeper (BC) and native habitat. nt: not tested, ns: not significant, * P< 0.05, ** P< 0.01, ***P< 0.001. + Parasitoid host taxa

Taxa	BC	Native	t-test
Arachnida			
Acarina (mites)	4991	6505	ns t=0.7890 P=0.4528)
Araneae (spiders) +	369	94	** (t=3.819 P=0.0051)
Pseudoscorpionida (pseudoscorpions)	0	1	nt
Diplopoda			
Julida (julid millipedes)	2	2	nt
Polyxenida (pin-cushion millipedes)	17	11	ns (t=0.9177 P=0.3856)
Collembola			
Collembola (springtails)	887	1040	ns (t=0.6074 P=0.5604)
Insecta (insects)			
Blattodea (cockroaches) +	14	7	ns (t=1.360 P=0.2110)
Coleoptera (beetles) +	734	347	*** (t=7.682 P<0.0001
Diptera (flies) +	11493	3592	*** (t=7.869 P<0.0001)
Hemiptera (aphids, scale insects, true bugs & whiteflies) +	636	465	ns (t=0.9233 P=0.3828)
Hymenoptera (ants)	222	233	ns (t=0.1923 P=0.8523)
(bees & wasps)	4659	1657	*** (t=5.225 P=0.0008)
Lepidoptera (butterflies & moths) +	273	156	* (t=2.742 P=0.0254)
Neuroptera (lacewings) +	92	49	ns (t=1.863 P=0.0995)
Orthoptera (crickets & grasshoppers) +	3	6	nt
Psocoptera (booklice) +	77	35	* t=2.903 P=0.0198)
Strepsiptera (stylops)	17	1	ns (t=1.809 P=0.1081)
Thysanoptera (thrips) +	490	328	ns (t=1.297 P=0.2309)
Thysanura (silverfish)	0	1	nt
TOTAL	25545	14572	** (t=3.919 P=0.0044)

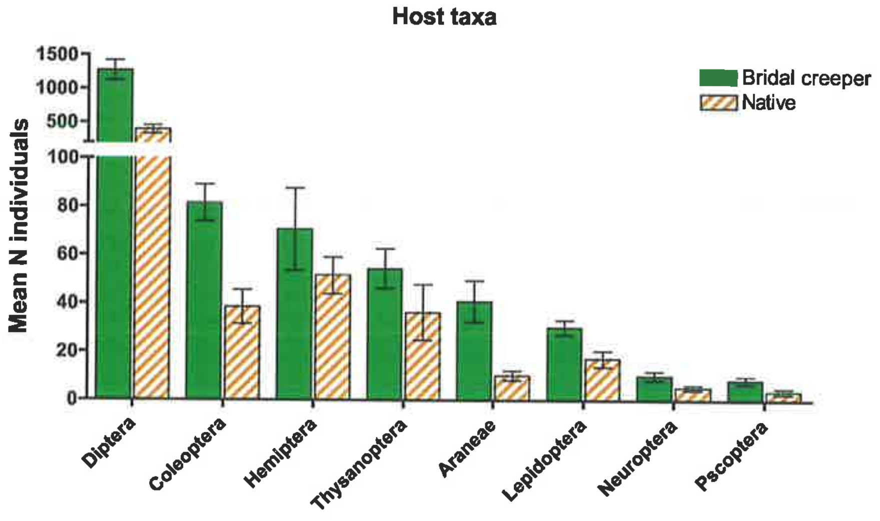


Figure 4.13 Mean number (±SE) of individuals of major host taxa collected from emergence traps in bridal creeper (n=9) and native (n=9) habitat. Orthoptera and Blattodea were not included due to very low numbers collected. For comparison, orders have been ranked by descending number individuals from bridal creeper traps.

4.3.5 Species temporal abundance patterns

The timing of when a parasitoid emerges as an adult is closely linked to the host species and microclimatic factors such as temperature and moisture. As the emergence traps were emptied weekly, the temporal emergence patterns of the most abundant species common to both habitats could be compared to infer if these developmental factors differed between habitats. The proportion of individuals collected, rather than the total number, were compared due to the large differences in abundance of many species between bridal creeper and native traps:

(a) Individuals of the plant/litter-associated parasitoid Braconidae sp.09 (*Cotesia* sp. a genus which parasitise a range of lepidopteran larvae) were present in both native and bridal creeper traps throughout the sample period (Figure 4.14a). Numbers peaked in April from native traps, but slightly later (during May) in invaded traps (Figure 4.14a);

(b) Braconidae sp. 44 (*Asogaster* sp.; a genus which parasitise egg-larval parasitoids of Lepidoptera), occurred in native and bridal creeper traps over the same time period however, it had a more restricted emergence period, emerging over two months from bridal creeper traps but only over two weeks from native traps (Figure 4.14b);

(c) Chalcidoidea sp. 05 (Eulophidae, *Euplectrus* sp.; a genus which parasitise exposed-feeding lepidopteran larvae on plants), emerged over the sampling period (Figure 4.14c). The emergence patterns across habitats was relatively similar, but with a peak in emergence in February in native habitat (Figure 4.14c);

(d) Chalcidoidea sp. 07 (Encyrtidae, *Copidosoma* sp.; a genus which parasitise lepidopteran larvae on plants), had very similar emergence patterns across native and bridal creeper traps, emerging in spring then peaking in numbers in autumn (Figure 4.14d);

(e) Individuals of Chalcidoidea sp. 33 (Pteromalidae, *Gastrancistrus* sp.; a genus of gall-associated wasps from *Acacia* and *Eucalyptus*), emerged from the leaf litter over late spring through summer in a similar pattern from both native and bridal creeper habitat (Figure 14e);

(f) Despite large differences in numbers, the abundant and widespread Diapriidae sp. 01 (*Rostropria inopicida*; which belongs to a subfamily that parasitise soil- and leaf litter-associated fly larvae), had almost identical emergence patterns from native and bridal creeper traps. Individuals emerged in two obvious peaks in numbers in December and January, with a smaller proportion emerging in spring, and low numbers present throughout the sample period (Figure 4.14f);

(g) Diapriidae sp. 04 (*Stylaclista* sp.; which belongs to a subfamily that parasitise soil- and leaf litter-associated Diptera), was present throughout the sampling period but peaked in numbers over November and December in both native and bridal creeper invaded habitat (Figure 4.14g);

(h) Ichneumonidae sp. 13 (*Paraphylax* sp.; a genus which parasitise a range of plant-associated arthropods), had very similar emergence patterns across native and bridal creeper traps, with a peak in emergence in November (Figure 4.14h); and

(i) The emergence pattern of Scelionidae sp. 01 (*Trissolcus* sp.; a genus which parasitise Pentatomidae (Hemiptera) eggs on plants), had a similar emergence pattern from both bridal creeper and native habitat, with the greatest numbers occurring in late summer and early autumn (Figure 4.14i).

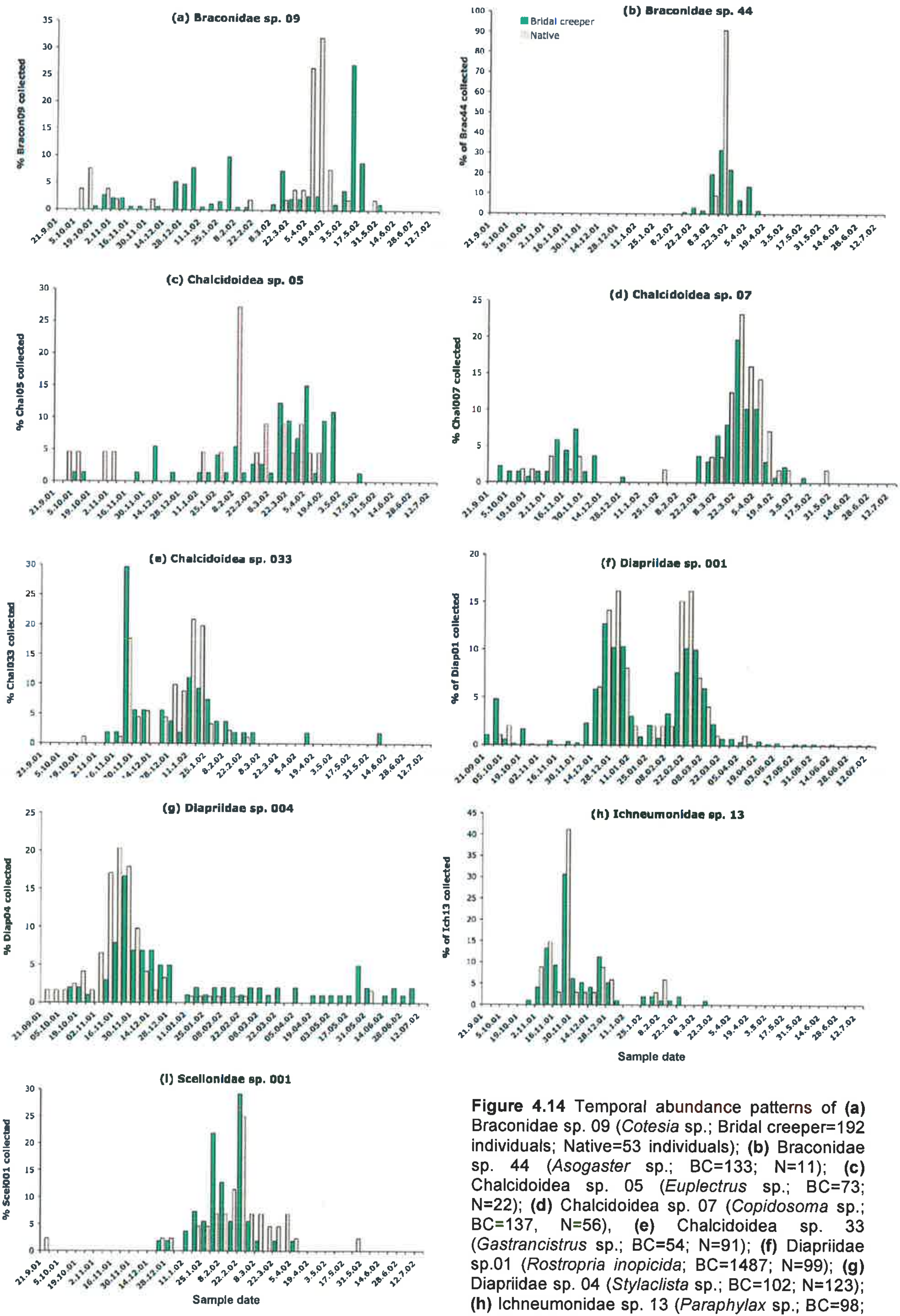


Figure 4.14 Temporal abundance patterns of **(a)** Braconidae sp. 09 (*Cotesia* sp.; Bridal creeper=192 individuals; Native=53 individuals); **(b)** Braconidae sp. 44 (*Asogaster* sp.; BC=133; N=11); **(c)** Chalcidoidea sp. 05 (*Euplectrus* sp.; BC=73; N=22); **(d)** Chalcidoidea sp. 07 (*Copidosoma* sp.; BC=137, N=56), **(e)** Chalcidoidea sp. 33 (*Gastrancistrus* sp.; BC=54; N=91); **(f)** Diapriidae sp.01 (*Rostropria inopicida*; BC=1487; N=99); **(g)** Diapriidae sp. 04 (*Stylaclista* sp.; BC=102; N=123); **(h)** Ichneumonidae sp. 13 (*Paraphylax* sp.; BC=98; N=34); **(i)** Scelionidae sp. 01 (*Trissolcus* sp.; BC=55; N=44).

4.3.6 Wasp assemblages and leaf litter

The dominance of soil- and leaf litter-associated parasitoids (Figure 4.2) and the higher levels of leaf litter under bridal creeper (Chapter 2) prompted an investigation of the effects of litter on wasp abundance and species-richness. The range in the amount of litter in bridal creeper invaded habitat, particularly the percent cover (Section 4.3.1), was not ideal for this comparison. However, this was a 'naturally' occurring ranges of leaf litter in the selected study areas with 100% bridal creeper cover.

Interestingly, the percent cover and depth of leaf litter had a significant influence on the number of individuals and species emerging from native habitat for several functional groups (Figure 4.15). Both the percent cover of litter and litter depth positively influenced the number of species and individuals collected in native traps of parasitoids associated with insects feeding inside plant tissue (Figure 4.15b), arthropods on plants (Figure 4.15c) and, not surprisingly, those associated with litter and soil (Figure 4.15e). Litter depth only had a significant positive effect on the number of species and individuals of gall-associated wasps (Figure 4.15d) and parasitoids of plant/ litter associated arthropods (Figure 4.15f).

(a) Plant sucking

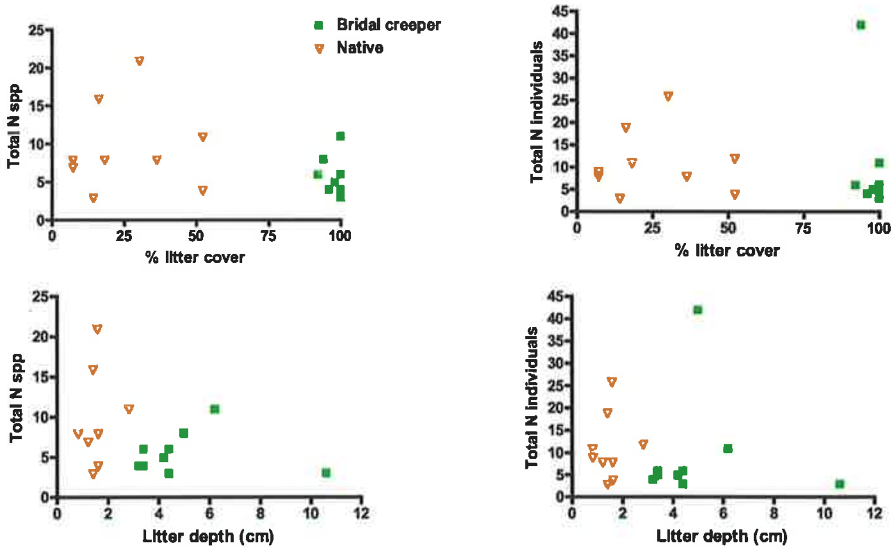
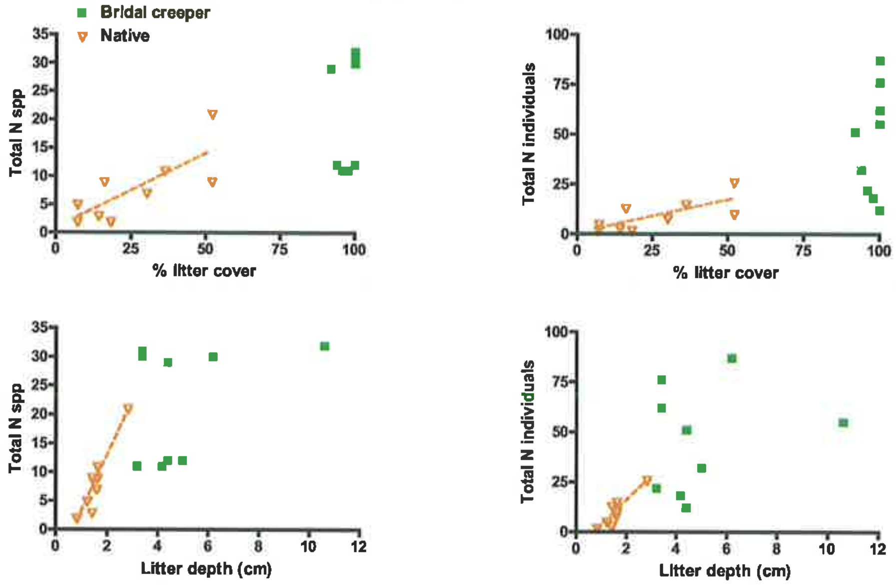
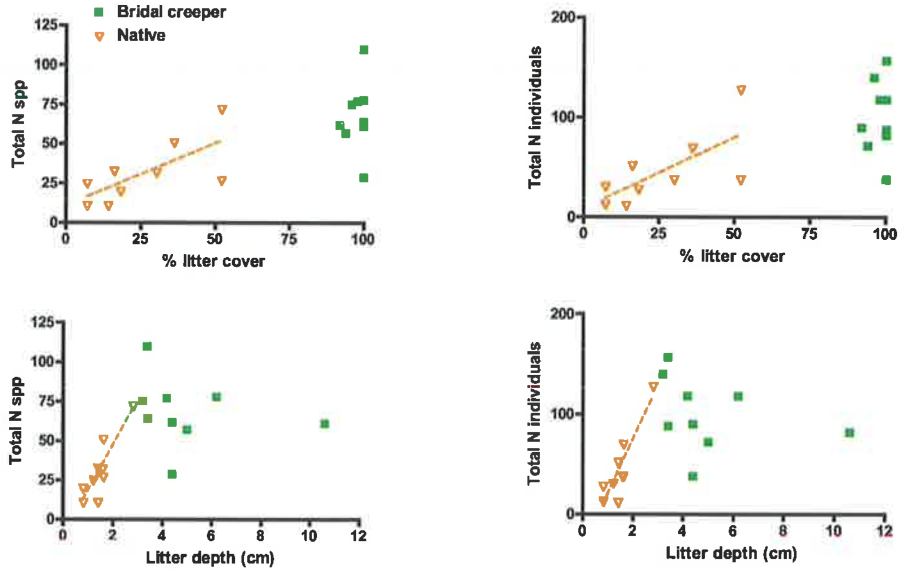


Figure 4.15 (a) Relationship between the percent cover of leaf litter and leaf litter depth and total number of species and number of individuals for plant sucking-associated parasitoids (litter cover and number of spp.: Bridal creeper: P=0.6617 r^2=0.02894; Native: P=0.9293, r^2=0.0012, litter cover and number of individuals: BC: P=0.2262 r^2=0.2009; N: P=0.9708, r^2=0.0002; litter depth and number of spp.: BC: P=0.9369 r^2=0.00096; N: P=0.6394, r^2=0.03310, litter depth and number of individuals: BC: P=0.9795, r^2=0.0001; N: P=0.7840, r^2=0.01145). The line of best fit has been drawn for significant relationships.



(b) Plant tissue

Figure 4.15 (b) Relationship between the percent cover of leaf litter and leaf litter depth and total number of species and number of individuals for plant tissue-associated parasitoids (litter cover and number of spp.: BC: P=0.4577, r^2=0.08107; N: P=0.0134, r^2=0.6068, litter cover and number of individuals: BC: P=0.4577, r^2=0.08107; N: P=0.0134, r^2=0.6068; litter depth and number of spp.: BC: P=0.3227, r^2=0.1392; N: P<0.0001, r^2=0.9006, litter depth and number of individuals: BC: P=0.5653, r^2=0.04944; N: P=0.0005, r^2=0.8433). The line of best fit has been drawn for significant relationships.



(c) Plant

Figure 4.15 (c) Relationship between the percent cover of leaf litter and leaf litter depth and total number of species and number of individuals for plant-associated parasitoids (litter cover and number of spp.: BC: P= 0.7347, r^2=0.01747; N: P=0.0313, r^2=0.5074, litter cover and number of individuals: BC: P= 0.8675, r^2= 0.004260; N: P=0.0363, r^2=0.4879; litter depth and number of spp.: BC: P=0.6010, r^2=0.04107; N: P=0.0023, r^2= 0.7565, litter depth and number of individuals: BC: P=0.4520 , r^2=0.08308; N: P=0.0013, r^2=0.7907). The line of best fit has been drawn for significant relationships.

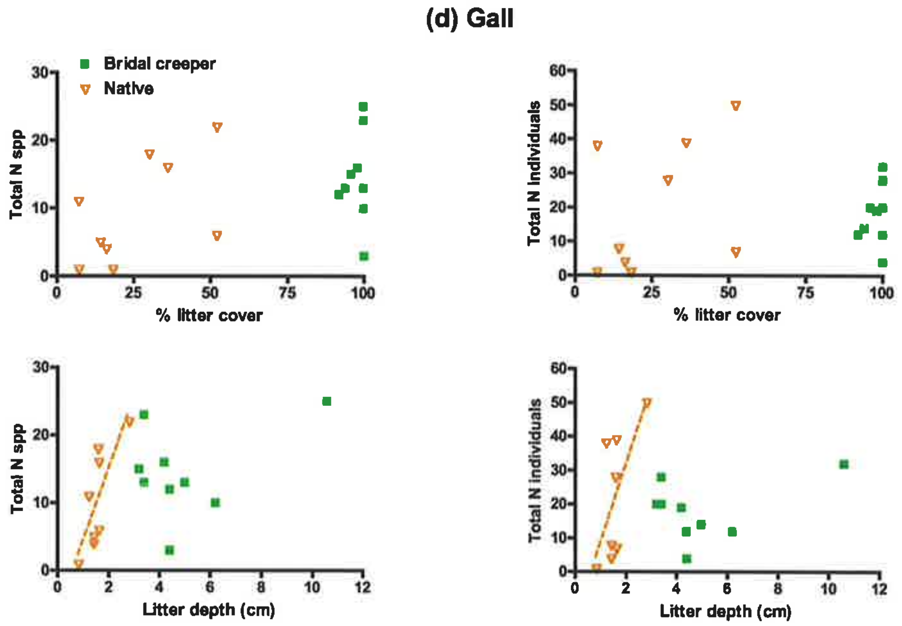


Figure 4.15 (d) Relationship between the percent cover of leaf litter and leaf litter depth and total number of species and number of individuals for gall-associated parasitoids and wasps (litter cover and number of spp.: BC: P=0.7173, r^2=0.01991; N: P=0.0966, r^2=0.3445, litter cover and number of individuals: BC: P= 0.4599, r^2=0.08031; N: P= 0.2602, r^2=0.1765; litter depth and number of spp.: BC: P=0.2881 r^2=0.1588; N: P=0.0086, r^2=0.6509, litter depth and number of individuals: BC: P=0.3179, r^2=0.1418; N: P=0.0333, r^2=0.4994). The line of best fit has been drawn for significant relationships.

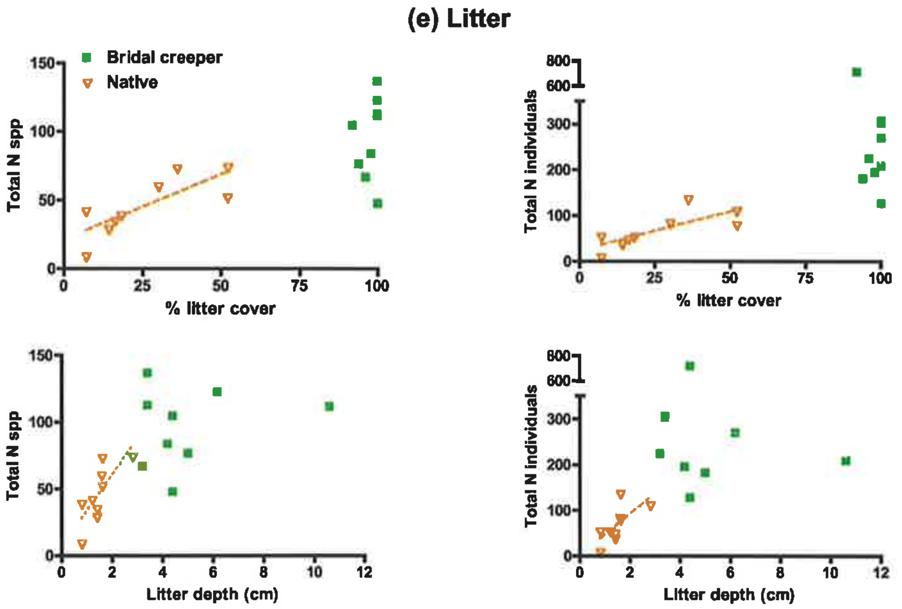
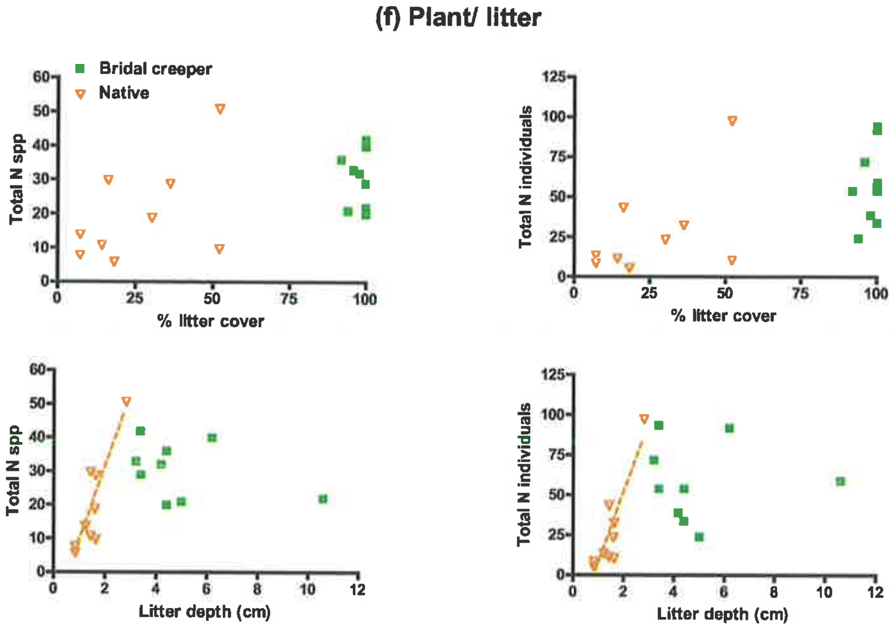


Figure 4.15 (e) Relationship between the percent cover of leaf litter and leaf litter depth and total number of species and number of individuals for litter and soil-associated parasitoids (litter cover and number of spp.: BC: P=0.4953, r^2=0.06882; N: P=0.0117, r^2=0.6207, litter cover and number of individuals: BC: P=0.0994, r^2=0.3399; N: P= 0.0149, r^2=0.5949; litter depth and number of spp.: BC: P=0.5791,r^2=0.04608; N: P=0.0190, r^2=0.5679, litter depth and number of individuals: BC: P=0.6925, r^2=0.02370; N: P=0.0420, r^2= 0.4685). The line of best fit has been drawn for significant relationships.



(f) Plant/ litter

Figure 4.15 (f) Relationship between the percent cover of leaf litter and leaf litter depth and total number of species and number of individuals for plant/ litter-associated parasitoids (litter cover and number of spp.: BC: P=0.9888, r^2=0.00003047; N: P=0.1415, r^2=0.2817, litter cover and number of individuals: BC: P=0.3370, r^2=0.1318; N: P=0.1284, r^2=0.2980; litter depth and number of spp.: BC: P=0.3362, r^2=0.1322; N: P=0.0023, r^2=0.7574, litter depth and number of individuals: BC: P=0.9910, r^2=0.00001; N: P=0.0013, r^2=0.7907). The line of best fit has been drawn for significant relationships.

4.4 Discussion

4.4.1 Effects of bridal creeper invasion on parasitic wasp assemblages

Following-on from the results of Chapter 3, this study also found that the absence of native ground-cover plant species due to bridal creeper invasion had not resulted in a decline in arthropod biodiversity. Moreover, in distinct contrast to the sweep net study, this investigation recorded significantly more wasps (both individuals and species) and their hosts emerging from bridal creeper-invaded habitat (Tables 4.1, 4.4; Figure 4.5, 4.13). Importantly, these findings revealed the use of invaded areas for arthropod reproduction and development. The general patterns of species abundance, richness and assemblage structure were similar to those recorded in Chapter 3. The same wasp families and functional groups were recorded in similar proportions. However, in this study, the most abundant and speciose families and functional groups emerged in significantly higher numbers from bridal creeper invaded habitat (Tables 4.1-2; Figures 4.5-6). The distribution patterns of wasp species across both native and invaded habitat for was the same as that found in Chapter 3, where the majority of species were collected from only one or two traps in low numbers (Figure 4.7a). The strong positive relationship between the abundance of a species and the number of transects it was recorded from (Figure 4.7b) was also the same for both bridal creeper and native habitat.

Although species frequency distributions from both habitats were left-skewed and, as found in Chapter 3, mostly followed a log-normal abundance distribution (Figure 4.8), one species (Diapriidae sp. 01: *Rostropria inopicida*) dominated the wasp assemblage emerging from bridal creeper invaded habitat (Figure 4.9a). Accordingly, a log-normal distribution could not be fitted to the rank abundances of parasitoids of soil and litter arthropods emerging from invaded habitat (Figure 4.8e). This species also contributed to the high number of individuals collected from all nine traps in bridal creeper (Figure 4.7b), the overall high numbers of Diapriidae (Table 4.1), as well as the high numbers of soil- and litter-associated parasitoids from bridal creeper traps (Table 4.2). When species have different tolerance levels to environmental change, the distribution patterns of species abundances can be altered, often resulting in high levels of dominance (Schowalter 2000; Castillo & Lobo 2004; Magurran 2004). It is possible that Diapriidae sp. 01 has been able to exploit the habitat changes caused by the invasion of bridal creeper. The exceptionally high numbers of this species, and other findings of the functional group analysis, are discussed below within the context of habitat and host associations.

4.4.2 Parasitic wasp assemblages and developmental habitat associations

In this study of the habitat covered by the emergence traps, leaf litter emerged as an important environmental variable influencing parasitic wasp assemblages. As found in Chapter 3, parasitic wasps associated with soil and litter arthropods were the most species-rich and abundant functional group across both native and invaded habitat (Table 4.2). The assemblage recorded from invaded habitat was characterised by habitat with high levels of litter cover (Figure 4.11). Interestingly however, across native habitat, the amount of litter was positively correlated with the abundance and species-richness of several other functional groups, not just soil- and litter-associated parasitoids (Figure 4.15), suggesting that the presence of leaf litter is a strong determining factor more generally in the abundance and diversity of parasitic Hymenoptera (and probably also their hosts). This relationship may not have been found in the bridal creeper assemblage simply because there was not the range of litter depth and, in particular, cover, under bridal creeper traps (Figure 4.15). An increase in the amount of leaf litter on the soil surface has been shown to increase the number detritivores and their predators (Blair, *et al.* 1994; Ponsard, *et al.* 2000). However, in addition to providing a food source for detrivorous arthropods, leaf litter also determines the microclimate of the upper soil layer and enhances structural diversity by providing microhabitats for shelter, camouflage, and hunting areas for members of both detritus- and plant-based compartments of food webs and their predators (Facelli 1994; Ulrich 1998; Langellotto & Denno 2004; Moore, *et al.* 2004; Sabo, *et al.* In Press). Thus, at Mt Billy CP, this finding indicates the significance of leaf litter on a range of biologically diverse wasps, not only those that parasitise soil- and leaf litter-associated arthropods.

Although many (abundant) species were shared between native and invaded areas (Figure 4.10), the ordination of species composition across traps revealed that wasp assemblages emerging from native and invaded habitat could be considered distinct based on species identity and abundance (Figure 4.11). Further examination of each functional group showed however, that only the assemblage composition of parasitoids of soil and leaf litter arthropods was distinct (Figure 4.12e). The other functional groups displayed considerable overlap in composition across native and invaded areas indicating that these groups had similar wasp assemblages across both habitat types. This may be due to their association with the canopy that was the same above both invaded and non-invaded areas, and/or the redistribution of leaf litter (discussed below). The spatial distribution of bridal creeper and native traps in the ordinations is of particular interest. In all the ordinations (except parasitoids of plant-sucking insects), the bridal creeper traps clustered closely together indicating that the assemblages emerging from bridal creeper invaded areas were reasonably similar. In contrast, the native traps were much more widely distributed, suggesting that more distinct assemblages emerged across non-invaded native habitat (Figures 4.11 and 4.12). This pattern of a widely dispersed native assemblage and more similar bridal creeper assemblage is comparable to that found in Chapter 3 (Figure 3.9), but is more well-defined using larval habitat associations. As suggested in Chapter 3, such a finding indicates that the invasion of bridal creeper has resulted in a more uniform or homogenous habitat compared to native habitat, hence influencing the composition of the wasp assemblages. Floristics data supports this, with a greater number of plant species and more open spaces with moss cover recorded in native habitat and the greater cover of leaf litter under bridal creeper (Figure 4.4; Chapter 2). Furthermore, only one species was found to be a significant indicator taxon for native habitat, whereas a number of wasps from a range of functional groups were indicators of bridal creeper (Table 4.3). Further sampling of more similar native areas (eg. same levels of moss and litter cover, same dominant plant species) may have produced more species indicative of native habitat. However, biotic homogenization, or the increase in species similarity among communities, commonly occurs with the invasion of exotic species (Olden & Poff 2003).

In a comparison of hymenopteran communities from burnt and un-burnt mature pine forest, Lockwood (1996) found that burnt sites had a much higher level of community similarity compared to non-burnt sites. This may indicate that mature native habitat, such as the non-invaded native patches at Mt Billy CP, have naturally high levels of distinct microhabitat patchiness that results in between-patch endemism, even at relatively small spatial scales. Accordingly, bridal creeper appears to be eliminating this habitat patchiness by making the habitat more homogeneous. The redistribution and accumulation of leaf litter under bridal creeper (Chapter 2) may also have resulted in the movement of larval parasitoids and their hosts. As leaf litter was collated from many different habitat patches, this in turn would have also contributed to the more homogenous habitat and more similar wasp assemblages occurring in bridal creeper areas. Thus, a significant impact of bridal creeper invasion is likely to be the homogenization of both the plant and insect communities.

Many insect populations exist in habitat patches as meta-populations and, as such, are highly vulnerable to stochastic changes in population density or environmental changes, relying on re-colonisation from other patches after local extinctions for the persistence of the species (Fisher 1998; Hunter 2002). Parasitoids, in particular, are known to lag behind their hosts in colonising or recolonising habitat patches (Kruess & Tscharntke 1994; Tscharntke, *et al.* 1998). The homogenisation of naturally patchy habitat matrices has been shown have an impact on host-parasitoid interactions by changing the movement and densities of both hosts and parasitoids leading to reduced parasitism rates and parasitoid persistence in habitat patches (Cronin & Haynes 2004). The reduction of native patches and homogenisation of remaining habitat due to bridal creeper therefore has the potential to modify specific host-parasitoid associations and, furthermore, eliminate the possibility of re-colonisation from other native patches.

The current patchiness of bridal creeper invasion may also explain the increase in wasp diversity in invaded areas. Species richness often increases, or is at its maximum, in areas with moderate levels of disturbance (the intermediate disturbance hypothesis) (Connell 1978; Petraitis, *et al.* 1989). For example, selective logging, that leaves some habitat undisturbed, and hence increasing the patchiness or heterogeneity of a forest, has shown that disturbed areas also provide habitat for opportunistic species which in turn results in an increase in species richness overall (Oliver, *et al.* 2000). An increase in the abundance and species-richness of braconid wasps was found in selectively logged pine forest in North America as newly open areas were colonised by early succession flowering plants that attracted both phytophagous insects and their parasitoids (Lewis & Whitfield 1999). Although disturbance is typically defined as a relatively discrete event in time that removes individuals, creating the opportunity for new individuals to become established (Begon, *et al.* 1990), similarities can be drawn with the invasion of bridal creeper. 'Gaps' in the habitat (ie. weed-invaded patches) have been created, but over a significantly more gradual temporal scale than disturbances such as fire or the removal of a tree. The impact on native plants reported in Chapter 2 indicates that the invasion of bridal creeper has significantly modified the native habitat. Accordingly, the patchy habitat created by the not-yet-complete invasion of bridal creeper suggests that the impact of this invasive weed could be compared to a medium-level habitat disturbance. This, in turn, may have allowed for an overall increase in biodiversity by providing 'new' habitat, such as bridal creeper's thick foliage and increased levels of leaf litter, as well as access to 'old' habitat, ie. uninvaded areas. This combination of old and new habitat can perhaps be seen as an overall increase in habitat complexity. Such increases in habitat complexity have been shown to significantly positively influence parasitic wasp abundance, diversity, assemblage composition and parasitism rates (Marino & Landis 1996; Schellhorn, *et al.* 2000; Tscharntke 2000; Langellotto & Denno 2004; Lassau & Hochuli 2005). It may be predicted therefore, that once bridal creeper covers the entire habitat, wasp diversity and abundance will decline.

4.4.3 Parasitic wasp host associations

Leaf litter- and soil-associated parasitoids

Parasitoid assemblages are influenced by a range of factors that can be broadly divided into habitat (e.g. habitat type and structural complexity, adult food plants, shelter from predators, and temperature and moisture), and host factors (e.g. host taxonomy, morphology, behaviour, distribution and abundance, and host resource distribution, structure and chemistry) (Dubbert, *et al.* 1998; Doak 2000; Shapiro & Pickering 2000; Tooker & Hanks 2000; Whitfield & Lewis 2001; Stireman & Singer 2003; Lassau & Hochuli 2005). Many of these factors may be directly influenced by both the quantity and type of leaf litter (Ulrich 1998, 2004). Insect parasitoids usually respond positively to host abundance, and rates of parasitism may increase in areas of higher host density as parasitoids are attracted to, and/or stay longer, in areas of high host density (the optimal foraging theory) (Hubabrd & Cook 1978; Ulrich 1998; Valladares & Salvo 2001; Stireman & Singer 2002; Kruess 2003; Thiel & Hoffmeister 2004). Therefore, the significantly higher numbers in bridal creeper of host taxa with soil- and litter-associated stages (Diptera, Coleoptera, Lepidoptera and Araneae) (Figure 4.13) are the likely explanation for the higher numbers of soil- and litter-associated parasitoids emerging from invaded habitat. In a German beech forest, the experimental addition and reduction of leaf litter resulted in associated significant increases and decreases, respectively, of parasitoids of soil- and litter-dwelling parasitoids and their hosts, particularly Diptera (Ulrich 1998). At Mt Billy CP, flies were by far the most abundant host group emerging from both habitats, and were significantly more abundant in bridal creeper traps (Figure 4.13; Table 4.4). Thus, the high numbers of Diapriidae, particularly from bridal creeper traps, is undoubtedly due to the greater numbers of their hosts, litter- and soil-dwelling fly larvae (Appendix C).

Of particular interest is Diapriidae sp. 01 (*R. inopicida*), that was by far the dominant parasitoid collected in this study (Figure 4.9). This species was widespread, collected from all but three (native) traps, and emerged in exceptionally high numbers from bridal creeper compared with native habitat (Figure 4.9). As discussed above, the numerical dominance of *R. inopicida* in invaded areas corresponds to the high numbers of its host taxa (Diptera), that in turn, may be responding to the habitat created by the high levels of litter under bridal creeper. A comparison of food webs comprised of plants, insect leaf miners and their parasitoids from native and horticultural habitats demonstrated the proliferation of those species best adapted to habitat modification (Valladares & Salvo 1999). The study found that the highly modified cultivated system had a disproportionate abundance of a single dominant species at each trophic level (a herbivore and its parasitoid) compared with the more pristine native habitat (Valladares & Salvo 1999). Species with more general resource requirements tend to respond better to disruptions such as habitat change than specialist species. Such species may be relatively insensitive to the removal (or addition) of one or more resources, or may have the ability to adapt to a variety of environmental conditions (Ehrlich & Mooney 1983; LaSalle 1993; Fraser & Lawton 1994; Hawkins & Sheehan 1994; Valladares & Salvo 1999; Memmott, *et al.* 2000; Memmott & Wasner 2002). Although the host range is known for comparatively few parasitoid species, evidence suggests there is considerable variation in host ranges, largely due to host feeding niche and mode of development (Hawkins & Lawton 1987; Hawkins, *et al.* 1992; Memmott, *et al.* 1994) and, therefore, level of specificity and response to habitat change. Idiobiont parasitoids (usually ectoparasitoids) kill or immobilise their hosts, terminating development and, thus avoiding host immune responses. As such, idiobionts usually have broader host ranges than koinibiont parasitoids (usually endoparasitoids) that, in contrast, allow the continued development of their hosts with specifically evolved adaptations to overcome the immune system of their actively developing hosts, leading to a narrower host range (Hawkins, *et al.* 1992). There are no specific host records for *R. inopicida*. However, like all Diapriidae, it would be an ectoparasitic idiobiont of dipteran prepupae and/or pupae (Masner 1993). Therefore, *R. inopicida* is likely to be a generalist, and as such, may have been able to move onto other hosts made available by litter accumulation, or has a wide range of hosts such that any adverse changes caused by bridal creeper was unlikely to affect it. Indeed, Ulrich (2004) suggests that current, albeit limited, data indicate that most soil- and litter-associated parasitoids are generalists with broad host ranges. Furthermore, the population of *R. inopicida* at Mt. Billy CP displayed significant wing polymorphism with individuals ranging from micropterous and brachypterous to fully-winged. This range of morphs may also explain the disproportionate dominance of *R. inopicida* in invaded areas, as it may be more 'adaptable' (Roff 1990, 1994). For example, wing polymorphism in a planthopper species (*Prokelisia dolus*) was shown to allow the species to exist across natural variations in vegetation structure and female density; flightless males discovered females more frequently in contiguous vegetation and more efficiently at higher female densities, whereas flight-capable males located females more often in sparse vegetation and more successfully at lower female densities (Langellotto & Denno 2001). In the case of *R. inopicida*, it may be advantageous to have reduced wings for dwelling in leaf litter (eg. (Nauman 1982; Galloway & Austin 1984; Austin 1986), but morphs with wings also allow greater mobility and hence patch colonisation. In addition, each morph may be able to attack different hosts, thereby also increasing the species polyphagy. The increased habitat homogeneity in invaded areas created by continuous coverage of bridal creeper and leaf litter (Section 4.4.2) may also be favouring the short winged morphs. Decreasing habitat heterogeneity seems to favour flightlessness, with wing-reduced females often being more fecund, because energy normally put into wing muscles can be allocated to egg production (Roff 1990; Zera & Denno 1997). Thus, the invasion of bridal creeper has indirectly, via litter accumulation, allowed for the dominance of a species that is undoubtedly contributing to the homogenization of the parasitoid community in invaded habitat.

Parasitoids of plant-associated hosts

Considering bridal creeper is unlikely to have herbivores feeding upon it (Chapter 3, Section 3.1) and many host records suggest tree canopy associations (Appendix C), the emergence of plant-associated wasps (parasitoids of plant-sucking insects, insects feeding inside plant tissue other plant-associated arthropods, and gall-associated wasps) from the ground-cover habitat may seem unexpected (Table 4.2). However, distant species can often influence the composition of local assemblages as adult holometabolous insects often inhabit areas for mating and feeding distinct to those they develop in, and subsequently emerge from. For example, Delettre, *et al.* (1998) found that less than half of the fly species they recorded actually emerged from the soil and litter in their study sites; the remainder developed elsewhere and moved into the area as adults. Thus, for many taxa, reproduction (and hence, emergence) sites can differ from those used by adults for mating and feeding. The high abundance and diversity of these plant-associated groups emerging from the soil and litter provides further evidence for multi-habitat use and the importance of the ground-level habitat at Mt Billy CP for the development of plant-associated parasitoids and their hosts. When ready to pupate, many wasp larvae, after bursting out of the plant-feeding host larvae, may drop to the ground to pupate in soil or leaf litter (eg. Shaw & Huddleston 1991; Pivnick 1993). Pupal parasitoids may hunt for fallen plant-feeding host pupae amongst low vegetation or litter (eg. Gauld 1984). Parasitoids that attack leaf-mining or other insects that feed inside plant tissue, such as those inside seeds and fruits, and pupate inside the plant tissue, can also become part of the leaf litter community if the leaf, seed or fruit falls from the plant (eg. Ovruski, *et al.* 2004). Similarly, gall-associated parasitoids can also be found in the leaf litter below their host plants (eg. Hayman, *et al.* 2003). Therefore, although a host may be plant-associated, often the developing larvae/pupae and their parasitoids can become part of the soil and litter community.

As in the current study, Harris, *et al.* (2004) found that an increase in litter and dead wood in gorse-invaded habitat led to an increase in detritus-feeding insects. However, in contrast to this research, they reported a reduction in herbivorous insects due to the loss of native plant species. At Mt Billy CP, three plant-associated functional groups were significantly more abundant in bridal creeper traps than native traps (parasitoids of plant-associated insects, plant- and litter-associated arthropods, and insects feeding inside plant tissue; Table 4.2, Figure 4.5). As there was no change to the canopy above bridal creeper invaded areas, a reduction in plant-associated wasps in this habitat may not be expected (Chapter 3). Therefore, the greater numbers in invaded areas was surprising considering the similar canopy cover above each trap. A possible hypothesis for this is the movement and accumulation of litter has also resulted in the subsequent movement of these wasps and their hosts. When actively moving forest leaf litter to experimentally investigate the effects of litter enhancement and reduction on parasitic Hymenoptera, Ulrich (1998) reported exceptionally high numbers of scale insect (Hemiptera, Sternorrhyncha) parasitoids emerging from increased leaf litter plots as an artefact of transporting the litter. The movement and accumulation of litter from many different habitat patches may also explain why there was considerable overlap in assemblage composition for the plant-associated functional groups from native and invaded habitat compared with the litter-associated wasps that would be choosing hosts to parasitise in the leaf litter (Figure 4.10). As highlighted above, it has also been shown that litter has strong positive effects on non-detrivorous arthropods, favourably enhancing the microhabitat for many taxa. Parasitoids are strongly influenced by temperature and moisture, and parasitism rates can be enhanced by increased habitat complexity provided by detritus (Langellotto & Denno 2004). As previously discussed, many of these plant-associated groups were significantly influenced by the extent of litter cover and depth (Figure 4.15), suggesting that leaf litter and associated habitat factors are also important for the development of non-litter associated parasitoids and their hosts.

Several plant-associated species found in non-invaded habitat were not recorded in invaded sites: for example, all Aphidiinae (Braconidae; aphid parasitoids), *Mymar* (Myrmaridae; egg parasitoids of mostly grass-feeding delphacids), *Elasmus* (Eulophidae; parasitoids of caterpillars on plants), a *Trissolcus* species (Scelionidae; parasitoids of pentatomoid eggs on leaves), and a *Synopeas* species (Platygastridae; parasitoids of plant-feeding cecidomyiids in galls). Indeed, indicator species analysis found Chalcidoidea sp. 10 (*Mymar* sp.) to be the only indicator of native habitat (Table 4.3). A more detailed examination of specific species-level host-parasitoid associations is required to investigate this further. As considered in Chapter 3, a more detailed food-web approach is needed to determine if any of the ground-cover native species at Mt Billy CP are important food plants for herbivorous taxa and hosts for parasitic wasps (eg. Memmott & Godfray 1994; Valladares & Salvo 1999). However, the host records for these species suggest that they have comparatively specialised host associations and that, as originally hypothesised, the displacement of native plant species by bridal creeper may be having an effect on perhaps the few herbivores associated with the ground-cover vegetation.

Bridal creeper has the potential to eventually completely cover the ground-cover habitat at Mt Billy CP, resulting in the total loss of native vegetation. The majority of the native habitat patches originally selected (in 2000) as non-invaded control areas had bridal creeper seedlings present by the completion of the research reported here (in 2003) (pers. obs.). As discussed in Chapter 3, most adult parasitoids feed on nectar from flowers, with species often visiting a limited range of plants. Species from all wasp families and many subfamilies and genera recorded in this study, from minute Chalcidoidea and Seclionidae to larger Ichnuemonidae and Tiphiidae, have been previously recorded feeding at flowers (Jervis, *et al.* 1993; Tooker & Hanks 2000). It has been shown in agricultural systems that the biological control of pest species in crops by parasitoids is enhanced by providing extra adult food sources, such as nectar-producing flowers near or inter-dispersed among crop plants (Schellhorn, *et al.* 2000; Gurr, *et al.* 2004). A similar effect may be occurring at Mt Billy CP where bridal creeper patches are inter-dispersed with native vegetation. As such, adult wasps, despite their development in invaded habitat, are likely to also be using the non-invaded areas. Once bridal creeper covers the entire habitat, these areas will be lost, having implications for the parasitoid species that use the native ground-cover flowering plants as a food source, particularly less mobile species that may not be able to use flowering canopy *Acacia* and *Eucalyptus* trees. The loss of plant-associated parasitoid species may then also have flow-on effects to the canopy trees where their herbivorous insects may be released from parasitic wasp regulation, leading to outbreaks and increased levels of herbivory (LaSalle & Gauld 1993).

Parasitism in bridal creeper invaded habitat

When locating a host, parasitoids respond to habitat factors such as temperature, shade, humidity, vegetation type and chemicals associated with plants and hosts (Gauld & Bolton 1996; Meiners & Obermaier 2004). As such, it was predicted that the thick growth of bridal creeper, and/or increased leaf litter, may influence host location, and hence, parasitism (Section 4.1). For example, a species of *Cotesia* (Braconidae) was almost completely unable to find its exposed host's (Lepidoptera: Pieridae) food plant when overgrown by weeds (Sato & Ohsaki 1987). However, the high number of parasitoids emerging from invaded habitat indirectly suggests that bridal creeper is having little influence on parasitism, and hence a parasitoid's ability to locate host habitat and hosts individuals. This may be because overall, there were limited changes to the arthropod habitat, particularly its structure, for parasitoids already suited to searching though ground-level vegetation, litter and soil for hosts. In addition, most groups were associated with the canopy that remained unchanged in the presence of bridal creeper. Thus, bridal creeper is unlikely to be significantly modifying host-parasitoid interactions (ie parasitism).

The temporal emergence patterns of several of the abundant parasitoid species that emerged from both invaded and native habitats (Figure 4.14) indicate that the same (or similar) hosts are being used in both bridal creeper and native habitat. The lifecycles of parasitoids have evolved to be seasonally synchronised with those of their hosts, particularly in habitats with pronounced seasonality (Godfray 1994; Gauld & Hanson 1995; Lalonde 2004). The very similar emergence patterns of several relatively abundant species recorded from both invaded and weed-free habitat (Figure 4.14) indirectly suggests that the same host(s) are being used across both habitats (eg. Chalcidoidea sp. 07, Chalcidoidea sp. 33, Diapriidae sp. 01, Ichneumonidae sp. 13, and Scelionidae sp. 01). The timing and patterns of parasitoid emergence is also determined by other factors influenced by microclimate such as temperature, humidity and predation (Orr, *et al.* 2000; Charlet 2002). Therefore, these similar emergence patterns also suggest that the microclimate provided by the ground-cover bridal creeper and some native habitat patches is also similar. Several other wasp species examined also had similar emergence patterns, but the emergence period was longer or the peaks in numbers were at slightly different times (eg. Braconidae sp. 09, Braconidae sp. 04, Chalcidoidea sp. 08 and Diapriidae sp. 04). These parasitoids may also be attacking the same hosts, as males and females can emerge at different times (eg. Gauthier, *et al.* 1997; Loch &

Walter 2002), as can parasitoids that have parasitised different host stages, eg. early compared to late instars (Hu, *et al.* 2003). Detailed examination of specific host-parasitoid association (eg. via rearing studies) is required to fully determine if the same host species are being parasitised in weed-invaded and weed-free habitat. However, these emergence patterns do suggest, that for some parasitoid taxa at least, it is likely that the same hosts were parasitised in both invaded and non-invaded areas. Thus, increased leaf litter across bridal creeper invaded areas has probably allowed for the expansion (and increase) of the litter and soil-associated arthropod community and their parasitoids.

4.5 Conclusion

As reported in Chapter 3, the invasion of bridal creeper and associated loss of native plant species is not having an obviously negative effect on arthropod biodiversity. This study showed that by investigating species relationships (host-parasitoid associations) the effect of bridal creeper on arthropod biodiversity could be more fully understood. Through the investigation of larval habitat associations it was revealed that there was no substantially negative impact on parasitoid (and hence host arthropod) reproduction and development. Indeed, a higher number of parasitoids emerged from invaded areas than native habitat revealing the use of invaded areas for arthropod reproduction and development. Leaf litter and soil-associated parasitoids were again a major functional group, with significantly greater numbers of individuals and species emerging from invaded habitat. The significantly higher numbers of host taxa with litter-associated life stages (Diptera, Coleoptera, Lepidoptera, and Araneae) also emerging from invaded habitat is a likely explanation for the increase in litter-associated parasitoids. This was highlighted by *R. inopicida*, a parasitoid that dominated the bridal creeper wasp assemblage, presumably responding to increased soil and leaf-litter host fly species.

Leaf litter appears to be an important determining factor for a range of wasp functional groups, not only soil- and litter-associated wasps (and their hosts). As such, bridal creeper's foliage has not only directly provided new arthropod habitat (Chapter 3), its invasion has also indirectly affected the entire arthropod food web. In the detritus-based compartment of the woodland food web, higher levels of leaf litter resulted in more detritivores, which in turn led to more parasitoids of soil and litter arthropods. For the plant-based compartment of the web, more litter also appears to influence the abundance of plant associated host taxa and their parasitoids (mostly from the canopy), that may be responding to the enhanced microclimate and/or are being moved about with the leaf litter and accumulating in invaded areas. In addition, similar temporal emergence patterns of parasitoid species indicated that the same hosts may have been used across both habitats. Thus, increased leaf litter across bridal creeper invaded areas may have allowed for the expansion and increase in abundance of the associated arthropod community. The recording of parasitoids of plant-associated hosts emerging from the ground-cover habitat also highlights the importance of heterogeneity of habitats and habitat complexity for many arthropod groups and illustrates that species richness emerging from a particular site (eg. ground-cover soil and leaf litter habitat) depends on the surrounding habitats (eg. canopy).

Despite the higher numbers of parasitoids and their hosts in invaded areas, the invasion of bridal creeper is having a homogenising effect on parasitoid assemblage composition for a range of wasp functional groups. This suggests that native habitat has naturally high levels of patchiness resulting in between patch endemism and that bridal creeper is eliminating this by making the habitat more homogeneous. It may be predicted that such small-scale habitat modification enhances biodiversity by increasing habitat complexity, and can perhaps even be seen as 'beneficial'. However, if these changes become too extensive (ie. as bridal creeper becomes more widespread), it may be detrimental due to the loss of patches containing resources such as nectar-providing flowers. Thus, the dominance of *R. inopicida* and the homogenisation of the wasp assemblage highlights how, indirectly via leaf litter accumulation, the invasion of bridal creeper has the potential to modify the structure and organization of the arthropod community in invaded habitat.

Stephens, C.J., Taylor, J.D., and Austin, A.D., (2003) Modification of insect-plant interactions: weed invasion and the pollination of an endangered orchid.
Records of the South Australian Museum, v. 7, pp. 193-201.

Chapter 6

Summary and general discussion

Documenting the impacts of environmental weeds on a range of native biota, their community structure and associated ecological processes has been infrequently undertaken (Adair & Groves 1998). By considering different taxa and trophic groups (plants, arthropods and parasitic Hymenoptera), high-level (orders and families) and low-level (species) taxonomic assemblages, and ecological processes (parasitism and pollination), this study has revealed the complex direct and indirect effects an invasive plant species can have in a native habitat.

The impact of bridal creeper on the native plant community was overwhelmingly detrimental, undoubtedly due to direct interactions with the weed, such as shading and root competition (Chapter 2). It was predicted therefore, that the replacement of an open, species-rich ground-cover habitat into a closed, homogenous one, would have a flow-on effect to other components of the system, such as plant-associated arthropods and their parasitoids. However, the impact of bridal creeper on native arthropods and parasitic wasps was less clear, and certainly more complex, due to both direct and indirect effects of weed invasion and the characteristics of the arthropod assemblage associated with the ground-cover habitat.

Very abundant and diverse arthropod and wasp communities were found to exist in habitat invaded by bridal creeper, presumably using the weed's foliage as habitat. However, there was some evidence that bridal creeper may not provide seasonally equivalent habitat to that of native vegetation for some herbivorous and nectar-feeding groups (Chapter 3). Invaded habitat was also being used for the reproduction and development of a diverse range of parasitic wasps and their hosts. Significantly though, the homogenous habitat produced by bridal creeper compared with native vegetation was reflected in the composition of the wasp assemblages occurring in invaded areas (Chapters 3 and 4). Furthermore, the indirect effect of higher levels of leaf litter associated with bridal creeper invasion resulted in greater numbers of litter-associated arthropods and their parasitoids and, in particular, the extreme abundance of one species that dominated the wasp assemblage emerging from invaded habitat (Chapter 4). These findings suggest that possibly the most significant impact of bridal creeper invasion is the gradual homogenization of both the plant and insect communities. Finally, the interaction between an orchid and its pollinator was not impacted upon by the presence of bridal creeper, and may have even been enhanced due the increase in the number of its soil- and litter-associated pollinator in weed-invaded areas (Chapter 5).

The unexpected result of few clear 'negative' effects due to the significant reduction in native plant diversity was because the commonly assumed link between native plant and arthropod diversity (Groves & Willis 1999; Knops, *et al.* 1999; Kruess & Tscharntke 2002, 2002) was considerably more complex than predicted. The main factors contributing to this are summarised below.

(i) *Naturally impoverished herbivore community.* The ground-cover plant community, that was so negatively affect by bridal creeper, was comprised of seasonally senescing annuals, geophytes and deciduous perennials that may have supported a naturally impoverished herbivore community (Lawton 1983). This was supported by parasitoid host records, which revealed that many of the plant-based host insects recorded from the ground-cover habitat were mostly associated with the canopy trees. Hence, their habitat and other resources remained largely unaffected by bridal creeper.

(ii) *Multi-habitat use.* Wasp functional group analysis based on host habitat associations, revealed the mobility and multi-habitat use of adult parasitic wasps. The collection from foliage of parasitoids of litter-associated arthropods and, in the absence of herbivores, the presence of parasitoids of plant-associated insects on bridal creeper, showed that many species use different habitat for juvenile development compared with that used by adults. Furthermore, the extent of bridal creeper invasion was such that non-invaded habitat remained within a patchy, open system that was still allowing mobile species access to native habitat if required. However, bridal creeper has the potential to eventually completely cover the ground-cover habitat at Mt Billy CP, resulting in the total loss of native vegetation. Once bridal creeper covers the entire habitat the native patches will be lost, having implications for species that use resources provided by the native ground-cover, for example, flowering plants as a food source.

(iii) *Importance of leaf litter.* Functional group analysis also revealed the dominance of soil and litter associated arthropods and the importance of the leaf litter microhabitat for taxa from both the detritus- and plant-based compartments of the food web. Consequently, the ground-cover plant community that was so completely altered by bridal creeper was not as important as other components of the woodland habitat, such as the soil, leaf litter and canopy microhabitats, for the reproduction and development of the majority of arthropod taxa recorded. The detection of leaf litter as an important factor was also of particular significance in the understanding of the effects of bridal creeper on *Pterostylis bryophila* pollination rates and pollinator abundance.

(iv) *Increase in habitat complexity*. The invasion of bridal creeper both removed and replaced arthropod habitat by supplanting native flora in a patchy mosaic, and indirectly created habitat by increasing leaf litter in invaded areas. As such, bridal creeper could be considered to have caused an overall increase in habitat complexity. It has been suggested that increases in species richness should be expected whenever an invasive species increases the complexity and/or heterogeneity of a habitat (Crooks 2002; Sax, *et al.* 2005). Based on the homogenisation of the wasp assemblages, it may be predicted however, that once bridal creeper covers the entire habitat, arthropod diversity and abundance will decline. These findings are important not only for considering the effects of weed invasion on native biota, but also in other situations where the structural complexity is modified via changes in the plant community in both agricultural and natural landscapes.

Parasitic Hymenoptera

Parasitic wasps are a major part of most terrestrial ecosystems, possibly contributing to 20% of all insect species (LaSalle & Gauld 1993), with estimates of over 31,000 species for Australia alone (Yeates, *et al.* 2003). Over 500 parasitic wasp morphospecies were recorded at Mt Billy CP using just two sampling techniques (Appendix B). Although the sampling techniques differ, this research collected a wasp assemblage with a similar order of magnitude to other comprehensive studies of temperate parasitic wasp assemblages (Owen, *et al.* 1981; Lockwood, *et al.* 1996; Lewis & Whitfield 1999), including that recorded from an Australian forest (Lassau & Hochuli 2005). Such figures demonstrate the potentially extreme richness and abundance of parasitic wasp assemblages in temperate habitats. The abundance and diversity of wasps recorded at Mt Billy CP also highlights the high levels of arthropod diversity that can occur in a remnant habitat and the conservation value of small reserves for terrestrial arthropods (Yen & Butcher 1997).

Despite their extreme diversity, high trophic level and species-specific host and niche associations, parasitic wasp assemblages have very rarely been used to investigate the effects of habitat change (Lockwood, *et al.* 1996; Lewis & Whitfield 1999; Lassau & Hochuli 2005). Because of their host and niche associations, parasitoids lend themselves to a functional approach that is often of more general relevance than the study of individual species and allows for an ecological interpretation of species richness and abundance (Simberloff & Dayan 1991; Didham, *et al.* 1996; Fisher 1998). In the research reported in this thesis, the use of parasitic wasps and their host-associations provided an ecological insight into the studied habitat. Particularly, the use of parasitoid functional groups supplied valuable information on host arthropod identity, their associated niches, biology and trophic levels, and a qualitative measurement of host-parasitoid interactions.

There is a diverse range of ecological research into hymenopteran parasitoid community structure and organisation (eg. Price, *et al.* 1980; Hawkins 1993; Memmott, *et al.* 1994; Shaw 1994; Rodriguez & Hawkins 2000). However, the focus of such investigations, and of many general hymenopteran reviews (eg. LaSalle & Gauld 1993; Hawkins & Sheehan 1994; Quicke 1997), is largely on herbivorous insects and their parasitoids. Such an emphasis on herbivore-parasitoid relationships is primarily due to the agricultural background of most parasitic wasp research. The research reported in this thesis, and others (eg. Samways 1995; Siemann, *et al.* 1998), have highlighted that at local scales, plant diversity does not always correlate with insect diversity. Despite this, vegetation is typically the first choice for biodiversity inventories (Danks 1996; Duelli & Obrist 1998). Furthermore, this research revealed the high abundance and diversity of litter- and soil-associated parasitoids (and thus their hosts) in a eucalypt woodland habitat. It has been suggested that this finding may turn out to be characteristic of temperate woodland ecosystems (Ulrich 1998, 2004). From an ecosystem functioning perspective, the activities of soil and litter arthropods affect detritus decay rates and microbial activity that, in turn, strongly influences nutrient supply and primary productivity (Seastedt & Crossley Jr. 1984; Moore, *et al.* 2004). This highlights how litter- and soil-associated parasitoids that regulate the populations of such detritus-associated arthropods warrant more emphasis in ecological studies. At Mt Billy CP, leaf litter was also found in be an important influence in the richness and abundance of non-detritus associated groups from the canopy. These results clearly illustrate how the canopy and soil/litter sub-communities are linked by species that feed on above ground foliage but pupate in the soil and/or litter, or feed on litter resources but disperse and bask on foliage, and by predators, parasitoids and detritivores that move among substrates in search of resources (Schowalter 2000). This emphasises how other habitat factors, such as complexity and patch heterogeneity rather than simply plant diversity per se, clearly need to be considered in the study, conservation and management of ecological systems and processes.

In addition to investigating ecological questions about the effect of weed invasion on arthropod communities, this work has also resulted in an insight into, and an inventory of, the native parasitic wasps and their host associations within a diverse native woodland community. It is expected that this will facilitate further studies and management strategies of Mt Billy CP and other similar woodland systems. For example, two foliage-feeding insect species have been introduced into Australia as biological control agents for bridal creeper: a leafhopper, *Zygina* sp. (Hemiptera, Cicadellidae) and a leaf beetle, *Crioceris* sp. (Coeloptera, Chrysomelidae) (CSIRO 2003). Several wasp genera recorded from both native and bridal creeper-invaded habitat at Mt Billy CP have been reported elsewhere as parasitoids of both Chrysomelidae and Cicadellidae species (Appendix C). This may have an impact on the success of these introduced biocontrol agents as it has been shown that many introduced herbivore species accumulate a considerable number of native parasitoids, often soon after introduction (Cornell & Hawkins 1993).

Future research

This study has described the impacts of weed invasion on species richness and abundance patterns and gained a significant insight into the complexities of a natural system. Explanations and hypotheses for these observations have been presented and developed throughout pertinent chapters of this thesis. Further investigations that could usefully test these hypotheses and help identify the ecological processes behind the observed patterns are outlined below.

(i) *Leaf litter*. Considering the importance of leaf litter for the arthropods in the studied system, and its influence on decomposition and nutrient and soil dynamics, a more targeted study into bridal creeper growth and litter accumulation is required. The experimental addition and/or removal of leaf litter (see Ulrich 1998) would be useful to examine the hypothesis that the accumulation of leaf litter is causing an increase in arthropod abundance and species richness. Such a study could also investigate what litter-associated factors are important for arthropod and parasitoid communities, such as the amount of leaf litter, densities of hosts or feeding substrates, shelter, microclimatic conditions, and soil depth, structure and composition. As host food plants can have a strong influence on parasitism, for example, plant nutritional status, chemicals and physical attributes (Price, *et al.* 1980; Quicke 1997), equivalent characteristics of litter may also prove important in host-parasitoid associations and community structure.

(ii) *Intensity of bridal creeper invasion.* Different levels (percent cover) of bridal creeper clearly influences the number of native plant species, with low levels of invasion having little effect. As highlighted previously, the patchy invasion of bridal creeper may have allowed arthropods access to non-invaded habitat. This suggests that the research presented here may have examined invasion levels much lower than that for plants simply because of arthropod movement. Therefore, the effect of different levels of bridal creeper invasion on arthropod communities would be a useful investigation and may be particularly valuable for management decisions such as prioritising areas for weed control.

(iii) *Host-parasitoid interactions.* When determining the impacts of habitat change on native biota, simple species lists are not as useful as "who does what and with whom" (Purvis & Hector 2000). Thus, a more specific understanding of individual parasitoid-host relationships would be of particular value and would allow for the comparison of underlying processes such as decomposition, herbivory and parasitism between invaded and non-invaded habitats. Food webs can provide a rich source of information in addition to species diversity and abundance as they provide data on species interactions and, by identifying both direct and indirect effects, can be used to investigate the impact of perturbation on a community (Cohen, *et al.* 1993; Memmott & Godfray 1993; Crowder, *et al.* 1996). Of particular use would be the development of quantitative parasitoid webs that identify specific host-parasitoid species-level interactions via detailed observations and host-rearing studies (eg. Memmott & Godfray 1993, 1994; Valladares & Salvo 1999). The construction and comparison of such webs among specifically targeted canopy and ground-cover plants, detritus, arthropods and their associated parasitoids from native and weed invaded habitats would identify the species interactions that shaped the abundance and diversity patterns recorded in this study.

References

Ackerman J.D., Meléndez-Ackerman E.J. and Salguero-Faria J. 1997. Variation in pollinator abundance and selection of fragrance phenotypes in an epiphytic orchid. *American Journal of Botany* 84: 1383-90.

Adair R.J. and Groves R.H. 1998. *Impact of Environmental Weeds on Biodiversity: A Review and Development of a Methodology*. National Weeds Program, Environment Australia, Canberra.

Adams P.B. and Lawson S.D. 1993. Pollination in Australian orchids: a critical assessment of the literature 1882-1992. *Australian Journal of Botany* 41: 553-75.

Agriculture & Resource Management Council of Australia & New Zealand, Australian & New Zealand Environment & Conservation Council and Forestry Ministers. 2001. *Weeds of National Significance: Bridal Creeper (*Asparagus asparagoides*) Strategic Plan*, National Weeds Strategy Executive Committee, Launceston.

Alekseev V.N. 1987. Superfamily Ceraphronoidea (Ceraphronoids). In *Keys to the Insects of the European Part of the USSR*, ed. G.S. Medvedev, pp. 1213-57. New Delhi, Amerind Publishing.

Allen M.F., Morris S.J., Edwards E. and Allen E.B. 1995. Microbe-plant interactions in Mediterranean-type habitats: shifts in fungal symbiotic and saprophytic functioning in response to global change. In *Global Change and Mediterranean-type Ecosystems*, ed. J.M. Moreno, W.C. Oechel, pp. 287-305. New York, Springer-Verlag.

Andersen A.N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* 16: 347-57.

Andersen A.N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* 22: 15-29.

Andersen A.N., Ludwig J.A., Lowe L.M. and Rentz D.C.F. 2001. Grasshopper biodiversity and bioindicators in Australian tropical savannas: responses to disturbance in Kakadu National Park. *Austral Ecology* 26: 213-22.

Andow D.A. and Imura O. 1994. Specialization of phytophagous arthropod communities on introduced plants. *Ecology* 75: 296-300.

Anthelme F., Grossi J.L., Brun J.J. and Didier L. 2001. Consequences of green alder expansion on vegetation changes and arthropod communities removal in the northern French Alps. *Forest Ecology and Management* 145: 57-65.

Askew R.R. 1980. The diversity of insect communities in leaf-mines and plant galls. *Journal of Animal Ecology* 49: 817-29.

Austin A.D. 1985. The function of spider egg sacs in relation to parasitoids and predators, with special reference to the Australian fauna. *Journal of Natural History* 19: 359-76.

Austin A.D. 1986. A taxonomic revision of the genus *Mirobaeoides* Dodd (Hymenoptera: Scelionidae). *Australian Journal of Zoology* 34: 315-37.

Austin A.D. 1999. The importance of 'species' in biodiversity studies: lessons from a mega-diverse group- the parasitic Hymenoptera. In *The Other 99%; The Conservation and Biodiversity of Invertebrates,* ed. W. Ponder and D. Lunney, pp 159-165. Transactions of the Royal Zoological Society of NSW, Mosman.

Austin A.D. and Dangerfield P.C. 1992. Synopsis of Australian Microgastrinae (Hymenoptera: Braconidae), with a key to genera and description of new taxa. *Invertebrate Taxonomy* 6: 1-76.

Austin A.D. and Field S.A. 1997. The ovipositor system of Scelionid and Platygastrid wasps (Hymenoptera: Platygastroidea): comparative morphology and phylogenetic implications. *Invertebrate Taxonomy* 11: 1-87.

Austin A.D., Jennings J.T., Iqbal M. and Stevens N.B. 2002. *BioEd 'An Interactive Training Tool for Taxonomy': Key to the Australian Families of Hymenoptera.* CD-ROM.

Balderson J. 1991. Mantodea (Praying mantids). In *The Insects of Australia: A Textbook for Students and Research Workers*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 348-56. Melbourne, Melbourne University Press.

Barbosa O. and Marquet P.A. 2002. Effects of forest fragmentation on the beetle assemblage at the relict of Fray Jorge, Chile. *Oecologia* Online 5 June 2002.

Bartareau T. and Jakes B.R. 1994. Some observations on the flowering and pollination of *Pterostylis procera* M. Clements & D Jones in north-east Queensland. *The Orchadian* 11: 198-201.

Bates R. 1989. Pollination biology and ecology of the orchid *Pterostylis cucullata* (leafy greenhood) in South Australia. *South Australian Naturalist* 63: 85-9.

Bates R.J. and Weber J.Z. 1990. *Orchids of South Australia.* South Australia, Flora and Fauna of South Australia Handbooks Committee. 182 pp.

Beardsell D.V. and Bernhardt P. 1982. Pollination biology of Australian terrestrial orchids. In *Pollination '82*, ed. E.G. Williams, R.B. Knox, J.H. Gilbert, P. Bernhardt, pp. 166-83. Parkville, University of Melbourne.

Begon M., Harper J.L. and Townsend C.R. 1990. *Ecology: Individuals, Populations and Communities.* Cambridge, Blackwell. 945 pp.

Bickerton D. 2001. *Draft Recovery Plan for* Pterostylis bryophila *(Hindmarsh Valley greenhood)*, National Parks and Wildlfe SA, Adelaide.

Bickerton D. 2003. *The Common White Spider-Orchid: Common No More*, Threatened Flora, Department for Environment and Heritage.

Blair J.M., Parmelee R.W. and Wyman R.L. 1994. A comparison of the forest floor invertebrate communities of four forest types in the northeastern U.S. *Pedobiologia* 38: 146-60.

Blossey B., Skinner L.C. and Taylor J. 2001. Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. *Biodiversity and Conservation* 10: 1787-807.

Boeken B. and Orenstein D. 2001. The effect of plant litter on ecosystem properties in a patchy Mediterranean semi-arid shrubland. *Journal of Vegetation Sciences* 12: 825-32.

Boerner R.E.J. and Kooser J.G. 1989. Leaf litter redistribution among forest patches within an Allegheny Plateau. *Landscape Ecology* 2: 81-92.

Bond W.J. 1994. Keystone species. In *Biodiversity and Ecosystem Function*, ed. E.D. Schulze, H.A. Mooney, pp. 237-53. Berlin, Springer-Verlag.

Boucek Z. 1988. *Australasian Chalcidoidea (Hymenoptera): A Biosystematic Revision of Genera of Fourteen Families with a Reclassification of Species.* Wallingford, CAB International. 832 pp.

Braithwaite R.W., Lonsdale W.M. and Estbergs J.A. 1989. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra. Biological Conservation* 48: 189-210.

Brown B.J. and Mitchell R.J. 2001. Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* 129: 43-9.

Brown J.H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124: 255-79.

Brown J.H. and Sax D.F. 2004. An essay on some topics concerning invasive species. *Austral Ecology* 29: 530-6.

Burbidge A.H., Leicester K., McDavitt A. and Majer J.D. 1992. Ants as indicators of disturbance at Yanchep National Park, Western Australia. *Journal of the Royal Society of Western Australia* 75: 89-95.

Burks B.D. 1979. Chalcididae. In *Catalog of Hymenoptera in America North of Mexico*, ed. K. V. Krombein, P. D. Hurd Jr, D. R. Smith, B. D. Burks, pp. 860-74. Washington, Smithson Institution Press.

Burks B.D. 1979. Mymaridae. In *Catalogue of Hymenoptera in America North of Mexico*, ed. K. V. Krombein, P. D. Hurd Jr, D. R. Smith, B. D. Burks, pp. 1022-33. Washington, Smithson Institution Press.

Burks R.A. 2003. *Key to the Nearctic genera of Eulophidae, Subfamilies: Entedoninae, Euderinae, and Eulophinae (Hymenoptera: Chalcidoidea).* http://cache.ucr.edu/~heraty/Eulophidae/index.html.

Byers G.W. 1991. Mecoptera (Scorpion-flies, hanging-flies). In *The Insects of Australia: A Textbook for Students and Research Workers*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 696-704. Melbourne, Melbourne University Press.

Cady L. 1988. The genus *Pterostylis* in Australia and New Zealand: Part 2. *The Orchadian* 9: 52-61.

Cane J.H. and Tepedino V.J. 2001. Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conservation Ecology [online]* 5.

Carson W.P. and Root R.B. 2000. Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs* 70: 73-99.

Carver M., Gross G.F. and Woodward T.E. 1991. Hemiptera (Bugs, leafhoppers, cicadas, aphids, scale insects etc.). In *The Insects of Australia*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 429-509. Carlton, Melbourne University Press.

Castillo M.L. and Lobo J.M. 2004. A comparision of Passalidae (Coleoptera, Lamellicornia) diversity and community structure between primary and secondary tropical forest in Los Tuxtlas, Veracruz, Mexico. *Biodiversity and Conservation* 13: 1257-69.

Chapin F.S., Schulze E.D. and Mooney H.A. 1992. Biodiversity and ecosystem processes. *Trends in Ecology and Evoloution* 7: 107-8.

Chapin F.S., Zavaleta E.S., Eviners V.T., Naylor R.L., Vitousek P.M., Reynolds H.L., Hooper D.U., Lavorel S., Sala O.E., Hobbie S.E., Mack M.C. and Diaz S. 2000. Consequences of changing biodiversity. *Nature* 405: 234-42.

Charlet L.D. 2002. Parasitization of the red sunflower seed weevil (Coleoptera: Curculionidae) by its larval parasitoid *Triaspis aequoris* (Hymenoptera: Braconidae) in cultivated sunflower. *Environmental Entomology* 31: 844-51.

Clouse R. 1999. Leaf-litter inhabitants of a Brazilian pepper stand in Everglades National Park. *Florida Entomologist* 82: 388-403.

Cohen J.E., Bever R.A., Cousins S.H., DeAngelis D.L., Goldwasser L., Lawton K.L., MArtinez N., O'Malley R., Page L.M., Patten B.C., Pimm S.L., Polis G.A., Rejmánek M., Schoener T.W., Schoenly K., Sprules E.G., Teal J.M., Ulanowicz R.E., Warren P.H., Wilbur H.M. and Yodzis P. 1993. Improving food webs. *Ecology* 74: 252-8.

Cohen J.E., Schoenly K., Heong K.L., Justo H., Arida G., Barrion A.T. and Litsinger J.A. 1994. A food web approach to evaluating the effect of insecticide spraying on insect pest population dynamics in a Philippine irrigated rice ecosystem. *Journal of Applied Ecology* 31: 747-63.

Colautti R.I., Ricciardi A., Grigorovich I.A. and MacIsaac H.J. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7: 721–33.

Coll M. and Bottrell D.G. 1996. Movement of an insect parasitoid in simple and diverse plant assemblages. *Ecological Entomology* 21: 141-9.

Colless D.H. and McAlpine D.K. 1991. Diptera (Flies). In *Insects of Australia*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 717-86. Carlton, Melbourne University Press.

Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-10.

Corff J.L., Marquis R.J. and Whitfield J.B. 2000. Temporal and spatial variation in a parasitoid community associated with the herbivores that feed on Missouri *Quercus*. *Environmental Entomology* 29: 1-14.

Cornell H.V. and Hawkins B.A. 1993. Accumulation of native parasitoids species on introduced herbivores: a comparison of hosts as natives and as invaders. *American Naturalist* 141: 847-65.

Costello S.L., Pratt P.D., Rayamajhi M.B. and Centre T.D. 2003. Arthropods associated with above-ground portions of the invasive tree *Melaleuca quinquenervia* in South Florida, USA. *Florida Entomologist* 86: 300-22.

Cronin J.T. and Haynes K.J. 2004. An invasive plant promotes unstable host-parasitoid patch dynamics. *Ecology* 85: 2772-82.

Crooks J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97: 153-66.

Crowder L.B., Reagan D.P. and Freckman D.W. 1996. Food web dynamics and applied problems. In *Food Webs. Integration of Patterns and Dynamics*, ed. G.A. Polis, K.O. Winemiller, pp. 327-36. New York, Chapman & Hall.

CSIRO. 2003. *What is Bridal Creeper?* Web page. http://www.ento.csiro.au/bridalcreeper/.

Cumber R.A. 1967. Factors influencing egg survivial of *Scolypopa australia* Walker (Hemiptera-Homoptera: Ricaniidae) in the Sydney area. *New Zealand Journal of Science*: 639-43.

D'Antonio C.M. and Vitousek P.M. 1992. Biological invasions by exotic grasses, the grass-fire cycle and global change. *Annual Review of Ecology and Systematics* 23: 63-87.

Dafni A. and Bernhardt P. 1990. Pollination of terrestrial orchids of Southern Australia and the mediterranean region: systematic, ecological and evolutionary implications. *Evolutionary Biology* 24: 193-253.

Dahms E.C. 1984. Revision of the genus *Melittobia* (Chalcidoidea: Eulophidae) with the description of seven new species. *Memoirs of the Queensland Museum* 21: 271-336.

Danks H.V. 1996. *How to assess insect biodiversity without wasting your time*. Document Series No. 5, Biological Survey of Canada (Terrestrial Arthropods), Canada.

Darling D.C. and Johnson N.F. 1984. Synopsis of Nearctic Azotinae (Hymenoptera: Aphelinidae). *Proceedings of the Entomological Society of Washington* 86: 552-62.

Davies R.G. 2002. Feeding group responses of a Neotropical termite assemblage to rainforest fragmentation. *Oecologia* Online.

Day M.C. 1988. *Spider Wasps, Hymenoptera: Pompilidae*. London, British Museum (Natural History).

Delettre Y.R., Morvan N., Tréhen P. and Grpptaert P. 1998. Local biodiversity and multi-habitat use in empidoid flies (Insecta: Diptera, Empidoidea). *Biodiversity and Conservation* 7: 9-25.

Denys C. and Tscharntke T. 2002. Plant-insect communities and the predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia* 130: 315-24.

Dessart P. 1995. The Evaniomorph parasitoid families: Ceraphronidae. In *The Hymenoptera of Costa Rica*, ed. P.E. Hanson, I.D. Gauld, pp. 199-203. Oxford, Oxford University Press.

di Castri F. 1989. History of biological invasions with special emphasis on the Old World. In *Biological Invasions: a Global Perspective*, ed. J.A. Drake, H. Mooney, F.D. Castri, R.H. Groves, F.J. Kruger, *et al*, pp. 1-30, John Wiley & sons.

Didham R.K., Ghazoul J., Stork N.E. and Davis A.J. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology & Evolution* 11: 255-60.

Didham R.K., Lawton J.H., Hammond P.M. and Eggleton P. 1998. Trophic structure and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences* 353: 437-51.

Dighton J., Bonillas A.S.M., Jimînez-Nûnez R.A. and Martînez N. 2000. Determinates of leaf litter patchiness in mixed species New Jersey pine barrens forest and its possible influence on soil and soil biota. *Biology and Fertility of Soils* 31: 288-93.

Doak P. 2000. The effects of plant dispersion and prey density on parasitism rates in a naturally patchy habitat. *Oecologia* 122.

Donaldson J., Nänni I., Zachariades C. and Kemper J. 2002. Effects of habitat fragmentation on pollinator diversity and plant reproductive success in Renosterveld shrublands of South Africa. *Conservation Biology* 16: 1267-76.

Donnelly S.E., Lortie C.J. and Aarssen L.W. 1998. Pollination in *Verbascum thapsus* (Scrophulariaceae): the advantage of being tall. *American Journal of Botany* 85: 1618-25.

Dubbert M., Tscharntke T. and Vidal S. 1998. Stem-boring insects of fragmented *Calamagrostis* habitats: herbivore-parasitiod community structure and the unpredictability of grass shoot abundance. *Ecological Entomology* 23: 271-80.

Duelli P. and Obrist M.K. 1998. In search of the best correlates for local organismal biodiversity in cultivated areas. *Biodiversity and Conservation* 7: 297-309.

Dufrêne M. and Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345-66.

Dukes J.S. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia* 126: 563-8.

Dukes J.S. and Mooney H.A. 2003. Disruption of ecosystem processes in western North America by invasive species. In *How Landscapes Change: Human Disturbance and Ecosystem Disruption in the Americas*, ed. G.A. Bradshaw, P.A. Marquet, H.A. Mooney. Berlin Heidelberg, Springer-Verlag.

Dyer L.A. and Letourneau D.K. 1999. Trophic cascades in a complex terrestrial community. *Proceedings of the National Academy of Sciences of the United States of America* 96: 5072-6.

Ehrlich P.R. and Ehrlich A.H. 1981. *Extinction. The Causes and Consequences of the Disappearance of Species*. New York, Random House.

Ehrlich P.R. and Mooney H.A. 1983. Extinction, substitution, and ecosystem services. *BioScience* 33: 248-54.

Elton C.S. 1958. *The Ecology of Invasions by Animals and Plants*. London, Methuen & Co.

Evans H.E. 1978. The Bethylidae of America North of Mexico. *Memoirs of the American Entomological Institute* 27: 332.

Facelli J.M. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings on old fields. *Ecology* 75: 1727-35.

Fergusson N.D.M. 1995. The Cynipoid Famlies: Figitidae. In *The Hymenoptera of Costa Rica*, ed. P.E. Hanson, I.D. Gauld, pp. 259-65. Oxford, Oxford University Press.

Finnamore A. and Gauld I.D. 1995. The Chrysidoid Families: Bethylidae. In *The Hymenoptera of Costa Rica*, ed. P.E. Hanson, I.D. Gauld, pp. 470-9. Oxford, Oxford University Press.

Finnamore A.T. and Brothers D.J. 1993. Superfamily Chrysidoidea. In *Hymenoptera of the World: An Identification Guide to Families*, ed. H. Goulet, J.T. Huber, pp. 130-60. Ontario, Centre for Land and Biological Resources Research, Agriculture Canada.

Fisher B.L. 1998. Insect behaviour and ecology in conservation - preserving functional species interactions. *Annals of the Entomological Society of America* 91: 155-8.

Florentine S.K. and Fox J.E.D. 2003. Allelopathic effects of *Eucalyptus victrix* on *Eucalyptus* and grasses. *Allelopathy Journal* 11: 77 – 84.

Foster B.L. and Gross K.L. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology* 79: 2593-602.

Fraser S.M. and Lawton J.H. 1994. Host range expansion by British moths onto introduced conifers. *Ecological Entomolgy* 19: 127-37.

French K. and Eardley K. 1997. The impact of weed infestations on litter invertebrates in coastal vegetation. In *Frontiers in Ecology: Building the Links*, ed. N. Klomp, I. Lunt, pp. 89-102. New York, Elsevier.

French K. and Major R.E. 2001. The effect of exotic *Acacia* (Fabaceae) invasion on ant assemblages in South African Fynbos. *Austral Ecology* 26: 303-10.

French K. and Zubovic A. 1997. Effect of the weed *Chrysanthemoides monilifera* (Bitou Bush) on bird communities. *Wildlife Research* 24: 727-35.

Galloway I.D. and Austin A.D. 1984. Revision of the Scelioninae (Hymneoptera: Scelionidae) in Australia. *Australian Journal of Zoology Supplementary Series* 99: 1-138.

Gaston K.J. 2000. Global patterns in biodiversity. *Nature* 405: 220-7.

Gauld I. and Bolton B., ed. 1996. *The Hymenoptera*. New York, Oxford University Press. 332 pp.

Gauld I.D. 1984. *An Introduction to the Ichneumonidae of Australia.* London, British Museum (Natural History).

Gauld I.D. 1995. The ichneumonoid families: Ichneumonidae. In *The Hymenoptera of Costa Rica*, ed. P.E. Hanson, I.D. Gauld, pp. 390-430. Oxford, Oxford University Press.

Gauld I.D. and Hanson P.E. 1995. The biology of Hymenoptera: The parasitoid and its interactions with its host. In *The Hymenoptera of Costa Rica*, ed. P.E. Hanson, I.D. Gauld, pp. 45-88. Oxford, Oxford University Press.

Gauthier N., Monge J. and Huignard J. 1997. Sex-allocation behaviour of a solitary ectoparasitoid: effects of host-patch characteristics and female density. *Entomologia Experimentalis et Applicata* 82: 167–74.

Gibson G.A.P. 1993. Superfamilies Mymarommatoidea and Chalcidoidea. In *Hymenoptera of the World: An Identification Guide to Families*, ed. H. Goulet, J.T. Huber, pp. 570-655. Ontario, Centre for Land and Biological Resources Research, Agriculture Canada.

Godfray H.C.J. 1994. *Parasitoids. Behavioral and Evolutionary Ecology.* Princeton, Princeton University Press. 473 pp.

Goodwin J. 1992. The role of mycorrhizal fungi in competitive interactions among native bunchgrass and alien weeds: a review and synthesis. *Northwest Scientist* 66: 251-60.

Gordh G. and Moczar L. 1990. A catalog of the world Bethylidae (Hymenoptera: Aculeata). *Memoirs of the American Entomological Institute* 46.

Gotelli N.J. and Colwell R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379-91.

Goulet H. and Huber J.T., ed. 1993. *Hymenoptera of the world: an identification guide to families.* Ontario, Centre for Land and Biological Resources Research, Agriculture Canada. 668 pp.

Greenwood H., O'Dowd D.J. and Lake P.S. 2004. Willow (*Salix* x *rubens*) invasion of the riparian zone in south-eastern Australia: reduced abundance and altered composition of terrestrial arthropods. *Diversity and Distributions* 10: 485-92.

Griffin G.F., Stafford Smith D.M., Morton S.R., Allan G.E., Masters K.A. and Preece N. 1989. Status and implications of the invasion of Tamarisk (*Tamarix aphylla*) on the Finke River, Northern Territory, Australia. *Journal of Environmental Management* 29: 297-315.

Gross C.L. and Mackay D. 1998. Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biological Conservation* 86: 169-78.

Groves R.H. and Willis A.J. 1999. Weeds and loss of native plant biodiversity: some Australian examples. *Australian Journal of Environmental Management* 6: 156-63.

Gullan P.J. and Cranston P.S. 2004. *The Insects: An Outline of Entomology.* London, Blackwell Publishing. 528 pp.

Gurevitch J. and Padilla D.K. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* Volume 19: 470-4.

Gurr G.M., Wratten S.D. and Altieri M.A., ed. 2004. *Ecological Engineering for Pest Management.* Collingwood, CSIRO Publishing.

Gómez J.M. and Zamora R. 1994. Top-down effects in a tritrophic system: parasitoids enhance plant fitness. *Ecology* 75: 1023-30.

Hammond P.C. and Miller J.C. 1998. Comparison of the biodiversity of Lepidoptera within three forested ecosystems. *Annals of the Entomological Society of America* 91: 323-8.

Harper J.L. and Hawksworth D.L. 1995. Preface. In *Biodiversity. Measurement and Estimation*, ed. DL Hawksworth, pp. 5-12. London, Chapman & Hall.

Harris A.C. 1987. *Pompilidae (Insecta: Hymenoptera).* Wellington, Science Information Publishing Centre.

Harris R.J., Toft R.J., Dugdale J.S., Williams P.A. and Rees J.S. 2004. Insect assemblages in a native (kanuka- *Kunzea ericoides*) and an invasive (gorse- *Ulex europaeus*) shrubland. *New Zealand Journal of Ecology* 28: 35-47.

Harvey M.S. and Yen A.L. 1989. *Worms to Wasps: An Illustrated Guide to Australia's Terrestrial Invertebrates.* Melbourne, Oxford University Press. 203 pp.

Haslett J.R. 2001. Biodiversity and conservation of Diptera in heterogeneous land mosaics: a fly's eye view. *Journal of Insect Conservation* 5: 71-5.

Hastings A. 2000. Parasitoid spread: lessons for and from invasion biology. In *Parasitoid Population Biology*, ed. ME Hochberg, AR Ives. New Jersey, Princeton University Press.

Hawkins B.A. 1993. Refuges, host population dynamics and the genesis of parasitoid diversity. In *Hymenoptera and Biodiversity*, ed. J. LaSalle, I.D. Gauld, pp. 235-56. Wallingford, CAB International.

Hawkins B.A. and Lawton J.H. 1987. Species richness for parasitoids of British phytophagous insects. *Nature* 326: 788-90.

Hawkins B.A., Shaw M.R. and Askew R.R. 1992. Relations among assemblage size, host specialization, and climatic variability in North American parasitoid communities. *The American Naturalist* 139: 58-79.

Hawkins B.A. and Sheehan W. 1994. *Parasitoid Community Ecology.* Oxford, Oxford University Press. 516 pp.

Hawksworth D.L. 1991. The fungal dimention of biodiversity: magnitude, significance and conservation. *Journal of Mycological Research* 95: 641-55.

Hawksworth D.L., ed. 1995. *Biodiversity. Mesurement and Estimation.* London, Chapman & Hall. 140 pp.

Hayman D.I., MacKenzie K.E. and Reekie E.G. 2003. The infuence of pruning on wasp inhabitants of galls induced by *Hemadas nubilipennis* Ashmead (Hymenoptera: Pteromalidae) on lowbush blueberry. *Journal of Economic Entomology* 96: 1245-53.

Hobbs R.J. 1989. The nature and effects of disturbance relative to invasions. In *Biological Invasions: A Global Perspective*, ed. J.A. Drake, H. Mooney, F.D. Castri, R.H. Groves, F.J. Kruger, *et al*, pp. 389-405, John Wiley & Sons.

Holt V. 2005. *The Impact of Bridal Creeper (*Asparagus asparagoides*) on Ground-Dwelling and Leaf Litter Insect Biodiversity*. Unpublished Honours thesis. The University of Adelaide, Adelaide.

Hooper D.U. and Vitousek P.M. 1997. The effects on plant composition and diveristy on ecosystem processes. *Science* 277: 1302-5.

Hu J.S., Gelman D.B. and Blackburn M.B. 2003. Age-specific interaction between the parasitoid, *Encarsia formosa* and its host, the silverleaf whitefly, *Bemisia tabaci* (Strain B). *Journal of Insect Science* 3: 1–10.

Hubabrd S.F. and Cook R.M. 1978. Optimal foraging by parasitoid wasps. *Journal of Animal Ecology* 47: 593-604.

Hughes J.B., Daily G.C. and Ehrlich P.R. 2000. Conservation of insect diversity: a habitat approach. *Conservation Biology* 14: 1788-97.

Hunter. 2002. Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology* 4: 159-66.

Hövemeyer K. 1999. Diversity patterns in dipteran communities. *Journal of Animal Ecology* 68: 400-16.

Jennersten O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* 2: 359-65.

Jervis M.A., Kidd N.A.C., Fitton M.G., Huddleston T. and Dawah H.A. 1993. Flower-visiting by hymenopteran parasitoids. *Journal of Natural History* 27: 67-105.

Joern A. 1982. Vegetation structure and microhabitat selection in grasshoppers (Orthoptera, Acrididae). *The Southwestern Naturalist* 27: 197-209.

Joern A. and Lawlor L.R. 1981. Guild structure in grasshopper assemblages based on food and microhabitat resources. *Oikos* 37: 93-104.

Johnson N.F. 1984. Systematics of Nearctic *Telenomus*: classification and revisions of the *podisi* and *phymatae* species groups (Hymenoptera: Scelionidae). *Bulletin of the Ohio Biological Survey* 6: 1-113.

Johnson N.F. and Bin F. 1982. Species of *Telenomus* (Hym., Scelionidae), parasitoids of stalked eggs of Neuroptera (Chrysopidae & Berothidae). *Redia* 65: 189-206.

Johnson S.D. and Bond W.J. 1992. Habitat dependent pollination success in a Cape orchid. *Oecologia* 91: 455-6.

Jones D.L. 1988. *Native Orchids of Australia*. Frenchs Forest, Reed Books. 656 pp.

Jones D.L. 1997. Two rare new species of *Pterostylis* R. Br. (Orchidaceae) allied to *P. alveata*. *The Orchadian* 12: 180-4.

Jones T.H., Godfray H.C.J. and Hassell M.P. 1996. Relative movement patterns of a tephritid fly and its parasitoid wasps. *Oecologia* 106: 317 - 24.

Kato M. 1994. Structure, organization, and response of a species-rich parasitoid community to host leafminner population dynamics. *Oecologia* 97: 12-25.

Keane R.M. and Crawley M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164-70.

Kearns C.A., Inouye D.W. and Waser N.M. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* 29: 83-112.

Kemp W.P. and Harvey S.J. 1990. Patterns of vegetation and grasshopper community composition. *Oecologia* 83: 299-308.

Kemp W.P., Harvey S.J. and O'Neill K.M. 1990. Habitat and insect biology revisited: the search for patterns. *American Entomologist* Spring: 44-9.

Kennedy T.A., Naeem S., Howe K.M., Knops J.M.H., Tilman D. and Reich P. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417: 636-8.

Knops J.M.H., Griffin J.R. and Royalty A.C. 1995. Introduced and native plants of the Hastings Reservation, central coast California: a comparison. *Biological Conservation* 71: 115-23.

Knops J.M.H., Tilman D., Haddad N.M., Naeem S., Mitchell C.E., Haarstad J., Richie M.E., Howe K.M., Reich P.B., Siemann E. and Groth J. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundance and diversity. *Ecology Letters* 2: 286-93.

Knops J.M.H., Wedin D. and Tilman D. 2001. Biodiversity and decomposition in experimental grassland ecosystems. *Oecologia* 126: 429-33.

Komonen A., Penttila R., Lindgren M. and Hansk I. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* 90: 119-26.

Kremen C., Colwell R.K., Erwin T.L., Murphy D.D., Noss R.F. and Sanjayan M.A. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7: 796-808.

Kruess A. 2003. Effects of lanscape structure and habitat type on a plant-herbivore-parasitoid communtiy. *Ecography* 26: 283-90.

Kruess A. and Tscharntke T. 1994. Habitat fragmentation, species loss, and biological control. *Science* 264: 1581-4.

Kruess A. and Tscharntke T. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* 106: 293-302.

Kruess A. and Tscharntke T. 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology* 16: 1570-80.

Köchy M. and Wilson S.D. 1997. Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. *Ecology* 78: 732-9.

Lalonde R.G. 2004. Some dynamical consequences of parasitoid diapause. *Oikos* 107: 338.

Landsberg J., James C.D., Morton S.R., Hobbs T., Stol J., Drew A. and Tongway H. 1997. *The Effects of Artificial Sources of Water on Rangeland Biodiversity.* Canberra, Environment Australia and CSIRO. 208 pp.

Langellotto G.A. and Denno R.F. 2001. Benefits of dispersal in patchy environments: mate location by males of a wing-dimorphic insect. *Ecology* 82: 1870-8.

Langellotto G.A. and Denno R.F. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139: 1-10.

LaSalle J. 1993. Parasitic Hymenoptera, biological control and biodiversity. In *Hymenoptera and Biodiversity*, ed. J. LaSalle, I.D. Gauld, pp. 197-215. Wallingford, CAB International.

LaSalle J. and Gauld I.D., ed. 1993. *Hymenoptera and Biodiversity.* Wallingford, CABI.

LaSalle J. and Gauld I.D. 1993. Hymenoptera: their diversity and their impact on the diversity of other organisms. In *Hymenoptera and Biodiversity*, ed. J. LaSalle, I.D. Gauld, pp. 1-26. Wallingford, CAB International.

Lassau S.A. and Hochuli D.F. 2005. Wasp community responses to habitat complexity in Sydney sandstone forests. *Austral Ecology* 30: 179 -- 87.

Lassau S.A., Hochuli D.F., Cassis G. and Reid C.A.M. 2005. Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity & Distributions* 11: 73-82.

Lawrence J.F. and Britton E.B. 1991. Coleoptera (Beetles). ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 534-683. Melbourne, Melbourne University Press.

Lawton J.H. 1978. Host-plant influences on insect diveristy: the effect of space and time. In *Diversity of Insect Faunas: 9th Symposium of the Royal Entomological Society.* pp. 105-25. Oxford, Blackwell.

Lawton J.H. 1983. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* 28: 23-39.

Lawton J.H. and Brown V.K. 1994. Redundancy in ecosystems. In *Biodiversity and Ecosystem Function*, ed. E.D. Schulze, H.A. Mooney, pp. 255-70. Berlin, Springer-Verlag.

Leigh J.H. and Briggs J.D. 1992. *Threatened Australian Plants. Overview and Case Studies*, Australian National Parks and Wildlife Service, Canberra.

Levine J.M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288: 852-4.

Lewis C.N. and Whitfield J.B. 1999. Braconid wasp (Hymenoptera: Braconidae) diversity in forest plots under different silvicultural methods. *Environmental Entomology* 28: 986-96.

Lipow S.R., Bernhardt P. and Vance N. 2002. Comparative rates of pollination and fruit set in widely separated populations of a rare orchid (*Cypripedium fasciculatum*). *International Journal of Plant Sciences* 163: 775-82.

Loch A.D. and Walter G.H. 2002. Mating behavior of *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae): potential for outbreeding in a predominantly inbreeding species. *Journal of Insect Behavior* 15: 13-23.

Lockwood J.A., Shaw A.R. and Struttmann J.M. 1996. Biodiversity of wasp species (Insecta: Hymenoptera) in burned and unburned habitats of Yellowstone National Park, Wyoming, USA. *Journal of Hymenoptera Research* 5: 1-15.

Lodge D.M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8: 133-7.

Loope L.L., Sanchez P.G., Tarr P.W., Loope W.L. and Andersen R.L. 1988. Biological invasions of arid land nature reserves. *Biological Conservation* 44: 95-118.

Lovejoy T.E. 1995. The quantification of biodiversity: an esoteric quest or a vital component of sustainable development? In *Biodiversity. Measurement and Estimation*, ed. D.L. Hawksworth, pp. 81-7. London, Chapman & Hall.

Lyons K.G. and Schwarta M.W. 2001. Rare species loss alters ecosystem function- invasion resistance. *Ecology Letters* 4: 358-65.

Mack M.C. and D'Antonio C.M. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evoloution* 13: 195-8.

Magurran A.E. 2004. *Measuring Biological Diversity*. Oxford, Blackwell Publishing. 256 pp.

Marino P.C. and Landis D.L. 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecological Applications* 6: 276-84.

Marsh P.M. 1997. Subfamily Doryctinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 206-33. Washington, The International Society of Hymenopterists.

Masner L. 1983. A revision of *Gryon* Haliday in North America (Hymneoptera: Proctotrupoidea: Scelionidae). *Canadian Entomologist* 115: 123-74.

Masner L. 1991. The Nearctic species of *Duta* Nixon (Hymenoptera: Scelionidae), egg parasitoids of ground crickets (Orthoptera: Gryllidae). *Canadian Entomologist* 123: 777-93.

Masner L. 1993. Superfamily Proctotrupoidea. In *Hymenoptera of the World: An Identification Guide to Families*, ed. H. Goulet, J.T. Huber, pp. 537-57. Ontario, Centre for Land and Biological Resources Research, Agriculture Canada.

Masner L. and Huggert L. 1989. World review and keys to genera of the subfamily Inostemmatinae with reassignment of the taxa to the Platygastrinae and Sceliotrachelinae (Hymenoptera: Platygastridae). *Memoirs of the Entomological Society of Canada* 147: 3-214.

Mason W.R.M. 1993. Superfamilies Evaniodea, Stephanoidea, Megalyroidea, and Trigonalyoidea. In *Hymenoptera of the World: an Identification Guide to Families*, ed. H. Goulet, J.T. Huber, pp. 510-20. Ottawa, Ontario, Agriculture Canada.

May F.E. and Ash J. 1990. An assessment of the allelopathic potential of *Eucalyptus. Australian Journal of Botany* 38: 245-54.

May R.M. 1995. Conceptual aspects of the quantification of the extent of biological diveristy. In *Biodiversity. Measurement and Estimation*, ed. D.L. Hawksworth, pp. 13-20. London, Chapman and Hall.

McCann K.S. 2000. The diversity-stability debate. *Nature* 405: 228-33.

McCune B. and Grace J.B. 2002. *Analysis of Ecological Communities.* Oregon, MJM Software Design. 300 pp.

Mcintyre S. and Lavorel S. 1994. How environmental and disturbance factors influence species composition in temperate Australian grasslands. *Journal of Vegetation Science* 5: 373-84.

Meiners T. and Obermaier E. 2004. Hide and seek on two spatial scales – vegetation structure effects herbivore oviposition and egg parasitism. *Basic and Applied Ecology* 5: 87–94.

Melbourne B.A. 1999. Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. *Austral Ecology* 24: 228-39.

Memmott J., Fowler S.V., Paynter Q., Sheppard A.W. and Syrett P. 2000. The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. *Acta Oecologica* 21: 213-22.

Memmott J. and Godfray H.C.J. 1993. Parasitoid webs. In *Hymenoptera and Biodiversity*, ed. J. LaSalle, I.D. Gauld, pp. 217-34. Wallingford, CAB International.

Memmott J. and Godfray H.C.J. 1994. The use and construction of parasitoid webs. In *Parasitoid Community Ecology*, ed. B.A. Hawkins, W. Sheehan, pp. 300-18. Oxford, Oxford University Press.

Memmott J., Godfray H.C.J. and Bolton B. 1993. Predation and parasitism in a tropical herbivore community. *Ecological Entomology* 18: 348-52.

Memmott J., Godfray H.C.J. and Gauld I.D. 1994. The structure of a tropical host-parasitoid community. *Journal of Animal Ecology* 63: 521-40.

Memmott J., Martinez N.D. and Cohen J.E. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology* 69: 1-15.

Memmott J. and Wasner N.M. 2002. Integration of alien plants into a native flower-pollinator visitation web. *Proceedings of the Royal Society of London B.* 269: 2395-9.

Mikola J. and Setälä H. 1998. Relating species diversity to ecosystem functioning: mechanistic backgrounds and experimental approach with a decomposer food web. *Oikos* 83: 180-94.

Miller J.C. 1993. Insect natural history, multi-species interactions and biodiversity in ecosystems. *Biodiversity and Conservation* 2: 233-41.

Mills L.S., Soule M.E. and Doak D.F. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43: 219-24.

Moore J.C., Berlow E.L., Coleman D.C., Ruiter P.C.d., Dong Q., Hastings A., Johnson N.C., McCann K.S., Melville K., Morin P.J., Nadelhoffer K., Rosemond A.D., Post D.M., Sabo K.L., Scow K.M., Vanni M.J. and Wall D.H. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7: 584-600.

Moran M.D. and Hurd L.E. 1998. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia* 113: 126-32.

Muesebeck C.F.W. 1979. Superfamily Ceraphronoidea. In *Catalogue of Hymenoptera in America North of Mexico*, ed. K.V. Krombein, P. D. Hurd, D.R. Smith, B.D. Burks, pp. 1187-95. Washington, Smithson Institution Press.

Muesebeck C.F.W. 1979. Superfamily Proctotrupoidea. In *Catalogue of Hymenoptera in America North of Mexico*, ed. K.V. Krombein, P. D. Hurd, D.R. Smith, B.D. Burks, pp. 1187-95. Washington, Smithson Institution Press.

Mustajarvi K., Siikamaki P., Rytkonen S. and Lammi A. 2001. Consequences of plant population size and density for plant-pollinator interactions and plant performance. *Journal of Ecology* 89: 80-7.

Myers N., Mittermeir R.A., Mittermeir C.G., da Fonseca G.A.B. and Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-8.

Müller C.B. and Godfray H.C.J. 1999. Indirect interactions in aphid-parasitoid communities. *Researches on Population Ecology* 41: 93-106.

Naeem S., III F.S.C., Costanza R., Ehrlich P.R., Golley F.B., Hooper D.U., Lawton J.H., OÂ'Neill R.V., Mooney H.A., Sala O.E., Symstad A. and Tilman D. 2001. Biodiversity and Ecosystem Functioning: Maintaining Natural Life Support Processes. *Issues in Ecology*.

Naeem S., Thompson L.J., Lawler S.P., Lawton J.H. and Woodfin R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-6.

Naumann I.D. 1982. Systematics of the Australian Ambositrinae (Hymenoptera: Diapriidae), with a synopsis on non-Australian Genera of the subfamily. *Australian Journal of Zoology Supplementary Series* 85.

Naumann I.D. 1988. *Ambositrinae (Insecta: Hymneoptera: Diapriidae)*. Fauna of New Zealand: 15. Wellington, Science Information Publishing Centre.

Naumann I.D. 1991. Hymenoptera (Wasps, bees, ants, and sawflies). In *The Insects of Australia: a textbook for students and research workers*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 916-1000. Melbourne, Melbourne University Press.

Naumann I.D., Carne P.B., Lawrence J.F., Nielsen E.S., Spradbery J.P., Taylor R.W., Whitten M.J. and Littlejohn M.J., ed. 1991. *The Insects of Australia: A Textbook for Students and Research Workers*, Volumes I & II. Melbourne, Melbourne University Press. 1137 pp.

New South Wales National Parks and Wildlife Service 2002. *Pterostylis gibbosa (R.Br.) Illawarra Greenhood Orchid Recovery Plan*, NSW National Parks and Wildlife Service, Hurstville.

New T.R. 1988. *Associations Between Insects and Plants*. Kensington, New South Wales University Press. 113 pp.

New T.R. 1991. Neuroptera (Lacewings). In *The Insects of Australia: A Textbook for Students and Research Workers*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 525-42. Melbourne, Melbourne University Press.

New T.R. 1998. *Invertebrate Surveys for Conservation*. Oxford, Oxford University Press. 240 pp.

Newell G.R. 1997. The abundance of ground-dwelling invertebrates in a Victorian forest affected by 'dieback' (*Phytophthora cinnamomi*) disease. *Australian Journal of Ecology* 22: 206-17.

Nielsen E.S. and Common I.F.B. 1991. Lepidoptera (Moths and butterflies). In *The Insects of Australia: A Textbook for Students and Research Workers*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 817-915. Melbourne, Melbourne University Press.

Niemelä J.K. and Spence J.R. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography* 17: 166-75.

Nixon G.E.J. 1980. *Diapriidae (Diapriinae) Hymenoptera, Proctotrupoidea*. London, British Museum (Natural History). 55 pp.

Noyes J.S. 1988. *Encyrtidae (Insecta: Hymenoptera)*. Fauna of New Zealand: 13. Wellington, Science Information Publishing Centre. 188 pp.

Noyes J.S. and Hayat M. 1984. A review of the genera of Indo-Pacific Encyrtidae (Hymenoptera: Chalcidoidea). *Bulletin of the British Museum (Natural History) Entomology Series* 48: 131-395.

Noyes J.S. and Valentine E.W. 1989. *Chalcidoidea (Insecta: Hymenoptera): Introduction, and Review of Genera in Smaller Families*. Fauna of New Zealand: 18. Wellington, Science Information Publishing Centre. 91 pp.

Noyes J.S. and Valentine E.W. 1989. *Mymaridae (Insecta: Hymenoptera): introduction, and review of genera*. Fauna of New Zealand: 17. Wellington, Science Information Publishing Centre. 95 pp.

Olden J. and Poff N.L. 2003. Toward a mechanistic understanding and prediction of biotic homogenization. *The American Naturalist* 162:442-60.

Oliver I. and Beattie A.J. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* 7: 562-8.

Oliver I. and Beattie A.J. 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* 10: 99-109.

Oliver I., Nally R.M. and York A. 2000. Identifying ground-active arthropod biodiversity performance indicators of the effects of forest management on ground active arthropod biodiversity using hierarchical partitioning and partial canonical correspondence analysis. *Forest Ecology and Management* 139: 21-40.

Orr D.B., Suh C.P.-C., McCravy K.W., Berisford C.W. and Debarr G.L. 2000. Evaluation of inundative releases of *Trichogramma exigum* (Hymenoptera: Trichogrammatidae) for suppression of Nantucket pine tip moth (Lepidoptera: Tortricidae) in pine (Pinaceae) plantations. *The Canadian Entomologist* 132: 373-86.

Ovruski S.M., Schliserman P. and Aluja M. 2004. Indigenous parasitoids (Hymenoptera) attacking *Anastrepha fraterculus* and *Ceratitia capita* (Diptera: Tephritidae) in native and exotic host plants in Northwestern Argentina. *Biological Control* 29: 43-57.

Owen J., Townes H. and Townes M. 1981. Species diversity of Ichneumonidae and Serphidae (Hymenoptera) in an English suburban garden. *Biological Journal of the Linnean Society* 16: 315-36.

Pace M.L., Cole J.J., Carpenter S.R. and Kitchell J.F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14: 483-8.

Parra-Tabla V., Vargas C.F., Magana-Rueda S. and Navarro J. 2000. Female and male pollination success of *Oncidium ascendens* Lindey (Orchidaceae) in two contrasting habitat patches: forest vs agricultural field. *Biological Conservation* 94: 335-40.

Peakall R. and Handel S.N. 1993. Pollinators discriminate among floral heights of a sexually deceptive orchid- implications for selection. *Evolution* 47: 1681-7.

Petraitis P.S., Latham R.E. and Niesenbaum R.A. 1989. The maintenance of species diversity by disturbance. *The Quarterly Review of Biology* 64: 393-418.

Pimm S.L. 1994. Biodiversity and the balance of nature. In *Biodiversity and Ecosystem Function*, ed. E.D. Schulze, H.A. Mooney, pp. 348-59. Berlin, Springer-Verlag.

Pimm S.L. and Lawton J.H. 1980. Are food webs divided into compartments? *Journal of Animal Ecology* 49: 879-98.

Pimm S.L. and Raven P. 2000. Extinction by numbers. *Nature* 403: 843-5.

Pivnick K.A. 1993. Diapause initiation and pupation site selection of the braconid parasitoid *Microplitis mediator* (Haliday): a case of manipulation of host behaviour. *Canadian Entomologist* 125: 825-30.

Polaszek A. 1991. Egg parasitism in Aphelinidae (Hymenoptera: Chalcidoidea) with special reference to *Centrodora* and *Encarsia* species. *Bulletin of Entomological Research* 81: 97-106.

Polis G.A. 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* 19: 121-36.

Polis G.A., Holt R.D., Menge B.A. and Winemiller K.O. 1996. Time, space, and life history: influences on food webs. In *Food Webs: Integration of Patterns and Dynamics*, ed. G.A. Polis, K.O. Winemiller, pp. 435-60. New York, Chapman & Hall.

Ponsard S., Arditi R. and Jost C. 2000. Assessing top-down and bottom-up control in a litter-based soil macroinvertebrate food chain. *Oikos* 89: 524-40.

Power M.E., Tilman D., Estes J.A., Menge B.A., Bond W.J., Mills L.S., Daily G., Castilla J.C., Lubchenco J. and Paine R. 1996. Challenges in the quest for keystones. *BioScience* 46: 609-20.

Price P.W., Bouton C.E., Gross P., McPheron B.A., Thompson J.N. and Weis A.E. 1980. Interactions among trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11: 41-65.

Prieur-Richard A. and Lavorel S. 2000. Invasions: the perspective of diverse plant communities. *Austral Ecology* 25: 1-7.

Threatened Flora and Fauna Program. 1993. *Leafy Greenhood Pterostylis cucullata.* Action Statement No. 54, Department of Natural Resources & Environment, East Melbourne.

Purvis A. and Hector A. 2000. Getting the measure of biodiversity. *Nature* 405: 212-9.

Quicke D.L.J. 1997. *Parasitic Wasps.* London, Chapman & Hall. 470 pp.

Quicke D.L.J. 1997. Subfamily Braconinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. RA Wharton, PM Marsh, MJ Sharkey, pp. 148-74. Washington, The International Society of Hymenopterists.

Rathcke B.J. and Jules E.S. 1993. Habitat fragmentation and plant-pollinator interactions. *Current Science* 65: 273-7.

Raymond K.L. 1999. *Ecology of* Asparagus asparagoides *(bridal creeper), an environmental weed of Southern Australia.* Unpublished PhD thesis. Monash University, Clayton. 252 pp.

Rentz D.C.F. 1991. Orthoptera (Grasshoppers, locusts, katydids, crickets). In *The Insects of Australia: a textbook for students and research workers*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 369-93. Melbourne, Melbourne University Press.

Richie A.J. 1993. Superfamily Cynipoidea. In *Hymenoptera of the World: An Identification Guide to Families*, ed. H. Goulet, J.T. Huber, pp. 521-30. Ottawa, Ontario, Agriculture Canada.

Rodriguez M.A. and Hawkins B.A. 2000. Diversity, function and stability in parasitoid communities. *Ecology Letters* 3: 35-40.

Roff D.A. 1990. The evolution of flightlessness in insects. *Ecological Mongraphs* 60: 389-421.

Roff D.A. 1994. Habitat persistence and the evolution of wing dimorphism in insects. *American Naturalist* 144: 772-98.

Roland J. and Taylor P.D. 1997. Insect parasitoids species respond to forest structure at different spatial scales. *Nature* 386: 710-3.

Ronquist F. 1995. Phylogeny and early evolution of the Cynipoidea (Hymenoptera). *Systematic Entomology* 20: 309-35.

Rosenfeld J.S. 2002. Functional redundancy in ecology and conservation. *Oikos* 98: 156-62.

Roth L.M. 1991. Blattodea (Cockroaches). In *The Insects of Australia*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 320-9. Carlton, Melbourne University Press.

Sabo J.L., Soykan C.U. and Keller A. In Press. Functional roles of leaf litter detritus in terrestrial food webs. In *Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change*, ed. P.C. de Ruiter, V. Wolters, J.C. Moore, Elsevier/Academic Press.

Saeed A., Austin A.D. and Dangerfield P.C. 1999. Systematic and host relationships of Australasian Diolcogaster (Hymenoptera: Braconidae: Microgastrinae). *Invertebrate Taxonomy* 13: 117-78.

Samways M.J. 1994. *Insect Conservation Biology*. London, Chapman and Hall.

Samways M.J. 1995. Southern Hemisphere insects: their variety and the environmental pressures upon them. In *Insects in the Changing Environment*, ed. N.E. Stork, R. Harrington, pp. 297-320. London, Academic Press.

Samways M.J., Caldwell P.M. and Osborn R. 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agriculture, Ecosystems and Environment* 59: 19-32.

Samways M.J. and Moore S.D. 1991. Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. *Biological Conservation* 57: 117-37.

Sanchez B.C. and Parmenter R.R. 2002. Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: a test of island biogeographic theory. *Journal of Arid Environments* 50: 247-65.

Sands D.P.A., Scott S.E. and Moffatt R. 1997. The threatened Richmond birdwing butterfly (*Ornithoptera richmondia* [Gray]): a community conservation project. *Memoirs of the Museum of Victoria* 56: 449-53.

Sato Y. and Ohsaki N. 1987. Host habitat location by *Apanteles glomeratus* and effect of food-plant exposure on host parasitism. *Ecological Entomology* 12: 291-7.

Sax D.F. 2002. Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California. *Global Ecology and Biogeography* 11: 49-57.

Sax D.F., Kinlan B.P. and Smith K.F. 2005. A conceptual framework for comparing species assemblages in native and exotic habitats. *Oikos* 108: 457-64.

Schellhorn N.A., Harmon J.P. and Andow D.A. 2000. Using cultural practices to enhance insect pest control by natural enemies. In *Insect Pest Management Techniques for Environmental Protection*, ed. J. Recheigl, N. Recheigl, CRC Press.

Schellhorn N.A. and Silberbauer L. 2003. The role of surrounding vegetation and refuges: increasing the effectiveness of predators and parasitoids in cotton and broccoli systems. Conference proceedings. Presented at the 1st International Symposium on Biological Control of Arthropods, Honolulu, Hawaii, USA.

Schoenly K., Bever R.A. and Heumier T.A. 1991. On the trophic relations of insects: a food web approach. *The American Naturalist* 137: 597-638.

Schowalter T.D. 2000. *Insect Ecology: an Ecosystem Approach.* San Diego, Academic Press. 483 pp.

Schwartz M.W., Brigham C.A., Hoeksema J.D., Lyons K.G., Mills M.H. and van Mantgem P.J. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122: 297-305.

Seastedt T.R. and Crossley Jr. D.A. 1984. The influence of arthropods on ecosystems. *Bioscience* 34: 157-61.

Shapiro B.A. and Pickering J. 2000. Rainfall and parasitic wasp (Hymenoptera: Ichneumonoidea) activity in successional forest stages in successional forest stages at Barro Colorado Nature Monument, Panama, and La Selva Biological Station, Costa Rica. *Agricultural and Forest Entomology* 2: 39-47.

Sharkey M.J. 1981. A revision of the Nearctic species of *Teleas* Latreille (Hymenoptera, Proctrotrupoidea, Scelionidae). *Canadian Entomologist* 113: 907-29.

Sharkey M.J. 1996. The Agathidinae (Hymenoptera: Braconidae) of Japan. *Bulletin of the National Institute of Agro-Environmental Sciences* 13: 1-100.

Sharkey M.J. 1997. Subfamily Agathidinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 68-83. Washington, The International Society of Hymenopterists.

Sharkey M.J. 1997. Subfamily Blacinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 140-7. Washington, The International Society of Hymenopterists.

Shaw M.R. 1994. Parasitoid host ranges. In *Parasitoid Community Ecology*, ed. B.A. Hawkins, W. Sheehan, pp. 111-44. Oxford, Oxford University Press.

Shaw M.R. and Huddleston T. 1991. *Classification and Biology of Braconid Wasps (Hymenoptera: Braconidae).* London, British Museum (Natural History). 126 pp.

Shaw S.R. 1983. A taxononmic study of Neartic *Ascogaster* and a decription of a new genus *Leptodrepana* (Hymenoptera: Braconidae). *Entomography* 2: 1-54.

Shaw S.R. 1985. A phylogenetic study of the subfamilies Metorinae and Euphorinae. *Entomography* 3: 277-370.

Shaw S.R. 1997. Subfamily Cheloninae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 192-201. Washington, The International Society of Hymenopterists.

Shaw S.R. 1997. Subfamily Euphorinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 234-54. Washington, The International Society of Hymenopterists.

Shaw S.R. 1997. Subfamily Rogadinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 402-12. Washington, The International Society of Hymenopterists.

Siemann E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79: 2057-70.

Siemann E., Tilman D., Haarstad J. and Richie M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist* 152: 738-50.

Simberloff D. and Dayan T. 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22: 115-43.

Smithers C.N. 1991. Pscoptera (Psocids, booklice). In *The Insects of Australia*, ed. I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, *et al*, pp. 412-20. Carlton, Melbourne University Press.

Sorensen B. and Jusaitis M. 1995. The impact of bridal creeper on an endangered orchid. In *Weeds of Conservation Concern*, ed. D. Cooke, J. Choate, pp. 27-30. Adelaide, Department of Environment and Natural Resources & Animal and Plant Control Commision, South Australia.

Stamou G.P., Stamou G.V., Papatheodorou E.M., Argyropoulou M.D. and Tzafestas S.G. 2004. Population dynamics and life history tactics of arthropods from Mediterranean-type ecosystems. *Oikos* 104: 98-108.

Standish R.J. 2004. Impact of an invasive clonal herb on epigaeic invertebrates in forest remnants in New Zealand. *Biological Conservation* 116: 49-58.

Standish R.J., Williams P.A., Robertson A.W., Scott N.A. and Hedderley D.I. 2004. Invasion by a perennial herb increases decomposition rate and alters nutrient availability in warm temperate lowland forest remnants. *Biological Invasions* 6: 71-81.

Stansbury C. 1996. Observations of birds feeding on bridal creeper (*Asparagus asparagoides*) fruits within Yanchep National Park, Western Australia. *Plant Protection Quarterly* 11: 59-60.

Steenkamp H.E. and Chown S.L. 1996. Influence of dense stands of an exotic tree, *Prosopis glandulosa* Benson, on a savanna dung beetle (Coleoptera: Scarabaeinae) assemblage in southern Africa. *Biological Conservation* 78: 305-11.

Steffan-Dewenter I. 2002. Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology* 27: 631-7.

Steffan-Dewenter I. and Tscharntke T. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121: 432-40.

Stinner R.E., Barfield C.S. and Stimac J.L. 1983. Dispersal and movement of insect pests. *Annual Review of Entomology* 28: 319-35.

Stireman J. and Singer M.S. 2002. Spatial and temporal variation in the parasitoid assemblage of an exophytic polyphagous caterpillar. *Ecological Entomology* 27: 588-600.

Stireman J. and Singer M.S. 2003. What determines host range in parasitoids? An analysis of a tachinid parasitoid community. *Oecologia* Online.

Stock W.D., Wienand K.T. and Baker A.C. 1995. Impacts of invading N_2-fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and ^{15}N natural abundance values. *Oecologia* 101: 375-82.

Stork N.E. 1999. Estimating the number of species on Earth. In *The Other 99%. The Conservation and Biodiversity of Invertebrates*, ed. W. Ponder, D. Lunney, pp. 1-7. Mosman, Transactions of the Royal Zoological Society of New South Wales.

Stork N.E. and Brendell M.J.D. 1993. Arthropod abundance in lowland rain forest of Seram. In *Natural History of Seram, Maluku, Indonesia*, ed. I.D. Edwards, A.A. MacDonald, J. Proctor, pp. 115-30. Andover, Intercept.

Strong D.R. 1974. Rapid asymptotic species accumulation in phytophagous insect communities: the pests of Cacao. *Science* 185: 1064-5.

Strong D.R., Lawton J.H. and Southwood R. 1984. *Insects on Plants. Community Patterns and Mechanisms.* Oxford, Blackwell Scientific. 313 pp.

Symstad A.J., Tilman D., Wilson J. and Knops J.M.H. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* 81: 389-97.

Taylor I.M.D. 1998. *Study of Herbivory and Pollination in the Endangered Illawarra Greenhood Orchid,* Pterostylis gibbosa. Unpublished Honours thesis. University of Wollongong, Wollongong. 76 pp.

Thiel A. and Hoffmeister T.S. 2004. Knowing your habitat: linking patch encounter-rate and patch exploitation in parasitoids. *Behavioural Ecology* 15: 419-25.

Tilman D. 2000. Causes, consequences and ethics of biodiversity. *Nature* 405: 208-11.

Tilman D., Knops J., Wedin D., Reich P., Ritchie M. and Siemann E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-2.

Todd M.C.L., Grierson P.F. and Adams M.A. 2000. Litter cover as an index of nitrogen availability in rehabilitated mine sites. *Australian Journal of Soil Research* 38: 423-33.

Toft R.J., Harris R.J. and Williams P.A. 2001. Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand. *Biological Conservation* 102: 31-46.

Tooker J.F. and Hanks L.M. 2000. Flowering plant hosts of adult Hymenopteran parasitoids of central Illinois. *Annals of the Entomological Society of America* 93: 580-8.

Tscharntke T. 1992. Fragmentation of *Phragmites* habitats, minimum viable population size, habitat suitability, and local extinction of moths, midges, flies, aphids, and birds. *Conservation Biology* 6: 530-6.

Tscharntke T. 2000. Parasitoid populations in the agricultural landscape. In *Parasitoid Population Biology*, ed. M.E. Hochberg, A.R. Ives, pp. 235-53. New Jersey, Princeton University Press.

Tscharntke T., Gathmann A. and Steffan-Dewenter I. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology* 35: 708-19.

Ulrich W. 1998. The parasitic hymenoptera in a beech forest on limestone III: the role of leaf litter for the parasitoid species. *Polish Journal of Ecology* 46: 311-26.

Ulrich W. 2004. Soil-living parasitic Hymenoptera: comparison between a forest and an open landscape habitat. *Pedobiologia* 48: 59-69.

Underwood A.J., Chapman M.G. and Connell S.D. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* 250: 97-115.

Valladares G.R. and Salvo A. 1999. Insect-plant food webs could provide new clues for pest management. *Environmental Entomology* 28: 539-43.

Valladares G.R. and Salvo A. 2001. Community dynamics of leafminers (Diptera: Agromyzidae) and their parasitoids (Hymenoptera) in a natural habitat from Central Argentina. *Acta Oecologica* 22: 301-9.

van Achterberg C. 1997. Subfamily Aphidiinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 118-34. Washington, The International Society of Hymenopterists.

van der Sommen F.J. 1986. Colonisation of forest and woodland communities by exotic plants. In *The Ecology of the Forests and Woodlands of South Australia*, ed. H.R. Wallace, pp. 248-67. Adelaide, Government Printer.

Viggiani G. 1984. Bionomics of the Aphelinidae. *Annual Review of Entomology* 29: 257-76.

Vitousek P.M. 1986. Biological invasions and ecosystem properties: can species make a difference? In *Biological Invasions of North America and Hawaii*, ed. H.A. Mooney, J. Drake, pp. 163-76, Springer.

Vitousek P.M. 1990. Biological invasions and ecosystem processes: towards an intergration of population biology and ecosystem studies. *Oikos* 57: 7-13.

Vitousek P.M., D'Antonio C.M., Loope L.L., Rejmánek M. and Westbrooks R. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21: 1-16.

Vlug H.J. 1995. *Catalogue of the Platygastridae (Platygastroidea) of the World (Insecta: Hymenoptera)*. Amsterdam, SPB Academic Publishing. 168 pp.

Wardle D.A. 1999. How soil food webs make plants grow. *Trends in Ecology and Evolution* 14: 418-20.

Wharton R.A. 1997. Subfamily Alysiinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 83-116. Washington, The International Society of Hymenopterists.

Wharton R.A. 1997. Subfamily Opiinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 378-95. Washington, The International Society of Hymenopterists.

Whitfield J.B. 1997. Subfamily Microgastrinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 332-64. Washington, The International Society of Hymenopterists.

Whitfield J.B. 1997. Subfamily Miracinae. In *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*, ed. R.A. Wharton, P.M. Marsh, M.J. Sharkey, pp. 370-3. Washington, The International Society of Hymenopterists.

Whitfield J.B. and Lewis C.N. 2001. Analytical survey of the braconid wasp fauna (Hymenoptera: Braconidae) on six midwestern US tall grass prairies. *Annals of the Entomological Society of America* 94: 230-8.

Wilson J.B. 1991. Methods for fitting dominance/diversity curves. *Journal of Vegetation Science* 2: 35-46.

Winemiller K.O. and Polis G.A. 1996. Food webs: what do they tell us about the world? In *Food Webs. Integration of Patterns and Dynamics*, ed. G.A. Polis, K.O. Winemiller. New York, Chapman & Hall.

Wolf A.T. and Harrison S.P. 2001. Effects of habitat size and patch isolation on reproductive success of the serpentine morning glory. *Conservation Biology* 15: 111-21.

Woolley J.B. 1988. Phylogeny and classification of the Signiphoridae (Hymenoptera: Chalcidoidea). *Systematic Entomology* 13: 465-501.

Wootton J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25: 443-66.

Xiong S. and Nilsson C. 1999. The effects of plant litter on vegetation: a meta-analysis. *Journal of Ecology* 87: 984-94.

Yeates D.K., Harvey M.S. and Austin A.D. 2003. New estimates for terrestrial arthropod species-richness in Australia. *Records of the South Australian Museum Monograph Series Number 7: Invertebrate Biodiversity and Conservation*, 231-41

Yela J.L. and Lawton J.H. 1997. Insect herbivore loads on native and introduced plants: a preliminary study. *Entomologia Experimentalis et Applicata* 85: 275-9.

Yen A. and Butcher R. 1997. *An overview of the conservation of non-marine invertebrates in Australia.* Canberra, Environment Australia.

Zabel J. and Tscharntke T. 1998. Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* 116: 419-25.

Zera A.J. and Denno R.F. 1997. Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology* 42: 207-30.

Appendix A

Plant species

Table A-1 Native and exotic (*) ground-cover plant species recorded from the ground-cover transects at Mt Billy CP.

Plant taxa	Common name	Life form
Adiantaceae		
Adiantum aethiopicum	common maiden-hair	perennial
Cheilanthes austrotenuifolia	annual/ green rock-fern	perennial
Anthericaceae		
Arthropodium strictum	chocolate-lily	geophyte
Chamaescilla corymbosa var. *corymbosa*	blue squill/ stars	geophyte
Thysanotus patersonii	twining fringe-lily	geophyte
Apiaceae		
Daucus glochidiatus	native carrot	annual
Hydrocotyle sp.	pennywort	annual
Asparagaceae		
*Asparagus asparagoides**	bridal creeper	geophyte
Asteraceae		
Bracteantha bracteata	golden everlasting	annual or biennial
*Cirsium vulgare**	spear thistle	annual or biennial
Cymbonotus preissianus	Australian/ austral bear's-ear	perennial
*Hypochaeris glabra**	smooth cat's ear	perennial
*Hypochaeris radicata**	rough cat's ear	perennial
Lagenifera huegelii	coarse bottle-daisy	perennial
*Scabiosa atropurpurea**	pincushion	annual or biennial
Senecio hispidulus var. *hispidulus*	rough groundsel	perennial
Senecio picridioides	purple-leaf groundsel	perennial
Senecio tenuiflorus	woodland groundsel	perennial
*Sonchus oleraceus**	common sow-thistle/ milk thistle	annual
Boraginaceae		
Myosotis australis	austral forget-me-not	perennial
Brassicaceae		
Cardamine sp.	bitter-cress	annual or perennial
Campanulaceae		
Wahlenbergia gracilis	sprawling bluebell	perennial
Wahlenbergia stricta ssp. *stricta*	tall bluebell	perennial
Caryophyllaceae		
*Cerastium glomeratum**	common mouse-ear chickweed	annual
*Moenchia erecta**	erect chickweed	annual
Silene gallica var. *gallica**	French catchfly	annual or biennial
*Stellaria media**	chickweed	annual
Stellaria palustris var. *palustris*	swamp starwort	perennial
Clusiaceae		
Hypericum gramineum	small St John's wort	perennial
Convolvulaceae		
Convolvulus erubescens	Australian/ pink bindweed	perennial
Dichondra repens	kidney weed	perennial
Cyperaceae		
Carex breviculmis	short-stem sedge	perennial
Isolepis marginata	little club-rush	annual
Droseraceae		
Drosera glanduligera	scarlet sundew	annual
Drosera peltata	pale sundew	geophyte
Epacridaceae		
Astroloma humifusum	cranberry heath	sm. prostrate shrub
Euphorbiaceae		
Poranthera microphylla	small poranthera	annual
Fabaceae		
Glycine latrobeana	clover glycine	perennial
*Trifolium dubium**	suckling clover	annual

Plant taxa	Common name	Life form
*Vicia monantha**	spurred vetch	annual
Geraniaceae		
Geranium retrorsum	grassland geranium	perennial
Hypoxidaceae		
Hypoxis vaginata var. *vaginata*	yellow star	geophyte
Iridaceae		
Romulea rosea var. *australis**	common onion-grass	geophyte
Juncaceae		
Juncus sp.	rush sp.	perennial
Luzula meridionalis	common wood-rush	perennial
Mimosaceae		
Acacia pycnantha	golden wattle	tree (seedling)
Myrtaceae		
Eucalyptus leucoxylon	South Australian blue gum	tree (seedling)
Eucalyptus viminalis ssp. *cygnetensis*	rough-bark manna gum	tree (seedling)
Ophioglossaceae		
Ophioglossum lusitanicum	austral adder's-tongue	geophyte
Orchidaceae		
Acianthus pusillus	mosquito/ gnat orchid	geophyte
Caladenia tentaculata	king green-comb spider-orchid	geophyte
Corybas dilatatus	common helmet-orchid	geophyte
Corybas sp.	helmet-orchid sp.	geophyte
Glossodia major	purple cockatoo/ wax-lip orchid	geophyte
Leptoceras menziesii	hare/ rabbit orchid	geophyte
Microtis sp.	onion-orchid sp.	geophyte
Pterostylis nutans	nodding greenhood	geophyte
Pterostylis pedunculata	maroon-hood orchid	geophyte
Oxalidaceae		
Oxalis perennans	native sorrel/ sour-sob	perennial
Plantaginaceae		
Plantago lanceolata var. *lanceolata**	ribwort/ ribgrass	perennial
Poaceae		
*Aira cupaniana**	small hair-grass	annual
*Avena barbata**	bearded oat	annual
*Briza maxima**	blowfly grass	annual
*Briza minor**	shivery grass	annual
*Bromus diandrus**	great brome	annual
Bromus hordeaceus ssp. *hordeaceus**	soft brome	annual
*Bromus madritensis**	Madrid brome	annual
*Cynosurus echinatus**	rough dog's-tail grass	annual
*Ehrharta longiflora**	annual veldt grass	annual
Lolium sp.*	ryegrass sp.	annual
Microlaena stipoides var. *stipoides*	weeping rice-grass	perennial
*Vulpia bromoides**	squirrel-tail fescue	annual
Polygonaceae		
Rumex brownii	slender dock	perennial
Primulaceae		
*Anagallis arvensis**	scarlet pimpernel	annual or biennial
Ranunculaceae		
Ranunculus lappaceus	native buttercup	perennial
Rosaceae		
Acaena echinata	sheep's burr	perennial
Rubiaceae		
Galium migrans	loose bedstraw	perennial
*Sherardia arvensis**	field madder	annual
Sapindaceae		
Dodonaea viscosa ssp. *spatulata*	sticky hop-bush	shrub (seedling)

Appendix B

Wasp morphospecies

Table A-2 Wasp morphospecies recorded from Mt Billy CP.

Morphospecies	Identification
CERAPHRONOIDEA	
Ceraphronidae	
Ceraph08	Ceraphronidae, *Aphanogmus*
Ceraph09	Ceraphronidae, *Aphanogmus*
Ceraph11	Ceraphronidae, *Aphanogmus*
Ceraph12	Ceraphronidae, *Aphanogmus*
Ceraph14	Ceraphronidae, *Aphanogmus*
Ceraph17	Ceraphronidae, *Aphanogmus*
Ceraph04	Ceraphronidae, *Aphanogmus*
Ceraph01	Ceraphronidae, *Ceraphron*
Ceraph02	Ceraphronidae, *Ceraphron*
Ceraph06	Ceraphronidae, *Ceraphron*
Ceraph13	Ceraphronidae, *Ceraphron*
Ceraph15	Ceraphronidae, *Ceraphron*
Megasp18	Ceraphronidae, *Ceraphron*
Megasp22	Ceraphronidae, *Ceraphron*
Megasp02	Ceraphronidae, *Ceraphron*
Megaspilidae	
Megasp03	Megaspilidae, ?*Conostigmus*
Megasp05	Megaspilidae, *Conostigmus*
Megasp07	Megaspilidae, *Lagynodes*
Meagsp01	Megaspilidae, *Megaspilus*
Megasp04	Megaspilidae, *Megaspilus*
Megasp09	Megaspilidae, *Megaspilus*
Megasp06	Megaspilidae,?*Plastomicrops*
Megasp21	Megaspilidae,?
Megasp16	Megaspilidae,?*Dendrocerus*
Megasp10	Megaspilidae, *Dendrocerus*
Megasp12	Megaspilidae, *Dendrocerus*
Megasp15	Megaspilidae, *Dendrocerus*
Megasp17	Megaspilidae, *Dendrocerus*
Megasp19	Megaspilidae, *Dendrocerus*
Beth 13	Megaspilidae, ?*Megaspilus*
CHALCIDOIDEA	
Aphelinidae	
Chal 067	Aphelinidae, Azotinae, *Ablerus*
Chal 075	Aphelinidae, Azotinae, *Ablerus*
Chal 076	Aphelinidae, Azotinae, *Ablerus*
Chal 081	Aphelinidae, Aphelininae, *Aphelinus*
Chal 056	Aphelinidae, *Centrodora*
Chal 154	Aphelinidae, *Centrodora*
Chal231	Aphelinidae, *Encarsia*(F) (1) Aphelinidae, *Coccophagus*(M) (2)
Chalcididae	
Chal243	Chalcididae, Chalcidinae, *Brachymeria*
Chal 036	Chalcididae, Haltichellinae, ? *Allochalcis*
Chal 102	Chalcididae, Haltichellinae, *Antrocephalus*
Chal210	Chalcididae, Haltichellinae, *Proconura*
Encyrtidae	
Chal239	Encyrtidae, Encyrtinae, ?*Bothriophryne*
Chal188	Encyrtidae, Encyrtinae, ?*Bothriophryne*
Chal 007	Encyrtidae, Encyrtinae, *Copidosoma*
Chal 114	Encyrtidae, Encyrtinae, ?*Copidosoma*
Chal219	Encyrtidae, Encyrtinae, ?*Copidosoma*
Chal 159	Encyrtidae, Encyrtinae, ?*Copidosoma*
Chal 117	Encyrtidae, Encyrtinae, *Discodes*
Chal 160	Encyrtidae, Encyrtinae, *Doddanusa*
Chal 128	Encyrtidae, Encyrtinae, ?*Homalotylus*
Chal270	Encyrtidae, Encyrtinae, ?*Mahencyrtus*
Chal 045	Encyrtidae, Encyrtinae, *Metaphycus.*
Chal 132	Encyrtidae, Encyrtinae, ?*Neanagyrus*

Morphospecies	Identification
Chal 162	Encyrtidae, Encyrtinae, *Paraenasomyia*
Chal 158	Encyrtidae, Encyrtinae, *Paralitomastix*
Chal 099	Encyrtidae, Encyrtinae, *Psyllaephagus*
Chal 091	Encyrtidae, Encyrtinae, *Psyllaephagus*
Chal181	Encyrtidae, Encyrtinae, *Psyllaephagus*
Chal 004	Encyrtidae, Encyrtinae, *Psyllaephagus*
Chal189	Encyrtidae, Encyrtinae, *Psyllaephagus*
Chal 107	Encyrtidae, Encyrtinae, *Psyllaephagus*.
Chal 169	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal 027	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal191	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal192	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal193	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal198	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal208	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal265	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal268	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal269	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal 009	Encyrtidae, Encyrtinae, ?*Psyllaephagus*
Chal 144	Encyrtidae, Encyrtinae, ?*Tachardiaephagus*
Chal 042	Encyrtidae, Encyrtinae, *Tachinaephagus*
Chal185	Encyrtidae, Encyrtinae, ?
Chal 104	Encyrtidae, Encyrtinae, ?
Chal267	Encyrtidae, Encyrtinae, ?
Chal 126	Encyrtidae, Encyrtinae, ?
Chal 032	Encyrtidae, Encyrtinae, ?
Chal 110	Encyrtidae, Encyrtinae, ?
Chal 041	Encyrtidae, Tetracneminae, Anagyrini
Chal204	Encyrtidae, Tetracneminae, Anagyrini
Chal 167	Encyrtidae, Tetrachneminae, Anagyrini
Chal 017	Encyrtidae, Tetracneminae, Anagyrini
Chal 131	Encyrtidae, Tetracneminae, Anagyrini
Chal 161	Encyrtidae, Tetracneminae, Anagyrini, ?*Anagyrus*
Chal 129	Encyrtidae, Tetracneminae, Anagyrini, ?*Anagyrus*
Chal 018	Encyrtidae, Tetracneminae, *Tetracnemoidea*
Chal 057	Encyrtidae, Tetracneminae, *Tetracnemoidea*
Chal 173	Encyrtidae, Tetracneminae, ?
Chal218	Encyrtidae, Tetracneminae, ?
Chal237	Encyrtidae, Tetracneminae, ?
Chal263	Encyrtidae, ?Tetracneminae, ?
Chal 090	Encyrtidae, ?Tetracneminae, ?
Eulophidae	
Chal245	Eulophidae, Entedoninae, ?*Asecodes*
Chal230	Eulophidae, Entedoninae, ?*Hispinocharis*
Chal 157	Eulophidae, Entedoninae, ?*Monteithius*
Chal194	Eulophidae, Entedontinae, *Omphale*
Chal183	Eulophidae, Entedontinae, *Omphale*
Chal 031	Eulophidae, Entedontinae, *Omphale*
Chal 011	Eulophidae, Entedontinae, *Omphale*
Chal 061	Eulophidae, Entodontinae, *Omphale*
Chal224	Eulophidae, Entedoninae, ?*Pleurotropopseus*
Chal199	Eulophidae, Entedoninae, ?
Chal 015	Eulophidae, Entedontinae, ?
Chal 002	Eulophidae, Euderinae, *Parasecodella*
Chal 038	Eulophidae, Eulophinae, ?*Diaulomorpha*
Chal 095	Eulophidae, Eulophinae, ?*Diaulomorpha*
Chal 097	Eulophidae, Eulophinae, ?*Diaulomorpha*
Chal 101	Eulophidae, Eulophinae, ?*Diaulomorpha*
Chal 094	Eulophidae, Eulophinae, ?*Diaulomorpha*
Chal 172	Eulophidae, Eulophinae, ?*Diaulomorpha*
Chal 043	Eulophidae, Eulophinae, ?*Diglyphomorphomyia*
Chal 021	Eulophidae, Eulophinae, *Elachertus* complex
Chal 171	Eulophidae, Eulophinae, *Elachertus* complex
Chal241	Eulophidae, Eulophinae, ?*Elachertus*
Chal 135	Eulophidae, Eulophinae, *Elasmus*
Chal 068	Eulophidae, Euderinae, *Euderus*
Chal 005	Eulophidae, Eulophinae, *Euplectrus*
Chal266	Eulophidae, Eulophinae, *Hemiptarsenus*
Chal222	Eulophidae, Eulophinae, *Ophelimus*
Chal 084	Eulophidae, Eulophinae, *Ophelimus*
Chal 123	Eulophidae, Eulophinae, *Ophelimus*

Morphospecies	Identification
Chal 133	Eulophidae, Eulophinae, *Ophelimus*
Chal 164	Eulophidae, Eulophinae, *Ophelimus*
Chal223	Eulophidae, Eulophinae, *Ophelimus*
Chal257	Eulophidae, Eulophinae, *Ophelimus*
Chal260	Eulophidae, Eulophinae, *Ophelimus*
Chal 006	Eulophidae, Eulophinae, ?*Ophelimus*
Chal 048	Eulophidae, Eulophinae, *Renaniana mirissima*
Chal 120	Eulophidae, Eulophinae, *Tooloomius*
Chal 150	Eulophidae, Tetrastichinae, ?*Aceratoneuromyia*
Chal182	Eulophidae, Tetrastichinae, ?*Aceratoneuromyia*
Chal186	Eulophidae, Tetrastichinae, ?*Aceratoneuromyia*
Chal228	Eulophidae, Tetrastichinae, ?*Aceratoneuromyia*
Chal258	Eulophidae, Tetrastichinae, ?*Aceratoneuromyia*
Chal 155	Eulophidae, Tetrastichinae, ?*Aceratoneuromyia*
Chal 073	Eulophidae, Tetrastichinae, ?*Aceratoneuromyia*
Chal 177	Eulophidae, Tetrastichinae, ?*Aprostocetus*
Chal262	Eulophidae, Tetrastichinae, *Aprostocetus*
Chal 034	Eulophidae, Tetrastichinae, ?*Ceratoneura*
Chal 024	Eulophidae, Tetrastichinae, *Epichrysocharis*
Chal 029	Eulophidae, Tetrastichinae, *Epichrysocharis*
Chal 145	Eulophidae, Tetrastichinae, *Epichrysocharis*
Chal 062	Eulophidae, Tetrastichinae, *Melittobia*.
Chal 064	Eulophidae, Tetrastichinae, ?*Neotrichoporoides*
Chal 072	Eulophidae, Tetrastichinae, *Quadrastichodella*
Chal 143	Eulophidae, Tetrastichinae, *Quadrastichodella*
Chal221	Eulophidae, Tetrastichinae, *Quadrastichodella*
Chal216	Eulophidae, Tetrastichinae, *Sigmophora*
Chal264	Eulophidae, Tetrastichinae, ?*Tamarixia*
Chal 054	Eulophidae, Tetrastichinae, ?*Tetrastichus*
Eupelmidae	
Chal 071	Eupelmidae, Eupelminae, *Anastatus*
Chal256	Eupelmidae, Eupelminae, ?*Brasema*
Chal179	Eupelmidae, Calosotinae, *Eusandalum*.
Eurytomidae	
Chal 052	Eurytomidae, Eurytominae, ?
Chal 074	Eurytomidae, Eurytominae, *Bruchophagus*
Mymaridae	
Chal226	Mymaridae, *Anagroidea*
Chal196	Mymaridae, ? *Anaphes*
Chal 078	Myrmaridae, ? *Australomymar*
Chal236	Mymaridae, *Gonatocerus*
Chal 010	Myrmaridae, *Mymar*
Chal195	Mymaridae, *Polynema*
Chal 013	Mymaridae, *Stethynium*
Chal 220	Mymaridae, ?*Stethynium*
Chal 028	Mymaridae, ?
Chal 070	Mymaridae, ?
Chal 106	Mymaridae, ?
Chal 174	Mymaridae, ?
Chal 187	Mymaridae, ?
Chal 190	Mymaridae, ?
Chal 201	Mymaridae, ?
Chal 229	Mymaridae, ?
Perilampidae	
Chal 069	Perilampidae, Chrysolampinae, *Chrysolampus*
Pteromalidae	
Chal234	Pteromalidae, Cleonyminae, *Notanisus*
Chal 051	Pteromalidae, Coelocybinae, *Coelocyboides*
Chal209	Pteromalidae, Coelocybinae, *Ormyromorpha*
Chal 112	Pteromalidae, Coelocybinae
Chal180	Pteromalidae, Coelocybinae
Chal 082	Pteromalidae, Diparinae, ?*Australolaelaps*
Chal 039	Pteromalidae, Diparinae, ?*Dipareta*
Chal 035	Pteromalidae, Diparinae, ?*Dipareta*
Chal 040	Pteromalidae, Diparinae
Chal244	Pteromalidae, Ditropinotellinae, *Ditropinotella*
Chal 055	Pteromalidae, Ditropinotellinae, *Ditropinotella*
Chal 001	Pteromalidae, Eunotinae
Chal 047	Pteromalidae, Eunotinae
Chal 103	Pteromalidae, Eunotinae
Chal 115	Pteromalidae, Eunotinae

Morphospecies	Identification
Chal 156	Pteromalidae, Eunotinae
Chal202	Pteromalidae, Macromesinae, *Macromesus*
Chal213	Pteromalidae, Ormocerinae
Chal 122	Pteromalidae, Ormocerinae, Melanosomellinae
Chal 033	Pteromalidae, Pireninae, *Gastrancistrus*
Chal 105	Pteromalidae, Pireninae, *Gastrancistrus*
Chal 146	Pteromalidae, Pireninae, *Gastrancistrus*
Chal 151	Pteromalidae, Pireninae, *Gastrancistrus*
Chal 163	Pteromalidae, Pireninae, *Trigonoderopsis*
Chal 020	Pteromalidae, Pireninae
Chal 037	Pteromalidae, Pireninae
Chal 140	Pteromalidae, Pireninae
Chal 149	Pteromalidae, Pireninae
Chal 176	Pteromalidae, Pireninae
Chal 014	Pteromalidae, Pteromalinae, ?*Callitula*
Chal 026	Pteromalidae, Pteromalinae, ?*Delislea*
Chal 008	Pteromalidae, Pteromalinae, *Isoplatoides*
Chal 148	Pteromalidae, Pteromalinae, *Isoplatoides*
Chal 165	Pteromalidae, Pteromalinae, *Isoplatoides*
Chal 086	Pteromalidae, Pteromalinae, *Isoplatoides*
Chal 113	Pteromalidae, Pteromalinae, *Isoplatoides*
Chal 127	Pteromalidae, Pteromalinae, *Isoplatoides*
Chal 044	Pteromalidae, Pteromalinae, *Pachyneuron*
Chal 093	Pteromalidae, Pteromalinae, ?*Pterisemoppa*
Chal 235	Pteromalidae, Pteromalinae, *Pteromalus*
Chal 168	Pteromalidae,Spalangiinae, *Spalangia*
Chal 063	Pteromalidae, ? Pteromalinae, ?
Chal 088	Pteromalidae, ? Pteromalinae, ?
Chal 206	Pteromalidae, Pteromalidae
Chal 096	Pteromalidae, Pteromalidae, ?
Chal 225	Pteromalidae, Pteromalidae, ?
Chal 233	Pteromalidae, Pteromalidae, ?
Chal 238	Pteromalidae, Pteromalidae, ?
Chal 184	Pteromalidae, Pteromalinae, ?
Chal 118	Pteromalidae, ?
Chal 214	Pteromalidae, ?
Signiphoridae	
Chal 136	Signiphoridae, *Chartocerus*
Torymidae	
Chal 058	Torymidae, Megastigminae, ?*Bootanomyia*
Chal 016	Torymidae, Megastigminae, *Megastigmus*
Chal 023	Torymidae, Monodontomerinae, *Torymoides*
Chal 217	Torymidae, Monodontomerinae, *Torymoides*
Trichogrammatidae	
Chal 147	Trichogrammatidae
Chal 152	Trichogrammatidae
Chal 153	Trichogrammatidae
Chal 111	Trichogrammatidae
Chal 207	Trichogrammatidae
Chal 242	Trichogrammatidae
CHRYSIDOIDEA	
Bethylidae	
Beth 01	Bethylidae, Bethylinae, *Eupsenella*
Beth 03	Bethylidae, Bethylinae, ?*Sierola*
Beth 05	Bethylidae, Bethylinae, *Sierola*
Beth 10	Bethylidae, Bethylinae, ?*Sierola*
Beth 12	Bethylidae, Bethylinae, ?*Sierola*
Beth 20	Bethylidae, Bethylinae, *Sierola*
Beth 27	Bethylidae, Bethylinae, *Sierola*
Beth 28	Bethylidae, Bethylinae, *Sierola*
Beth 29	Bethylidae, Bethylinae, *Eupsenella*
Beth 31	Bethylidae, Bethylinae, *Eupsenella*
Beth 42	Bethylidae, Bethylinae, *Sierola*
Beth 02	Bethylidae, Epyrinae
Beth 04	Bethylidae, Epyrinae
Beth 07	Bethylidae, Epyrinae
Beth 08	Bethylidae, Epyrinae
Beth 09	Bethylidae, Epyrinae
Beth 14	Bethylidae, Epyrinae
Beth 16	Bethylidae, Epyrinae
Beth 21	Bethylidae, Epyrinae

Morphospecies	Identification
Beth 22	Bethylidae, Epyrinae
Beth 23	Bethylidae, Epyrinae
Beth 33	Bethylidae, Epyrinae
Beth 34	Bethylidae, Epyrinae
Beth 51	Bethylidae, Epyrinae, *Plastanoxus*
Beth 54	Bethylidae, Epyrinae
Beth 19	Bethylidae, Pristocerinae
Beth 41	Bethylidae, Pristocerinae
Beth 52	Bethylidae, Pristocerinae
Beth 53	Bethylidae, Pristocerinae
Dryinidae	
Dryin 01	Dryinidae
Dryin 01	Dryinidae
Megasp21	Dryinidae
CYNIPOIDEA	
Cynipidae	
Cynip01	Cynipidae
Figitidae	
Char01	Figitidae, Charpinae
Eucoil01	Figitidae, Eucolinae
Eucoil02	Figitidae, Eucolinae
Eucoil03	Figitidae, Eucolinae
Eucoil05	Figitidae, Eucolinae
Eucoil07	Figitidae, Eucolinae
Eucoil08	Figitidae, Eucolinae
Eucoil10	Figitidae, Eucolinae
Eucoil11	Figitidae, Eucolinae
Eucoil13	Figitidae, Eucolinae
Figit01	Figitidae, Anacharitinae, *Anacharis*
EVANOIDEA	
Evaniidae	
Evan01	Evaniidae, *Acanthinevania*
Evan02	Evaniidae, *Szepligetella*
Evan03	Evaniidae, *Szepligetella*
Evan04	Evaniidae, *Acanthinevania*
Gasterupiidae	
Gaster01	Gasterupiidae
ICHNEUMONOIDEA	
Braconidae	
Bracon58	Braconidae, Agathadinae, *Bassus*
Bracon61	Braconidae, Agathadinae, *Bassus*
Bracon73	Braconidae, Alysiinae, Alysiini
Bracon 02	Braconidae, Alysiinae, Alysiini
Bracon04	Braconidae, Alysiinae, Alysiini
Bracon24	Braconidae, Alysiinae, Alysiini
Bracon28	Braconidae, Alysiinae, Alysiini
Bracon34	Braconidae, Alysiinae, Alysiini
Bracon38	Braconidae, Alysiinae, Alysiini
Bracon67	Braconidae, Alysiinae, Alysiini
Bracon74	Braconidae, Alysiinae, Alysiini
Bracon75	Braconidae, Alysiinae, Alysiini
Bracon80	Braconidae, Alysiinae, Alysiini
Bracon81	Braconidae, Alysiinae, Alysiini
Bracon92	Braconidae, Alysiinae, Alysiini
Procto02	Braconidae, Alysiinae, Alysiini
Bracon05	Braconidae, Aphidiinae, ?*Aphidius*
Bracon14	Braconidae, Aphidiinae
Bracon21	Braconidae, Aphidiinae
Bracon23	Braconidae,?Blacinae
Bracon11	Braconidae, Braconinae, *Bracon*
Bracon83	Braconidae, Braconinae, *Callibracon*
Bracon96	Braconidae, Braconinae, *Bracon*
Bracon46	Braconidae, Cheloninae, ?*Phanerotoma*
Bracon12	Braconidae, Cheloninae, *Ascogaster*
Bracon25	Braconidae, Cheloninae, ?*Chelonus*
Bracon44	Braconidae, Cheloninae, *Ascogaster*
Bracon60	Braconidae, Doryctinae, ?*Spathius*
Bracon30	Braconidae, Doryctinae
Bracon32	Doryctinae, *Spathius*
Bracon97	Braconidae, Doryctinae
Bracon39	Braconidae, Euphorinae, ?*Wesmaelia*

Morphospecies	Identification
Bracon49	Braconidae, Euphorinae, *Holdawayella*
Bracon66	Braconidae, Euphorinae, ?*Meteorus*
Bracon03	Braconidae, Euphorinae, *Leiophron*
Bracon07	Braconidae, Euphorinae, *Leiophron*
Bracon19	Braconidae, Euphorinae, ?*Leiophron*
Bracon20	Braconidae, Euphorinae, *Leiophron*
Bracon35	Braconidae, Euphorinae, *Leiophron*
Bracon41	Braconidae, Euphorinae, ?*Leiophron*
Bracon48	Braconidae, Euphorinae, ?*Leiophron*
Bracon53	Braconidae, Euphorinae, *Leiophron*
Bracon54	Braconidae, Euphorinae, *Leiophron*
Bracon82	Braconidae,?Euphorinae
Bracon15	Braconidae, Meteorinae, *Meteorus.*
Bracon52	Braconidae, Microgastrinae, *Dolichogenidea*
Bracon08	Braconidae, Microgastrinae, *Miropotes*
Bracon09	Braconidae, Microgastrinae, *Cotesia*
Bracon13	Braconidae, Microgastrinae, ?*Sathon*
Bracon22	Braconidae, Microgastrinae, ?*Diolcogaster*
Bracon31	Braconidae, *Microgastrinae, Dolichogenidea*
Bracon40	Braconidae, Microgastrinae, ?*Diolcogaster*
Bracon47	Braconidae, Microgastrinae, *Choeras*
Bracon62	Braconidae, Microgastrinae, *Sathon*
Bracon64	Braconidae, Microgastrinae, ?*Sathon*
Bracon77	Braconidae, Microgastrinae, *Miropotes*
Bracon89	Braconidae, Microgastrinae, *Miropotes*
Bracon51	Braconidae, Miracinae
Bracon 98	Braconidae, Miracinae
Bracon17	Braconidae, Opiinae
Bracon86	Braconidae, Opiinae
Bracon27	Braconidae, Opiinae
Bracon50	Braconidae, Opiinae
Bracon65	Braconidae, Opiinae
Bracon87	Braconidae, Opiinae
Bracon01	Braconidae, Opiinae
Bracon55	Braconidae, Rogadinae
Bracon88	Braconidae, Rogadinae
Bracon06	Braconidae, Rogadinae
Bracon43	Braconidae, Rogadinae
Bracon36	Braconidae,?
Bracon94	Braconidae,?
Bracon100	Braconidae,?
Ichneumonidae	
Ichneum46	Ichneumonidae, Anomaloninae, Gravenhorstiini, ? *Habronyx* or *Aphanistes*
Ichneum21	Ichneumonidae, Banchinae
Ichneum36	Ichneumonidae, Banchinae, *Lissonata*
Ichneum37	Ichneumonidae, Banchinae, *Lissonata*
Ichneum38	Ichneumonidae, Banchinae, *Lissonata*
Ichneum51	Ichneumonidae, Banchinae, *Lissonata*
Ichneum07	Ichneumonidae, Campopleginae, *Campoplex.*
Ichneum15	Ichneumonidae, Campopleginae
Ichneum50	Ichneumonidae, Campopleginae, *Venturia.*
Ichneum03	Ichneumonidae, Cryptinae
Ichneum06	Ichneumonidae, Cryptinae
Ichneum09	Ichneumonidae, Cryptinae, *Anacis.*
Ichneum13	Ichneumonidae, Cryptinae, *Paraphylax.*
Ichneum18	Ichneumonidae, Cryptinae, ?*Paraphylax.*
Ichneum29	Ichneumonidae, Cryptinae, ?
Ichneum44	Ichneumonidae, Cryptinae, ?
Ichneum47	Ichneumonidae, Cryptinae, ?
Ichneum20	Ichneumonidae, Diplazontinae
Ichneum48	Ichneumonidae, Diplazontinae ?*Diplazon laetatorius*
Ichneum01	Ichneumonidae, Ichneumoninae,?*Gavrana.*
Ichneum02	Ichneumonidae, Ichneumoninae
Ichneum26	Ichneumonidae, Ichneumoninae
Ichneum49	Ichneumonidae, Labeninae, *Labium*
Ichneum42	Ichneumonidae, Mesochorinae, *Mesochorus*
Ichneum04	Ichneumonidae, Metopiinae
Ichneum17	Ichneumonidae, Metopiinae
Bracon57	Ichneumonidae, Orthocentrinae, *Orthocentrus.*
Ichneum05	Ichneumonidae, Orthocentrinae, *Orthocentrus.*
Ichneum08	Ichneumonidae, Orthocentrinae, *Orthocentrus.*

Morphospecies	Identification
Ichneum27	Ichneumonidae, Orthocentrinae, *Orthocentrus*
Bracon37	Ichneumonidae, Orthocentrinae, *Orthocentrus*
Ichneum41	Ichneumonidae, Orthocentrinae, *Megastylus*
Ichneum24	Ichneumonidae, Pimplinae, *Lissopimpla*
Ichneum40	Ichneumonidae, Pimplinae, *Echthromorpha*
Ichneum35	Ichneumonidae, Tryphorinae, *Phytodietus*
Ichneum39	Ichneumonidae, Tryphoninae, *Netelia*
PLATYGASTROIDEA	
Platygastridae	
Platy47	Platygastridae, Platygastrinae, ?*Amblyaspis*
Platy08	Platygastridae, Platygastrinae, *Amblyaspis*
Platy11	Platygastridae, Platygastrinae, *Amblyaspis*
Platy50	Platygastridae, Platygastrinae, *Iphitrachelus*
Platy02	Platygastridae, Platygastrinae, *Inostemma*
Platy35	Platygastridae, Platygastrinae, *Inostemma*
Platy54	Platygastridae, Platygastrinae, *Inostemma*
Platy15	Platygastridae, Platygastrinae, ?*Isostasius*
Platy19	Platygastridae, Platygastrinae, ?*Isostasius*
Platy04	Platygastridae, Platygastrinae, *Isostasius*
Platy56	Platygastridae, Platygastrinae, *Isostasius*
Platy51	Platygastridae, Platygastrinae, ?*Metaclisis*
Platy36	Platygastridae, Platygastrinae, *Metanopedias*
Platy37	Platygastridae, Platygastrinae, *Metanopedias*
Platy03	Platygastridae, Platygastrinae, *Platygaster*
Platy05	Platygastridae, Platygastrinae, *Platygaster*
Platy13	Platygastridae, Platygastrinae, *Platygaster*
Platy24	Platygastridae, Platygastrinae, *Platygaster*
Platy25	Platygastridae, Platygastrinae, *Platygaster*
Platy32	Platygastridae, Platygastrinae, *Platygaster*
Platy40	Platygastridae, Platygastrinae, *Platygaster*
Platy43	Platygastridae, Platygastrinae, *Platygaster*
Platy45	Platygastridae, Platygastrinae, *Platygaster*
Platy53	Platygastridae, Platygastrinae, *Platygaster*
Platy26	Platygastridae, Platygastrinae, ?*Synopeas*
Platy06	Platygastridae, Platygastrinae, *Synopeas*
Platy07	Platygastridae, Platygastrinae, *Synopeas*
Platy09	Platygastridae, Platygastrinae, *Synopeas*
Platy10	Platygastridae, Platygastrinae, *Synopeas*
Platy16	Platygastridae, Platygastrinae, *Synopeas*
Platy17	Platygastridae, Platygastrinae, *Synopeas*
Platy20	Platygastridae, Platygastrinae, *Synopeas*
Platy21	Platygastridae, Platygastrinae, *Synopeas*
Platy22	Platygastridae, Platygastrinae, *Synopeas*
Platy27	Platygastridae, Platygastrinae, *Synopeas*
Platy28	Platygastridae, Platygastrinae, *Synopeas*
Platy30	Platygastridae, Platygastrinae, *Synopeas*
Platy33	Platygastridae, Platygastrinae, *Synopeas*
Platy34	Platygastridae, Platygastrinae, *Synopeas*
Platy38	Platygastridae, Platygastrinae, *Synopeas*
Platy39	Platygastridae, Platygastrinae, *Synopeas*
Platy48	Platygastridae, Platygastrinae, *Synopeas*
Platy49	Platygastridae, Platygastrinae, *Synopeas*
Platy52	Platygastridae, Platygastrinae, *Synopeas*
Platy55	Platygastridae, Platygastrinae, *Synopeas*
Platy58	Platygastridae, Platygastrinae, *Synopeas*
Platy62	Platygastridae, Platygastrinae, *Synopeas*
Platy41	Platygastridae, Sceliotrachelinae, *Allotropa*
Platy57	Platygastridae, Sceliotrachelinae, *Allotropa*
Platy61	Platygastridae, Sceliotrachelinae, *Allotropa*
Platy59	Platygastridae, Sceliotrachelinae, *Amitus*
Scel109	Platygastridae, Sceliotrachelinae, *Helava*
Platy01	Platygastridae, Sceliotrachelinae, *Platygastoides*
Platy29	Platygastridae, Sceliotrachelinae, *Platygastoides*
Platy31	Platygastridae, Sceliotrachelinae, *Platygastoides*
Platy18	Platygastridae, *Raopselaphus*
Platy23	Platygastridae, *Raopselaphus*
Scel020	Platygastridae,? genus
Scelionidae	
Scel 031	Scelionidae, Scelioninae, *Anteromorpha*
Scel 053	Scelionidae, Scelioninae, *Baeus leai*
Scel 036	Scelionidae, Scelioninae, *Baeus*

Morphospecies	Identification
Scel 003	Scelionidae, Scelioninae, *Baeus*
Scel 018	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 041	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 046	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 048	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 056	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 058	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 089	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 093	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 122	Scelionidae, Scelioninae, *Ceratobaeus*
Scel 096	Scelionidae, Scelioninae, ?*Duta*
Scel 006	Scelionidae, Scelioninae, *Gryon*
Scel 045	Scelionidae, Scelioninae, *Gryon*
Scel 107	Scelionidae, Scelioninae, *Gryon*
Scel 032	Scelionidae, Scelioninae, *Gryon*
Scel 076	Scelionidae, Scelioninae, *Gryon*
Scel 016	Scelionidae, Scelioninae, *Gryon*
Scel 055	Scelionidae, Scelioninae, *Gryon*
Scel 072	Scelionidae, Scelioninae, *Gryon*
Scel 077	Scelionidae, Scelioninae, *Gryon*
Scel 108	Scelionidae, Scelioninae, *Gryon*
Scel 004	Scelionidae, Scelioninae, *Gryon*
Scel 129	Scelionidae, Scelioninae, *Gryon*
Scel 022	Scelionidae, Scelioninae, *Idris*
Scel 025	Scelionidae, Scelioninae, *Idris*
Scel 037	Scelionidae, Scelioninae, *Idris*
Scel 044	Scelionidae, Scelioninae, *Idris*
Scel 047	Scelionidae, Scelioninae, *Idris*
Scel 062	Scelionidae, Scelioninae, *Idris*
Scel 063	Scelionidae, Scelioninae, *Idris*
Scel 064	Scelionidae, Scelioninae, *Idris*
Scel 078	Scelionidae, Scelioninae, *Idris*
Scel 035	Scelionidae, Scelioninae, *Idris*
Scel 083	Scelionidae, Scelioninae, *Idris*
Scel 114	Scelionidae, Scelioninae, *Idris*
Scel 057	Scelionidae, Scelioninae, ?*Idris*
Scel 080	Scelionidae, Scelioninae, ?*Idris/ Ceratobaeus* *
Scel 084	Scelionidae, Scelioninae, ?*Idris/ Ceratobaeus* *
Scel 097	Scelionidae, Scelioninae, ?*Idris/ Ceratobaeus* *
Scel 106	Scelionidae, Scelioninae, ?*Idris/ Ceratobaeus* * males difficult to determine
Scel 119	Scelionidae, Scelioninae, *Idris*
Scel 130	Scelionidae, Scelioninae, *Idris*
Scel 132	Scelionidae, Scelioninae, *Idris*
Scel 081	Scelionidae, Scelioninae, *Mirobaeoides*
Scel 104	Scelionidae, Scelioninae, *Mirobaeoides*
Scel 015	Scelionidae, Scelioninae, *Mirobaeoides*
Scel 049	Scelionidae, Scelioninae, *Mirobaeoides*
Scel 054	Scelionidae, Scelioninae, *Mirobaeoides*
Scel 009	Scelionidae, Scelioninae, *Dyscritobaeus*
Scel 113	Scelionidae, Scelioninae, *Dyscritobaeus*
Scel 102	Scelionidae, Scelioninae, *Dyscritobaeus*
Scel 019	Scelionidae, Scelioninae, *Dyscritobaeus*
Scel 095	Scelionidae, Scelioninae, *Dyscritobaeus*
Scel125	Scelionidae, Scelioninae, *Dyscritobaeus*
Scel117	Scelionidae, Scelioninae, *Dyscritobaeus*
Scel126	Scelionidae, Scelioninae, *Dyscritobaeus*
Scel 027	Scelionidae, Scelioninae, *Odontacolus*
Scel 070	Scelionidae, Scelioninae, *Odontacolus*
Scel 087	Scelionidae, Scelioninae, *Odontacolus*
Scel 029	Scelionidae, Scelioninae, *Probaryconus*
Scel 090	Scelionidae, Scelioninae, ?*Stylotelia.*
Scel 012	Scelionidae, Teleasinae, *Teleas*
Scel 010	Scelionidae, Teleasinae, *Trimorus*
Scel128	Scelionidae, Teleasinae, *Trimorus*
Scel124	Scelionidae, Teleasinae, *Trimorus*
Scel 002	Scelionidae, Teleasinae,
Scel 007	Scelionidae, Telenominae, *Telenomus*
Scel 042	Scelionidae, Telenominae, *Telenomus*
Scel 051	Scelionidae, Telenominae, *Telenomus*
Scel 005	Scelionidae, Telenominae, *Telenomus*
Scel 112	Scelionidae, Telenominae, *Telenomus*

Morphospecies	Identification
Scel 017	Scelionidae, Telenominae, *Telenomus*
Scel 052	Scelionidae, Telenominae, ?*Telenomus*
Scel 123	Scelionidae, Telenominae, *Telenomus*
Scel 127	Scelionidae, Telenominae, *Telenomus*
Scel 131	Scelionidae, Telenominae, *Telenomus*
Scel 001	Scelionidae, Telenominae, *Trissolcus*
Scel 034	Scelionidae, Telenominae, *Trissolcus*
Scel 039	Scelionidae, Telenominae, *Trissolcus*
Scel 040	Scelionidae, Telenominae, *Trissolcus*
Scel 059	Scelionidae, Telenominae, *Trissolcus*
Scel 060	Scelionidae, Telenominae, *Trissolcus*
Scel 065	Scelionidae, Telenominae, *Trissolcus*
Scel 071	Scelionidae, Telenominae, *Trissolcus*
Scel 094	Scelionidae, Telenominae, *Trissolcus*
Scel 105	Scelionidae,?
PROCTOTRUPOIDEA	
Diapriidae	
Diap 015	Diapriidae, Ambositrinae, *Acanthobetyla corystes*
Diap 023	Diapriidae, Ambositrinae, *Diphoropria* ?*nigricans*
Diap 033	Diapriidae, Ambositrinae, *Gwaihiria* ?*bifoveata*
Diap 103	Diapriidae, Ambositrinae, *Diphoropria* nr. *nigricans*
Diap 113	Diapriidae, Ambositrinae, *Diphoropria rufipes*
Diap 004	Diapriidae, Belytinae, *Stylaclista*
Diap 006	Diapriidae, Belytinae, nr. *Aclista*
Diap 012	Diapriidae, Belytinae, ?*Belyta*
Diap 035	Diapriidae, Belytinae, ?*Belyta*
Diap 060	Diapriidae, Belytinae, *Belyta*
Diap 110	Diapriidae, Belytinae, *Aclista*
Diap 116	Diapriidae, Belytinae, ?*Belyta*
Diap 001	Diapriidae, Diapriinae, Spilomicrini, *Rostropria inopicida*
Diap 007	Diapriidae, Diapriinae, Spilomicrini, *Neurogalesus*
Diap 013	Diapriidae, Diapriinae, Diapriini, *Idiotypa*
Diap 017	Diapriidae, Diapriinae, Spilomicrini, *Entomacis*
Diap 019	Diapriidae, Diapriinae, Spilomicrini, *Paramesius*
Diap 020	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 024	Diapriidae, Diapriinae, Diapriini, *Basalys*
Diap 025	Diapriidae, Diapriinae, Spilomicrini, *Entomacis*
Diap 031	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 032	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 034	Diapriidae, Diapriinae, Spilomicrini, *Entomacis*
Diap 037	Diapriidae, Diapriinae, Diapriini, *Basalys*
Diap 038	Diapriidae, Diapriinae, Diapriini, *Trichopria*
Diap 039	Diapriidae, Diapriinae, Diapriini, *Basalys*
Diap 069	Diapriidae, Diapriinae, Spilomicrini,?*Paramesius*
Diap 084	Diapriidae, Diapriinae, Diapriini, *Trichopria*
Diap 088	Diapriidae, Diapriinae, Spilomicrini, *Rostropria simplex*
Diap 092	Diapriidae, Diapriinae, Spilomicrini,?*Neurogalesus*
Diap 093	Diapriidae, Diapriinae, Spilomicrini, *Entomacis*
Diap 097	Diapriidae, Diapriinae, Diapriini, *Basalys*
Diap 099	Diapriidae, Diapriinae, *Austropria serraticeps*
Diap 101	Diapriidae, Diapriinae, Spilomicrini, *Pentapria*
Diap 041	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 107	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 027	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 029	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 116	Diapriidae, Diapriinae, Spilomicrini
Diap 112	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 118	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 098	Diapriidae, Diapriinae, Spilomicrini, *Spilomicrus*
Diap 097	Diapriidae, Diapriinae, Diapriini,? *Basalys*
Monomachidae	
Mono01	Monomachidae. *Monomachus*
Proctotrupoidae	
Procto 01	Proctotrupoidae
VESPOIDEA	
Mutillidae	
Mutil 01	Mutillidae, Sphaeropthalminae
Mutil 02	Mutillidae, Sphaeropthalminae
Mutil 03	Mutillidae, Sphaeropthalminae
Mutil 04	Mutillidae, Sphaeropthalminae
Pompilidae	

Morphospecies	Identification
Pomp 01	Pompilidae, Pepsinae, Chirodamini, *Sphictostethus ?aliciae*
Pomp 02	Pompilidae, Pepsinae, Chirodamini, *Austrosalius*
Pomp 03	Pompilidae, Pepsinae, Chirodamini, *Austrosalius*
Pomp 04	Pompilidae, Pepsinae, Chirodamini, *Naumannia*
Pomp 06	Pompilidae, Pepsinae, Ageniellini, *Fabriogenia*
Pomp 05	Pompilidae, Pepsinae, Chirodamini,?*Mimocurgus*
Pomp 13	Pompilidae, Pepsinae, Chirodamini,?*Mimocurgus*
Pomp 14	Pompilidae, Pepsinae, Chirodamini,?*Mimocurgus*
Pomp 15	Pompilidae, Pepsinae, Chirodamini,?*Mimocurgus*
Pomp 10	Pompilidae, Pompilinae, *Ctenostegus*
Tiphidae	
Tiph06	Tiphidae, Anthoboscinae
Tiph11	Tiphidae, Anthoboscinae
Tiph22	Tiphidae, Anthoboscinae
Tiph18	Tiphidae, Myzinnae
Tiph19	Tiphidae, Myzinnae
Tiph21	Tiphidae, Myzinnae
Tiph01	Tiphidae, Thynninae
Tiph03	Tiphidae, Thynninae
Tiph05	Tiphidae, Thynninae
Tiph07	Tiphidae, Thynninae
Tiph08	Tiphidae, Thynninae
Tiph09	Tiphidae, Thynninae
Tiph14	Tiphidae, Thynninae
Tiph15	Tiphidae, Thynninae
Tiph16	Tiphidae, Thynninae
Tiph17	Tiphidae, Thynninae
Tiph20	Tiphidae, Thynninae
Tiph23	Tiphidae, Thynninae

Where possible, wasp morphospecies were confirmed by hymenopteran taxonomists:

Ceraphronidae	-
Megaspilidae	-
CHALCIDOIDEA	Dr John LaSalle (Australian National Insect Collection, AUS), Dr Jim Wooley (Texas A&M University, USA)
Bethylidae	Dr Andrew Polaszek (The Natural History Museum, UK)
Dryinidae	-
Charipidae	-
Eucoilidae	-
Figitidae	-
Evaniidae	Andrew Deans (University of Illinois, USA)
Gasteruptidae	Dr John Jennings (The University of Adelaide, AUS)
Braconidae	Dr Jim Whitfield (University of Illinois, USA), Professor Andrew Austin (University of Adelaide, AUS)
Ichneumonidae	Dr Ian Gauld (The Natural History Museum, UK)
Platygastridae	Professor Andrew Austin (University of Adelaide, AUS), Dr Lubomír Masner (Agriculture and Agrifood, CAN)
Scelionidae	Professor Andrew Austin (University of Adelaide, AUS), Dr Lubomír Masner, (Agriculture and Agrifood, CAN)
Diapriidae	Matt Yoder (Texas A&M University, USA)
Monomachidae	-
Proctotrupidae	-
Mutillidae	-
Pompilidae	Mick Day (The Natural History Museum, UK)
Tiphidae	-

Appendix C

Wasp host and prey records

Table A-3 Wasp taxa recorded from Mt Billy CP and host records sourced from the literature subsequently used to allocate functional groups (Chapters 3 and 4). The level of identification and host record varies as the level of identification required to determine host associations differed among groups. In addition, many taxa do not have host information for Australian species, thus data reported here are from both Australian and non-Australian records.

Taxa	Host records
CERAPHRONOIDEA	
Ceraphronidae	
Aphanogmus	Recorded parasitoids of Diptera (especially Cecidomyiidae) and as hyperparasitoids via Braconidae in Lepidopteran larvae; also been found in cocoons of Neuroptera and in ant nests (Muesebeck 1979; Alekseev 1987; Naumann 1991).
Ceraphron	Recorded as parasitoids or hyperparasitoids of various Diptera (Cecidomyiidae, Drosophilidae, Phoridae, Sciaridae, and Syrphidae), Homoptera (Aleyrodidae, Aphidae, and Coccoidea), parasitic Hymenoptera (and recorded from ant nests), and Neuroptera (Muesebeck 1979; Alekseev 1987; Naumann 1991).
Megaspilidae	
Conostigmus	Parasitoids of Tachinidae, Syrphidae and Agromyzidae (Diptera); also recorded from Coleoptera (Coccinellidae), and from ant nests (where they may be parasitoids of myrmecophilous Diptera) (Muesebeck 1979; Alekseev 1987; Naumann 1991).
Dendrocerus	Hyperparasitoids of sternorrhynchous Homoptera (aphids, mealybugs, chermids and psyllids) via other parasitic hymenoptera (eg. Braconidae) or parasitoids of predatory (on Homoptera) Diptera larvae (Syrphidae and Chamaemyiidae); also recorded from phytophagous Diptera and Neuroptera (Coniopterygidae and Hemerobiidae) (Alekseev 1987; Naumann 1991; Dessart 1995).
Lagynodes	Have been recorded from ant nests, where they probably attack myrmecophilous Diptera (Muesebeck 1979; Alekseev 1987; Dessart 1995).
Megaspilus	Probably parasitiods of saprophytic Diptera (Alekseev 1987; Dessart 1995).
Plastomicrops	No records.
CHALCIDOIDEA	
Aphelinidae	Mostly parasitoids (primary and hyperparasitoids) of Homoptera, but also the eggs of Lepidoptera and Orthoptera, the eggs, larvae and pupae of Diptera and the larvae of Chalcidoidea and Drynidae (Hymenoptera) (Gibson 1993).
Azotinae	
Ablerus	Recorded from Homoptera (Cumber 1967) and Lepidoptera (Darling & Johnson 1984) eggs, and Chamaemyiidae (Diptera) pupae (Viggiani 1984).
Aphelininae	
Aphelinus	Recorded from Aphididae and Aleyrodidae (Hemiptera) nymphs and adults (Noyes & Valentine 1989).
Centrodora	Recorded from Homoptera, Acrididae (Orthoptera), and Cecidomyiidae (Diptera) eggs, and Dryinidae larvae and pupae (Viggiani 1984; Noyes & Valentine 1989; Polaszek 1991).
Encarsia	Recorded from Diaspididae (Hemiptera) and Aleyrodidae larvae (Noyes & Valentine 1989).
Coccophagus	Recorded from Coccidae and Pseudoccidae (Hemiptera) nymphs and adults, and Dryinidae and Aphelinidae (Hymenoptera) larvae and pupae (Viggiani 1984; Noyes 1989).
Chalcididae	
Chalcidinae	
Brachymeria	Mostly recorded from a wide range of Lepidoptera (eg. Arctiidae, Gelechiidae, Hesperiidae, Lasiocampidae, Megalopygidae,

Taxa	Host records
	Nymphalidae, Pieridae, Pyralidae, Tortricidae); but also Coleoptera (eg. Chrysomelidae), Hymenoptera (eg. Braconidae, Ichneumonidae, Symphyta), and Diptera (eg. Calliphoridae, Sarcophagidae, Tachinidae) pupae as both primary and hyperparasitoids (Burks 1979; Boucek 1988).
Haltichellinae	
Allochalcis	No records (Boucek 1988).
Antrocephalus	Recorded from Lepidoptera (eg. Psychidae, Pyralidae, Tortricidae) and some Diptera (eg. Muscidae) pupae (Boucek 1988).
Proconura	Recorded mostly from small Lepidoptera (eg. Pyralidae, Gelechiidae, Yponomeutidae), but also Coleoptera pupae (eg. Bruchidae) (Boucek 1988).
Encyrtidae	
Encyrtinae	
Aphycini	
Metaphycus	Parasitoids of Hemiptera (Coccidae, Diaspididae, Keriidae, Asterolecaniidae and Eriococcidae) (Noyes & Hayat 1984).
Bothriothoracini	
Tachinaephagus	Parasitoids of Diptera larvae (eg. Calliphoridae, Muscidae, Sarcophagidae, and Tephritidae) (Noyes & Hayat 1984).
Cheiloneurini	
Mahencyrtus	No records (Noyes & Hayat 1984).
Copidosomatini	
Copidosoma	Parasitoids (polyembryonic) of Lepidopteran larvae (eg. Gelechiidae, Geometridae, Noctuidae, Pyralidae) (Noyes & Hayat 1984; Noyes 1988).
Paralitomastix	Parasitoids (polyembryonic) of Lepidoptera (Pyralidae, Gelechiidae) larvae (Noyes & Hayat 1984)
Discodini	
Discodes	Parasitoids of Coccidae (Hemiptera) (Noyes & Hayat 1984)
Homalotylini	
Homalotylus	Parasitoids of Coccinellidae (Coleoptera) larvae (Noyes & Hayat 1984)
Microteryini	
Bothriophryne	Parasitoids of Coccidae (Hemiptera) (Noyes & Hayat 1984)
Doddanusa	No records (Noyes & Hayat 1984)
Paraenasomyia	Parasitoids of gall-forming Cecidomyiidae (Diptera) (Noyes & Hayat 1984)
Tachardiaephagus	Parasitoids of Keriidae (Noyes & Hayat 1984)
Trechnitini	
Neanagyrus	Parasitoids of lerp-forming Psyllidae (Hemiptera) (Noyes & Hayat 1984)
Psyllaephagus	Parasitoids or hyperparasitoids of Psyllidae (Hemiptera) (Noyes & Hayat 1984)
Tetracneminae	
Anagyrini	Parasitoids of Pseudococcidae (Hemiptera) (Noyes & Hayat 1984).
Anagyrus	Parasitoids of Pseudococcidae (Hemiptera) and Coccinellidae (Coleoptera) whose larvae produce a waxy secretion (Noyes & Hayat 1984).
Tetracnemini	
Tetracnemoidea	Parasitoids of Pseudococcidae (Noyes & Hayat 1984).
Eulophidae	
Entedoninae	
Asecodes	Parasitoids of Chrysomelidae (Coleoptera) eggs (Boucek 1988).
Hispinocharis	Hyperparasitoid (maybe a primary parasitoid) of hispine leafminers (Coleoptera: Chrysomelidae) (Boucek 1988).
Monteithius	No records (Boucek 1988).
Omphale	Parasitoids of Cecidomyiidae (Diptera) larvae (Boucek 1988).
Pleurotropopseus	No records (Boucek 1988).
Euderinae	
Parasecodella	No records (Boucek 1988).
Eulophinae	
Diaulomorpha	Parasitoids of Tenthredinidae (Hymenoptera) leaf miners and small Lepidoptera (Boucek 1988).
Diglyphomorphomyia	Possibly parasitoids of Lepidoptera stem borers (Boucek 1988).
Elachertus	Parasitoids of leaf-mining Lepidoptera and other small Lepidoptera (Boucek 1988).
Elasmus	Gregarious parasitoids of a range of Lepidoptera larvae in cases, spun

Taxa	Host records
	leaves, webs, or leaf mines (Noyes & Valentine 1989; Burks 2003).
Euderus	Parasitoids of Lepidoptera and Coleoptera (eg. Buprestidae) larvae, Cerambycidae and Curculionidae (Coleoptera) eggs, and hyperparasitic via Braconidae (Boucek 1988).
Euplectrus	Gregarious parasitoids of exposed-feeding Lepidoptera larvae (eg. Noctuidae) (Boucek 1988; Naumann 1991).
Hemiptarsenus	Parasitoids of Diptera leafminers on herbaceous plants (Boucek 1988)
Ophelimus	Develop in *Eucalyptus* galls; considered to be gall-formers (Boucek 1988)
Renaniana mirissima	No records (Boucek 1988)
Toolomius	No records, but may be parasitoids of Lepidopteran leafminners (Boucek 1988)
Tetrastichinae	
Aceratoneuromyia	Gregarious parasitoids of brachycerous Diptera larvae and pupae, especially of Tephritidae, Calliphoridae, and Muscidae (Boucek 1988)
Aprostocetus	Develop in plant galls casued by other insects, mostly Cecidomyiidae, as egg or larval parasitoids or as phytopagous inquilines. Many are host or gall specialists, or attack several galls in ecologically similar niches (Boucek 1988)
Ceratoneura	Gall-formers or inquilines in flower galls on various plant species (Boucek 1988)
Epichrysocharis	Possibly associated with galls on *Eucalyptus* (Boucek 1988)
Melittobia	Gregarious parasitoids of larvae and pupae of solitary or (more rarely) social bees and wasps. Also may attack other hosts in the vicinity of bee and wasp nests, such as Lepidoptera and Coleoptera larvae and brachycerous Diptera pupae (Dahms 1984)
Neotrichoporoides	Parasitoids of stem-boring Diptera, especially in stiff-stemed Gramineae (grasses) (Boucek 1988)
Quadrastichodella	Phytophagous gall-formers on *Eucalyptus* (Boucek 1988)
Sigmophora	Parasitoids of gall-forming Cecidomyiidae (Boucek 1988)
Tamarixia	Parasitoids of Psylloidea (Hemiptera) (Boucek 1988)
Tetrastichus	Parasitoids of Chrysomelidae and Lepidoptera pupae and sawfly larvae and pupae (Boucek 1988)
Eupelmidae	
Eupelminae	
Anastatus	Parasitoids of Lepidoptera (eg. Thaumetopoeidae) and Heteroptera (Hemiptera) (eg. Pentatomidae) eggs, and less commonly Blattodea, Diptera, Orthoptera, and Mantodea eggs. Species are generally host-specific, but some parasitise a range of hosts within the same niche (Boucek 1988)
Brasema	Possibly parasitoids of Coleoptera associated with wood (Boucek 1988)
Calosotinae	
Eusandalum	Parasitoids of wood-boring Coleoptera larvae, especially Buprestidae and Cerambycidae (Boucek 1988).
Eurytomidae	
Eurytominae	
Bruchophagus	Phytophagous in galls and seeds (Boucek 1988).
Eurytoma	Phytophagous, parasitoids in plant tissue/ galls or as hyperparsitoids via Braconidae and Ichneumonidae of Lepidoptera (Boucek 1988).
Mymaridae	
Anagroidea	No records (Noyes & Valentine 1989).
Anaphes	Parasitoids of eggs of Coleoptera (eg. Chrysomelidae, Coccinellidae, Curculionidae), Hemiptera (Miridae), Diptera, and Lepidoptera (Burks 1979; Noyes & Valentine 1989).
Australomymar	No records (Noyes & Valentine 1989).
Gonatocerus	Egg parasitoids of Homoptera (Hemiptera), mostly Cicadellidae and Membracidae (Noyes & Valentine 1989).
Mymar	Egg parasitoids of Delphacidae (Hemiptera) (Noyes & Valentine 1989).
Polynema	Parasitoids of eggs of Coleoptera (Curculionidae), Hemiptera (eg. Cicadellidae, Lygaeidae, Membracidae), Diptera, and Lepidoptera (Burks 1979; Noyes & Valentine 1989).
Stethynium	Recorded from eggs of Membracidae (Hemiptera) (Noyes & Valentine 1989).
Perilampidae	
Chrysolampinae	
Chrysolampus	Parasitoids of Bostrichidae and Nitidulidae (Coleoptera) (Boucek 1988).
Pteromalidae	

Taxa	Host records
Cleonyminae	Mostly develop as parasitoids of beetle larvae in wood; a few attack insects in grass and thistle stems, cockroach oothecae under bark, and bees nesting in dead wood (Boucek 1988).
Notanisus	Parasitoids and hyperparasitoids of insects in grass stems (Boucek 1988).
Coelocybinae	Associated with tree galls (Boucek 1988).
Coelocyboides	Reared from various tree galls (Boucek 1988).
Ormyromorpha	Parasitoids in galls from *Acacia* and *Eucalyptus* (Boucek 1988).
Diparinae	Only one record: a species reared from a Curculionid beetle; often found in leaf litter or soil (Boucek 1988).
Australolaelaps	No records (Boucek 1988).
Dipareta	No records (Boucek 1988).
Ditropinotellinae	Associated with galls on trees and shrubs (Boucek 1988).
Ditropinotella	Develop in galls on *Eucalyptus*, *Acacia* and *Casuarina* (Boucek 1988).
Eunotinae	Mostly predators (or parasitoids) of Coccoidea (Hemiptera) eggs, and more rarely Aphididae and Psylloidea (Hemiptera) eggs (Boucek 1988).
Macromesinae	
Macromesus	Parasitoids of wood-boring beetles in small twigs (Boucek 1988).
Ormocerinae	Associated with plant galls as parasitoids, inquilines or gall-formers (Boucek 1988).
Melanosomelli	Reared from galls of various trees (Boucek 1988).
Pireninae	Parasitoids of Cecidomyiidae (Diptera) in plant tissue (Boucek 1988).
Gastrancistrus	Recorded from galls from *Acacia*, *Melaleuca* and *Syncarpia* (Boucek 1988).
Trigonoderopsis	No records (Boucek 1988).
Pteromalinae	
Callitula	Parasitoids of small Diptera, especially stem- and leaf-mining Agromyzidae (Boucek 1988).
Delislea	No records (Boucek 1988).
Isoplatoides	Associated with trees: recorded from Pergidae (sawfly) mines on fallen leaves, *Eucalypt* and *Acacia* galls, Lepidopteran pupae, and in the nest of tree-dwelling ants (Boucek 1988).
Pachyneuron	Parasitoids of aphidophagous Syrphidae, Aphididae, Coccoidae, Coccinellidae and occasionally as hyperparasitoids from other hosts such as Aphidiinae or Chamaemyiidae (Diptera) (Boucek 1988).
Pterisemoppa	No host records (probably parasitoids of Diptera) (Boucek 1988).
Pteromalus	Parasitoids of Lepidoptera (eg. Coleophoridae, Nymphalidae, Pieridae) prepupae and pupae, Tephritidae (Diptera) and Curculionidae (Coleoptera) in galls, and insects in coccons, including Braconidae and Ichneumonidae (Hymenoptera) (Boucek 1988).
Spalangiinae	
Spalangia	Parasitoids of Diptera (eg. Calliphoridae, Muscidae, Sarcophagidae,) (Boucek 1988).
Signiphoridae	
Chartocerus	Hyperparasites of Encyrtidae and Aphelinidae (Hymenoptera) from Pseudococcidae, Coccidae, Psyllidae, and Aphididae (Hemiptera) and parasitoids of Chamaemyiidae (Diptera) pupae that are predators of mealybugs (Woolley 1988).
Torymidae	
Megastigminae	Most species are associated with various plant galls (Boucek 1988).
Bootanomyia	No records (Boucek 1988).
Megastigmus	Parasitic or phytophagous; associated with galls especially on *Eucalyptus* and *Acacia* (Boucek 1988).
Monodontomerinae	
Torymoides	Parasitiods of Cecidomyiidae (Diptera) in galls on *Eucalyptus* and *Acacia* (Boucek 1988)
Trichogrammatidae	Egg parasitoids of Lepidoptera, Hemiptera, Thysanoptera, and less commonly Coleoptera, Neuroptera, Diptera and Odonata (Naumann 1991). Species seem to be more habitat specific than host specific (Gibson 1993).
CHRYSIDOIDEA	
Bethylidae	
Bethylinae	Parasitoids of Lepidoptera (moth & butterfly) larvae in concealed situations (eg. leaf-rollers, case-bearers, bud-borers) or exposed caterpillars which are then concealed by the wasp mostly from the superfamilies Tineoidea, Gelechioidea, Tortricoidea, Pyraloidea (Finnamore & Gauld 1995).

Taxa	Host records
Eupsenella	No records (Gordh & Moczar 1990).
Goniozus	Recorded from species of Agonoxenidae, Blastobasidae, Choreutidae, Coleophoridae, Cosmopterigidae, Gelechiidae, Geometridae, Gracillariidae, Heliozelidae, Hyblaeidae, Incurvariidae, Oecophoridae, Psychidae, Pyralidae, Tineidae, and Tortricidae (Gordh & Moczar 1990).
Sierola	Recorded from species of Lepidoptera (eg. Gelechiidae, Gracillariidae, Lyonetiidae, Pyralidae, and Tortricidae) (Gordh & Moczar 1990).
Epyrinae	Parasitoids of Coleoptera larvae in concealed situations, eg. Anobiidae, Anthribidae, Bostrichidae, Bruchidae, Buprestidae, Dermestidae, Cerambyciidae, Ciidae, Cucujidae, Curculionidae, Tenebrionidae (Evans 1978; Gordh & Moczar 1990; Finnamore & Brothers 1993).
Pristocerinae	Parasitoids of wood-boring and soil-dwelling Coleoptera (beetle) larvae, eg. Anobiidae, Anthribidae, Bostrichidae, Bruchidae, Buprestidae, Dermestidae, Cerambyciidae, Ciidae, Cucujidae, Curculionidae, Tenebrionidae (Finnamore & Gauld 1995).
Dryinidae	Parasitoids of Auchenorrhyncha (Hemiptera) (eg. Dictyopharidae, Flatidae, Fulgoridae, Nogodinidae, Ricaniidae) adults and nymphs (Naumann 1991).
CYNIPOIDEA	
Charipidae	
Charipinae	Hyperparasitoids of Psylloidea (Hemiptera) through Braconidae and Chalcidoidea (Richie 1993; Ronquist 1995)
Cynpidae	Phytophagous gall formers or inquilines (Naumann 1991; Richie 1993; Ronquist 1995).
Eucoilidae	Parasitoids of a wide range of Diptera from both plant tissue, eg. Tephritidae, Chloropidae, Agromyzidae, and more often from rotting fruit, vegetation, carrion and dung, eg. Drosophilidae, Sepsidae, Phoridae, Muscidae, Calliphoridae, Sarcophagidae (Naumann 1991; Richie 1993; Fergusson 1995).
Figitidae	
Anacharitinae	Parasitoid of Hemerobiidae and Chrysopidae (lacewing) larvae (Naumann 1991; Richie 1993; Ronquist 1995).
EVANOIDEA	
Evaniidae	Solitary parasitoids of Blattodea (cockroach) eggs (Naumann 1991; Mason 1993).
Gasterupiidae	Egg and larval predators in nests of Apoidea (Hymenoptera- bees) and Vespoidea (Hymenoptera- wasps) in soil or wood, eg. Masarinae, Stenotritidae, Halicitade, Megachilidae, Colletidae, Vespidae (Naumann 1991; Mason 1993).
ICHNEUMONOIDEA	
Braconidae	
Agathidinae	Parasitoids of Lepidoptera larvae in consealed situations, except for the tribe Disophrini which parasitise exposed larvae (Sharkey 1997).
Bassus	Recorded from Lepidoptera larvae in concealed situations, (eg. Coleophoridae, Gelechiidae, Pieridae, Pyralidae, Totricidae, and Yponomeutidae) (Sharkey 1996).
Alysiinae	Parasitoids of cyclorrhaphous Diptera eggs or larvae (Wharton 1997).
Alysiini	Mostly attack Diptera living in ephemeral and odoriferous substrates such as dung, carrion, fungi, and rotting or fermenting plant matter (eg. Drosophilidae, Phoridae, Sarcophagidae) (Shaw & Huddleston 1991).
Aphidiinae	Parasitoids of Aphididae nymphs and adults (van Achterberg 1997).
Blacinae	Few host records; recorded as parasitoids of Coleoptera (eg. Cerambycidae, Curculionidae) larvae and Mecoptera larvae (Sharkey 1997).
Braconinae	Parasitoids of Lepidoptera and Coleoptera larvae in concealed situations, plus a few species recorded from Diptera and Pergidae (sawfly) (Quicke 1997).
Bracon	Parasitoids of a wide range of Lepidoptera, Coleoptera, Diptera, and phytophagous Hymenoptera, usually concealed in plant tissue such as stems, galls, and seed heads, or case bearers, leaf-rollers or under bark or in wood (Shaw & Huddleston 1991).
Callibracon	Parasitoid of Cerambycidae (Coleoptera) (Naumann 1991).
Cheloninae	Parasitoids of Lepidoptera larvae in concealed situations, or exposed or concealed eggs (Shaw 1997).
Ascogaster	Commonly recorded from species of Tortricidae, and rarely from

Taxa	Host records
	Geometridae (Lepidoptera) (Shaw 1983).
Chelonus	Recorded from species of Lepidoptera (eg. Lyonetiidae, Gracillariidae, Coleophoridae, Cosmopterigidae, Gelechiidae, Yponomeutidae, Pyralidae, Tortricidae, Noctuidae) (Shaw 1997, McComb, 1968 #322).
Phanerotoma	Recorded from species of Lepidoptera (eg. Gelechiidae, Pyralidae, and Tortricidae) (Shaw 1997).
Doryctinae	Parasitoids of wood-boring Coleoptera larvae, plus a few species recorded from stem-boring Lepidoptera and Pergidae (Hymenoptera) larvae (Marsh 1997).
Spathius	Recorded from species of Coleoptera (eg. Buprestidae, Cerambycidae, Curculionidae) (Marsh 1997, Matthews, 1970 #325).
Euphorinae	Parasitoids of adult Coleoptera, Hymenoptera, Neuroptera, and nymphal and adult Heteroptera (Hemiptera) and Pscoptera (Shaw 1997).
Euphoriella	Parasitoids of Pscoptera (booklice) nymphs (Shaw 1985).
Holawayella	Parasitoids of Tingidae (Hemiptera) (Shaw 1985).
Leiophron	Parasitoids of Miridae (Hemiptera) (Shaw 1985).
Wesmaelia	Parasitoids of Nabidae (Hemiptera) (Shaw 1985).
Meteorinae	
Meteorus	Mostly attack exposed-feeding soiltary macro-Lepidoptera larvae, but also concealed Coleoptera (in wood, bark, and fungi) and Lepidoptera (leaf rolls, mosses, fungi, and organic matter) (Shaw 1985; Shaw & Huddleston 1991).
Microgastrinae	Parasitoids of a very wide range of Lepidoptera larvae (Whitfield 1997).
Dolichogenidea	Mostly solitary on various microlepidoptera, some gregarious on macrolepidoptera (Whitfield 1997), eg. Agonoxenidae, Anthelidae, Batrachedridae, Galleriidae, Limacodidae, Lycaenidae, Noctuidae, Oecophoridae, Plutellidae, Psychidae (Austin & Dangerfield 1992).
Choeras	Solitary on microlepidoptera (Whitfield 1997) eg. Oecophoridae (Austin & Dangerfield 1992).
Cotesia	Solitary or gregarious on a wide range of macrolepidoptera (Whitfield 1997), eg. Anthelidae, Hesperiidae, Lycaenidae, Noctuidae, Pieridae, Plutellidae, Saturniidae, Tortricidae (Austin & Dangerfield 1992).
Sathon	Solitary or gregarious on a wide range of micro- and macrolepidoptera (Whitfield 1997), eg. Psychidae (Austin & Dangerfield 1992).
Diologaster	Solitary or gregarious on various macrolepidoptera (Whitfield 1997) (eg. Anthelidae, Arctiidae, Geometridae, Lasiocampidae, Limacodidae, Lymantriidae, Noctuidae, Notodontidae, Nymphalidae, Pyralidae, Thaumetopoeidae, Tortricidae) (Saeed, *et al.* 1999).
Miropotes	Solitary parasitoid of Pyralidae (Austin & Dangerfield 1992).
Miracine	Recorded from leaf-mining Lepidoptera (eg. Nepticulida, Heliozelidae, Gracillariidae, Tischeriidae) (Whitfield 1997).
Opiinae	Parasitoids of phytophagous cyclorrhaphous Diptera eggs or larvae (eg. Agromyzidae, Anthomyiidae, Tephritidae) (Wharton 1997).
Rogadinae	Parasitoids of exposed feeding macrolepidopteran larvae (Lasiocampidae, Lycaenidae, Zygaenidae), except for the one group which parasitises leaf-mining Lepidopteran larvae (eg. Lyonetiidae, Gracillariidae) (Shaw 1997).
Ichneumonidae	
Anomaloninae	
Gravenhorstiini	
Aphanistes	Parasitoids of Lepidoptera (eg. Geometridae) (Gauld 1984).
Habronyx	Parasitoids of Lepidoptera (eg. Geometridae, Psychidae, Saturniidae) (Gauld 1984)
Banchinae	Solitary parasitoids of Lepidopera larvae (Gauld 1984)
Lissonata	Recorded from species of Pyralidae (Gauld 1984)
Campopleginae	Solitary parasitoids of holometabolous insect larvae (Gauld 1984)
Campoplex	Parasitoids of Lepidopteran larvae (eg. Noctuidae) (Gauld 1984)
Venturia	Parasitoids of Lepidopteran larvae (eg. Pyralidae) (Gauld 1984)
Cryptinae	Parasitoids of holometabolous pupae, prepupae and less often larvae (Gauld 1984)
Anacis	Parasitoids of Lepidoptera (eg. Coleophoridae, Lymantriidae) (Gauld 1984)
Paraphylax	Parasitoids of small cocoons (presence of silk is important), eg. Araneidae (orb weaver spiders), and Lepidoptera (eg. Pieridae, Plutellidae, Psychidae, Pergidae, Saturniidae) (Gauld 1984)
Diplazontinae	Parasitoids of apidophagous Syrphidae (Diptera) and some phytophagous

Taxa	Host records
	syrphids (Gauld 1984)
Diplazon	Parasitoids of apidophagous Syrphidae (Diptera) (Gauld 1984)
Ichneumoninae	Parasitoids of Lepidoptera larvae or pupae (usually amongst ground vegetation and litter) (Gauld 1984)
Gavrana	No records
Labeninae	Mostly parasitoids of concealed Coleoptera larvae in plant tissue such as wood stems and galls; others attack solitary bees or small cocoons and spider egg sacs (Gauld 1984)
Labium	Parasitoid of solitary ground nesting bees, eg. Halictidae (Gauld 1984)
Mesochorinae	Hyperparasites, usually of Braconidae (Hymenoptera), and less frequently Ichneumonidae (Hymenoptera) and Tachinidae (Diptera) (Gauld 1984)
Mesochorus	Common parasitoid of Microgasterinae (Hymenoptera, Braconidae), also recorded from Tachinidae (Diptera) in Chrysomelidae (Coleoptera) and as a secondary parasite of Lasiocampidae (Lepidoptera) (Gauld 1984)
Metopiinae	Parasitoids of exposed or lightly concealed (eg. in leaf rolls) Lepidopteran larvae (Gauld 1984)
Orthocentrinae	Parasitoids of Diptera, mostly Mycetophilidae and related genera (Gauld 1984, 1995)
Orthocentrus	Parasitoids of Mycetophilidae and Sciaridae (Diptera) (I D Gauld pers comm; (Gauld 1995).
Megastylus	Parasitoids of Mycetophilidae (Diptera) (I D Gauld pers comm)
Pimplinae	Parasitoids of a wide range of holometabolous insect larvae and pupae, and spiders and spider egg sacs (Gauld 1984)
Echthromorpha	Parasitoids of Lepidoptera (eg. Hesperiidae, Tortricidae, Anthelidae, Bombycidae, Lycaenidae, Lymantriidae, Noctuidae, Nymphalidae, Psychidae, Xylorctidae, Papilionidae, Saturniidae) (Gauld 1984).
Lissopimpla	Parasitoids of Lepidoptera (eg. Anthelidae, Noctuidae, Pyralidae) (Gauld 1984).
Tryphoninae	Mostly parasitoids of Symphya (Hymenoptera), but some attack Lepidoptera larvae (Gauld 1984).
Netelia	Parasitoid of Lepidoptera larvae (eg. Noctuidae, Pieridae, Pyralidae) (Gauld 1984).
Phytodietus	Parasitoid of Lepidoptera larvae (eg. Geometridae, Tortricidae, Xylorctidae) (Gauld 1984).
PLATYGASTEROIDEA	
Platygastridae	
Platygastrinae	Egg and early larval parasitoids of Cecidomyiidae (Diptera) in galls (Masner & Huggert 1989).
Allostemma	No records (Masner & Huggert 1989).
Iphitrachelus	No records (Masner & Huggert 1989).
Inostemma	Parasitoids of Cecidomyiidae (Diptera) in galls (Masner & Huggert 1989).
Leptacis	Parasitoids of Cecidomyiidae (Diptera) (Vlug 1995).
Metaclisis	Parasitoids of Cecidomyiidae (Diptera) in galls (Masner & Huggert 1989).
Platygaster	Parasitoids of Cecidomyiidae (Diptera) (Vlug 1995).
Synopeas	Parasitoids of Cecidomyiidae (Diptera) (Austin & Field 1997).
Sceliotrachelinae	Egg and larval parasitoids of Hemiptera and Coleoptera (Masner & Huggert 1989).
Amitus	Parasitoids of Aleyrodidae (Hemiptera) (Masner & Huggert 1989).
Helava	Possibly parasitoids of Aphididae (Hemiptera) (Masner & Huggert 1989).
Platygastoides	Hosts not known, but possibly attacks Coleoptera eggs. Often collected in leaf litter (Masner & Huggert 1989).
Scelionidae	
Scelioninae	
Baeini	
Baeus	Parasitoid of Araneae eggs (Austin 1985).
Ceratobaeus	Parasitoid of Araneae eggs (Austin 1985).
Idris	Parasitoid of Araneae eggs (Austin 1985).
Mirobaeoides	Parasitoid of Araneae eggs (Austin 1985).
Odontacolus	Parasitoid of Araneae eggs (Austin 1985).
Calliscelionini	
Anteromorpha	Parasitoid of Gryllidae eggs (Austin & Field 1997).
Probaryconus	Parasitoid of Gryllidae eggs (Galloway & Austin 1984).
Gryonini	
Dyscritobaeus	No records (Austin & Field 1997), but possibly attacks Heteroptera (Hemiptera) eggs similar to other Gryonini (Naumann 1991).
Gryon	Recorded from Hemiptera eggs (eg. Alydidae, Coreidae, Largidae,

Taxa	Host records
	Lygaeidae, Pentatomidae, and Reduviidae) (Masner 1983).
Psilanteridini	
Duta	Recorded from Gryllidae eggs (Masner 1991).
Styloteleia	No records (Austin & Field 1997).
Teleasinae	
Teleasini	
Teleas	Recorded from Carabidae (Coleoptera) eggs (Sharkey 1981).
Trimorus	Recorded from Carabidae (Coleoptera) eggs (Muesebeck 1979).
Telenominae	
Telenomini	
Telenomus	Parasitoid of Heteroptera (eg. Pentatomidae, Reduviidae) or Lepidoptera (eg. Geometridae, Lasiocampidae, Lymantriidae, Noctuidae, Pyralidae, Sphingidae, Zygaenidae) and rarely Neuroptera or Diptera eggs (Johnson & Bin 1982; Johnson 1984;).
Trissolcus	Recorded from species of Pentatomoidea, mostly Pentatomidae (Hemiptera) eggs (Johnson 1984).
PROCTOTRUPOIDEA	
Diapriidae	
Ambositrinae	Parasitoids of Mycetophilid (Diptera) (only a few host records, but commonly collected in moist, shaded habitats from litter, moss, and low vegetation) (Naumann 1982; 1988).
Belytinae	Parasitoids of Mycetophilid and Sciaridae (Diptera) (Naumann 1991; Masner 1993).
Diapriinae	Mostly parasitoids of Diptera (eg. Stratiomyidae, Syrphidae, Tephritidae, Calliphoridae, Sarcophagidae, Muscidae, and Tachinidae) but also recorded from Coleoptera, (eg. Staphylinidae, Psephenidae), and Isoptera and Formicidae nests (Nixon 1980; Naumann 1991; Masner 1993).
Monomachidae	
Monomachus	Parasitoids of Stratiomyidae (Diptera) eggs (Naumann 1991)
Proctotrupidae	Mostly parasitoids of Coleopteran larvae in soil, litter, and rotten wood, but some species have also been recorded from Mycetophilidae (Diptera) (Masner 1993).
VESPOIDEA	
Mutillidae	Parasitoids in nests of Sphecidae, Vespidae (wasps) and, Apoidea (bees) (Naumann 1991)
Sphaeropthalminae	
Pompilidae	Predators of Araneae (spiders) (Harris 1987; Day 1988)
Tiphidae	Solitary parasitoids of soil-dwelling Coleoptera (beetle) larvae (Naumann 1991; Masner 1993).

Appendix D

General biology of wasp host and prey taxa

Table A-4 General biology and niches of wasp hosts and prey used to allocate functional groups. Emphasis is placed on the biology of the life stage(s) attacked, eg. larval biology for holometabolous hosts.

Host taxa	General biology	Tropic level
ARANEAE	**Spiders** (Harvey & Yen 1989) Carnivorous; may be found in most terrestrial habitats (and some semi-aquatic) in leaf litter, under bark, rock, logs, in burrows in the soil, or in aerial webs. Females lay eggs into a silk egg sac that is often guarded.	Predator
BLATTODEA	**Cockroaches** (Roth 1991) Mostly detritus-feeding ground-dwelling under bark, logs or stones, and some arboreal phytophagous species. Oothecae are dropped on the ground, glued to bark, or to the substrate and covered.	Detritivore/ herbivore
COLEOPTERA	**Beetles** (Lawrence & Britton 1991)	
Anobiidae	Deathwatch beetles. Larvae mostly bore into the wood or bark of dead trees, but some feed on fungal fruiting bodies, seeds and dry animal and plant matter.	Detritvore/ fungivore
Anthribidae	Fungus weevils. Larvae of most species feed in dead wood, but some feed on the fruiting bodies of fungi, and others on seeds.	Detritvore/ fungivore/ herbivore
Bostrichidae	Powder-post beetles. Larvae usually feed in the sapwood of dead or dying trees, or other types of dry plant material containing starches and sugars.	Detritvore
Buprestidae	Jewel beetles. Larvae usually feed in the wood or root systems of trees or shrubs with some feeding in herbaceous stems, galls, or leaf mines.	Herbivore
Carabidae	Ground beetles. Predacious larvae that live in wood and soil.	Predator
Cerambycidae	Longicorn beetles. Larvae usually feed internally on the wood of trees and shrubs, while some feed on herbs, roots, seeds and cones, or are gall formers.	Herbivore
Chrysomelidae	Leaf beetles. Adults feed externally and larvae externally or internally on a wide range of higher plants tissues (roots, foliage, herbaceous stems, growing tips, leaves, flowers, pollen, fruit, and seeds).	Herbivore
Ciidae	Tree-fungus beetles. Most larvae feed on fungi, but some feed in rotten vines and branches.	Fungivore/ detritvore
Coccinellidae	Ladybird beetles. Adults and larvae are mostly predacious on aphids, mealybugs, scales or other small insects and mites.	Predator
Cucujidae	Cucujid beetles. Adults and larvae live under bark or in tunnels of wood boring-insects.	Predator
Curculionidae	Weevils. Larvae can be soil-dwelling root-feeders, wood-borers, feed in galls, under bark, in seed pods, and leaf mines, and occasionally externally on foliage.	Herbivore
Dermestidae	Skin beetles. Larvae are generally scavengers on dead, dry animal material.	Detritivore
Nitidulidae	Sap beetles. May be found in leaf litter, rotten fruits, flowers, seeds, fungi, bark or tree wounds or preying on scale insects.	Fungivore/ detritvore/ predator
Tenebrionidae	Darkling beetles. Scavengers on dead plant and fungal material. Larvae live under bark, in rotten wood, in leaf litter, or the soil.	Detritivore
DIPTERA	**Flies** (Colless & McAlpine 1991)	
Agromyzidae	Leafmining flies. Larvae are leaf- or stem-miners and gall makers.	Herbivore

Host taxa	General biology	Tropic level
Anthomyiidae	Root flies. Some have larvae that feed on plants especially roots, others feed on dung, or are aquatic. Several are important pests of vegetables like the cabbage maggot and onion maggot.	Herbivore
Calliphoridae	Blow flies, bluebottles. Larvae feed in carrion or are parasitoids of earthworms, land snails, or are associated with ant or termite nests.	Detritivore/ parasitoid
Cecidomyiidae	Gall midges. Larvae are mostly found in galls in living plants, either feeding on the plant or fungi inside the gall. Others live in decomposing organic matter.	Herbivore/ fungivore/ detritivore
Chamaemyiidae	Aphid flies. Larvae are predators of coccids and psyllids.	Predator
Drosophilidae	Vinegar flies. Larvae are mostly fungivores, but can also feed on decaying fruit, flowers, dung etc.	Fungivore/ detritivore
Muscidae	House, stable flies. Larvae occur in manure, carrion, decaying organic matter, boring in plant stems, fresh & salt water, and as parasites feeding on the blood of bird nestlings	Detritivore/ herbivore/ parasite
Mycetophilidae	Fungus gnats. Larvae are mostly associated with fungi.	Fungivore
Phoridae	Scuttle flies. Larvae feed in carrion and other decomposing organic matter and fungi.	Detritivore
Sarcophagidae	Flesh flies. Larvae feed in carrion and other decomposing organic matter.	Detritivore
Sciaridae	Fungus gnats. Larvae occur in rotting vegetable matter of highly organic soils.	Detritivore
Stratiomyidae	Soldierflies. Larvae mostly occur in damp soil or rotting vegetation.	Detritivore
Syrphidae	Hover flies. Larvae mostly found in rotting vegetation, fruit or liquid, or predators of aphids.	Detritivore/ predator
Tachinidae	Tachinid flies. Parasitoids of arthropods, mostly insects (principally Lepidoptera, Coleoptera, Hemiptera, and Orthoptera)	Parasitoid
Tephritidae	Fruit flies. Larvae occur in fruit, seeds, and flower-heads.	Herbivore
Cyclorrhaphous Diptera	Phytophagous, parasitic or predacious larvae, typically occurring in decaying organic matter.	Detritivore/ herbivore/ parasite
HEMIPTERA (Homoptera) Sternorrhyncha	**Bugs** (Carver *et al.*, 1991)	
Aleyrodidae	Whiteflies. Hosts are almost exclusively angiosperms, mostly woody dicots. Nymphs under scales.	Herbivore
Aphididae	Aphids. Free-living plant feeders on the foliage of various plants, with some species feeding on the roots.	Herbivore
Asterolecaniidae	Pit scales. Feed on plants forming scales, sometimes gall-formers.	Herbivore
Coccidae	Soft scales. Plant feeders on a wide range of plants under scales.	Herbivore
Diaspididae	Armoured scales. Plant feeders on a wide range of plants, mostly under scales, but some in galls.	Herbivore
Eriococcidae	Gall-formers on trees and shrubs.	Herbivore
Keriidae	Lac insects. Plant feeders on a range of trees and shrubs under scales.	Herbivore
Pseudococcidae	Mealy bugs. Plant feeders on a wide range of plants, above and below ground covered in wax.	Herbivore
Psyllidae	Lerps. Feed on a range of trees and shrubs under lerps, in galls or free-living.	Herbivore
Auchenorrhyncha		
Cicadellidae	Leafhoppers. Free-living plant feeders on a wide range of plants.	Herbivore
Delphacidae	Planthoppers. Mostly feed on monocots.	Herbivore
Dictyopharidae	Planthoppers. Phloem-feeders on angiosperms.	Herbivore
Flatidae	Planthoppers. Phloem-feeders on angiosperms (including *Eucalyptus* sp).	Herbivore
Fulgoridae	Planthoppers. Feed on woody shrubs and trees.	Herbivore
Membracidae	Treehoppers. Free-living plant feeders on a range of trees and shrubs.	Herbivore
Nogodinidae	Planthoppers. Phloem-feeders on angiosperms (including *Eucalyptus* sp).	Herbivore

Host taxa	General biology	Tropic level
Heteroptera		
Alydidae	Broad-headed bugs. Nymphs and adults feed on various plants and seed pods. Eggs are usually glued in groups on leaves.	Herbivore
Coreidae	Leaf-footed bugs. Nymphs and adults feed on the foliage of various plants. Eggs are usually glued in groups on leaves.	Herbivore
Largidae	Largid bugs. Nymphs and adults feed on various plants. Eggs may be laid embedded in plant tissue or between plant parts, or in the soil or litter.	Herbivore
Lygaeidae	Seed bugs. Most species feed on seeds, while a few are sap-sucking, predacious or feed on vertebrate blood. Eggs may be laid embeded in plant tissue or between plant parts, or in the soil or litter.	Herbivore/ predator
Miridae	Plant bugs. Most are phytophagous on a range of plants, but some prey on small, soft-bodied insects or insect eggs.	Herbivore/ predator
Nabidae	Damsel bugs. Predacious; eggs are oviposited into grass stems.	Predator
Pentatomidae	Shield bugs. Nymphs and adults feed on various plants or are predacious. Eggs are usually glued in groups on leaves.	Herbivore/ predator
Reduviidae	Assassin bugs. Nymphs and adults are predacious. Eggs usually laid embeded in plant tissue or between plant parts.	Predator
Tingidae	Lace bugs. Phytophagous; found on a range of trees and shrubs, and also found from moss and leaf litter and in ant nests. Eggs laid in masses.	Herbivore
HYMENOPTERA	**Wasps, bees, and ants** (Naumann 1991)	
Symphyta	Sawflies. Larvae are almost exclusively phytophagous, either as exposed feeders on foliage, or as concealed feeders in leaf mines or tunnels in stems or wood.	Herbivore
Formicidae	Ants. Eusocial with perennial colonies in the soil or rotting wood, some in trees or other plants.	Predators/ herbivores/ detrivores
	For other Apocrita host biology see Appendix C	
LEPIDOPTERA	**Moths and butterflies** (Nielsen & Common 1991)	
Agonoxenidae	Palm moths. Larvae live under the leaves of foodplant in thin silken web.	Herbivore
Anthelidae	Larvae feed on various plants including trees and grasses, some pupate in the soil.	Herbivore
Arctiidae	Tiger moths. Larvae are external feeders feeders on herbaceous plants, or on lichens or fallen leaves and flowers.	Herbivore
Batrachedridae	Larvae feed on plants, seeds, and scale insects.	Herbivore/ predator
Blastobasidae	Scavenger moths. Larvae feed in fallen woody fruits, seeds, reproductive parts of cycads and dry organic matter, rarely on aphids and scale insects (mostly tropical species).	Herbivore/ predator
Bombycidae	Feed on trees; pupate in a dense silk coccon.	Herbivore
Choreutidae	Sun moths. Larvae live under the leaves of various food plants in a thin silken web.	Herbivore
Coleophoridae	Case-bearer moths. Larvae a leaf-miner in 1st instar then a case-bearer feeding externally on leaves or flowers, or mining in leaves.	Herbivore
Cosmopterigidae	Cosmet moths. Larvae are leaf-miners, borers in stems, seeds or fungi, tying leaves, forming galls, or predatory on scale insects.	Herbivore/ predator
Galleriidae	Larvae usually feed consealed, for example in grass-tree flower spikes, under loose bark or in the tunnels of wood-boring lepidopteran larvae or in ant nests.	Herbivore
Gelechiidae	Twirler moths. Larvae feed in joined leaves, seeds, leaf mines or stems; pupate in a silken cocoon in a larval shelter or in leaf litter.	Herbivore
Geometridae	Looper moths. Larvae often twig- or leaf-like, mostly feeding exposed, rarely in a loose shelter; usually pupate in a cocoon in litter or soil.	Herbivore
Gracillariidae	Leaf-miner moths. Larvae are leaf- or gall-mining and pupate inside mines or leaf rolls.	Herbivore
Heliozelidae	Shield-bearer moths. Larvae are leaf- or petiole-miners in trees and shrubs, finally cutting out flat, oval cases from the mine	Herbivore

Host taxa	General biology	Tropic level
	which either drop to the ground or attach to the host plant prior to pupation.	
Hesperiidae	Skippers. Larvae occur in a silk-lined shelter between joined leaves or in a rolled leaf. Feed on a range of plants from trees to grasses.	Herbivore
Hyblaeidae	Teak moths. Larvae occur in shelter between joined leaves; pupates in a silken cocoon among foliage, fallen leaves, or in soil.	Herbivore
Incurvariidae	Leaf-cutter moths. Larvae feed on trees and shrubs of Proteacea and Myrtaceae and are either leaf-miners until mature, when they cut a flat case from the mine for pupation, or mine at first and then cut out cases which they use as shelter when feeding. Pupation may occur in the case on the food plant or on the ground.	Herbivore
Lasiocampidae	Lappet moths. Larvae lie along twigs on twigs on food plants; parchment-like cocoons are often spun amongst foligae of food plant.	Herbivore
Limacodidae	Cup moths. Larvae feed exposed on various trees and shrubs (eg. *Eucalyptus*); pupate in a cup shaped cocoon attached to twigs or bark.	Herbivore
Lycaenidae	Gossamer-winged butterflies. Larvae mostly ant attended; feed on a variety of plants, some feeding exposed during the day, other noctural species hiding during the day under bark or in holes or crevices or in attendant ant nests.	Herbivore
Lymantriidae	Tussock moths. Larvae feed on a range of plants, often sheltering under bark or in crevices.	Herbivore
Lyonetiidae	Lyonet moths. Larvae are leaf-miners, often pupate exposed on the outside of the leaf.	Herbivore
Noctuidae	Hawk moths. Larvae mostly phytophagous on a very variety of plants, sometimes stem boring or predacious on coccoids. Pupate in a cell in the soil or in a silken coccon.	Herbivore/ predator
Notodontidae	Prominent moths. Larvae feed exposed, pupate in cell in soil or in tough coccon.	Herbivore
Nymphalidae	Brush-footed butterflies. Larvae feed exposed on a variety of plants; pupae suspended in foliage or less often in litter below.	Herbivore
Oecophoridae	Concealer moths. Larvae tunnel in wood, stems branches, flowers or galls, among leaf litter, or in tunnels in soil, some form portable cases, and a few are leaf miners.	Herbivore
Papilionidae	Swallowtail butterflies. Larvae feed exposed on a variety of plants; pupae exposed attached to food plant	Herbivore
Pieridae	Whites & sulphurs. Larvae feed exposed on a variety of plants; pupae exposed attached to food plant	Herbivore
Plutellidae	Diamondback moths. Larvae shelter in a loose web of leaves and pupate in an open mesh cocoon.	Herbivore
Psychidae	Bagworm moths. Larvae are case-bearing and feed on a wide range of flowering plants but also gymnosperms, lichens and mosses.	Herbivore
Pyralidae	Snout moths. Larvae occur in shelters of webbed leaves or shoots, in tunnels in shoots, stems, seed heads, fruits or galls, or in silken galleries among mosses, herbaceous plants or fresh water aqautic plants, or in stored products, or in Hymenoptera nests, or rarely predacious on coccoids.	Herbivore
Saturniidae	Emperor moths. Larvae feed exposed on a variety of plants; pupae exposed attached to food plant	Herbivore
Sphingidae	Hawk moths. Larvae feed exposed during the day; pupate in cell in soil or cocoon in leaf litter.	Herbivore
Thaumetopoeidae	Processionary caterpillars. Larvae are exposed nocturnal feeders, often gregarious living in silk bags and display processionary behaviour; pupate in soil.	Herbivore
Tineidae	Fungus moths. Larvae usually feed on dried organic matter, or on fungi, some are case-bearers or leaf-tiers; pupate in larval shelter of cocoon.	Herbivore
Tortricidae	Leaf-roller moths. Larvae usually leaf- or shoot-joiners, rarely leaf-mining (usually in early instars), or tunnelling in flower spikes, fruits, stems, or galls. Some feed on dead leaves in	Herbivore/ detritivore

Host taxa	General biology	Tropic level
	leaf-litter.	
Yponomeutidae	Ermine moths. Larvae live singly on slight webbing on leaves or gregariously in extensive webs; pupate in larval web or nearby.	Herbivore
Zygaenidae	Burnet moths, foresters. Larvae live in a web beneath the leaves of the food plant or in a silk shelter.	Herbivore
MANTODEA	**Praying mantids** (Balderson 1991) Carnivorous on smaller arthropods; found in most terrestrial habitats from trees and shrubs to grasses or on the ground. Eggs are laid in an ootheca that is attached to various substrates such as a twig or grass stem, in the ground, or under a rock or wood on the ground.	Predator
MECOPTERA	**Scorpion flies** (Byers 1991) Eggs are laid on or in moist soil or leaf-litter; larvae feed on dead insects; adults often found in low vegetation, feed on small arthropods and nectar.	Detritivore/ predator
ORTHOPTERA	**Grasshoppers & crickets** (Rentz 1991)	
Acrididae	Grasshoppers. Phytophagous, free living, mostly on the ground, eggs mostly laid in groups in the soil.	Herbivore
Gryllidae	Crickets. Live either in foliage or on the ground among leaf-litter and plants or in the ground. Eggs laid in groups in the soil.	Herbivore/ detritivore
NEUROPTERA	**Lacewings** (New 1991)	
Chrysopida	Green lacewings. Most are arboreal; eggs on stalks laid on foliage, branches etc. Larvae are active, generalist predators which sometimes cover themselves in debris. The pupal cocoon may also be covered in debris. Adults are mostly predacious, but some feed on honeydew.	Predator
Coniopterygidae	Dusty lacewings. Mainly arboreal. Eggs are laid singly on foliage or bark; pupate in flat silk cocoons spun on vegetation.	Predator
Hemerobiidae	Brown lacewings. Mostly found in trees and shrubs, but some are found on lower vegetation; eggs are laid on vegetation. Adults and larvae are active, generalist predators. Pupation occurs in a loosely woven silk cocoon on vegetation or under bark.	Predator
PSCOPTERA	**Booklice** (Smithers 1991) Adults and nymphs occur on foliage or branches of trees and shrubs, on or under bark, in leaf litter, and under or on rocks and feed on unicellular algae, lichens, fungal hyphae, spores, and insect and plant fragments.	Detritivore/ herbivore/ fungivore

Appendix E

Parasitoid functional groups

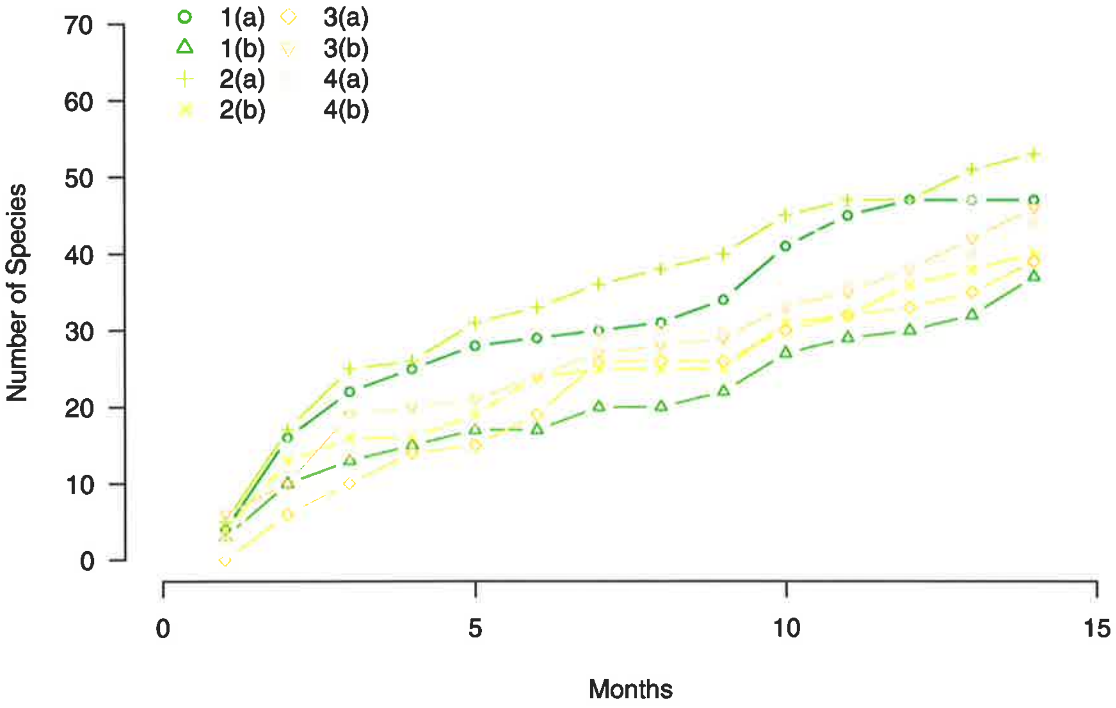
Table A-5 Functional groups allocated to parasitic wasp taxa recorded from Mt Billy CP. Functional groups are based on niche/habitat preference from available host and general biology records (Appendices C and D).

	Functional group	Taxa
1	Parasitoid (or hyperparasitoid) of plant-sucking insects (herbivores) or insects associated with plant-sucking insects (predators)	Aphelinidae (*Aphelinus, Coccophagus, Encarsia*), Encyrtidae (Anagyrini, *Homalotylus*, *Metaphycus*, *Discodes*, *Bothriophryne*, *Tachardiaephagus*, *Neanagyrus*, *Psyllaephagus*, *Tetracnemoidea*), Eulophidae (*Tamarixia*), Mymaridae (*Gonatocerus, Stethynium, Mymar*), Pteromalidae (Eunotinae), Signiphoridae (*Chartocerus*), Charipidae (Charipinae), Dryinidae, Braconidae (Aphidiinae), Ichneumonidae (Diplazontinae), Platygastridae (*Amitus*, *Helava*)
2	Parasitoid (or hyperparasitoid) of insects feeding inside plant tissue, eg. leaf or stem mines, fruit, seeds (herbivores)	Eulophidae (*Diaulomorpha, Diglyphomorphomyia*, *Elachertus*, *Hemiptarsenus*, *Neotrichoporoides*), Pteromalidae (*Notanisus*), Braconidae (Miracine), Braconidae (Opiinae)
3	Parasitoid (or hyperparasitoid) of free-living plant-associated insects (herbivores or predators)	Ceraphronidae (*Aphanogmus*), Megaspilidae (*Dendrocerus*), Aphelinidae (*Ablerus*, *Centrodora*), Encyrtidae (*Copidosoma*, *Paralitomastix*), Eulophidae (*Asecodes*, *Hispinocharis*, *Elasmus*, *Euplectrus, Tetrastichus*), Eupelmidae (*Anastatus*) Eurytomidae (*Eurytoma*), Mymaridae (*Anaphes*, *Polynema*), Pteromalidae (*Callitula, Isoplatoides, Pachyneuron, Pteromalus*), Braconidae (Euphorinae, Rogadinae), Ichneumonidae (Anomaloninae, Banchinae, Campopleginae, Cryptinae, Metopiinae), Scelionidae (*Dyscritobaeus*, *Gryon*, *Telenomus*, *Trissolcus*), Figitidae (Anacharitinae)
4	Plant gall-associated (as parasitoids or phytophagous inquelines or gall-formers)	Encyrtidae (*Paraenasomyia*), Eulophidae (*Ophelimus*, *Omphale, Aprostocetus*, *Ceratoneura*, *Epichrysocharis*, *Quadrastichodella*, *Sigmophora*), Eurytomidae (*Bruchophagus*), Pteromalidae (*Coelocyboides, Ormyromorpha, Ditropinotella*, Ormocerinae, *Gastrancistrus*), Torymidae (*Megastigmus*, *Torymoides*), Platygastridae (Platygastrinae), Cynpidae
5	Parasitoid of wood-boring insects (detritivores, predators)	Eupelmidae (*Brasema*, *Eusandalum*), Eurytomidae, Pteromalidae (*Macromesus*), Braconidae (*Callibracon*, Doryctinae)
6	Parasitoid of detritvores and other soil- and litter-associated arthropods (detritivores, predators)	Encyrtidae (*Tachinaephagus*), Eulophidae (*Aceratoneuromyia*) Braconidae (Alysiini), Tiphidae, Pteromalidae (Diparinae, *Spalangia*), Bethylidae (Epyrinae, Pristocerinae), Evaniidae, Ichneumonidae (Orthocentrinae), Ichneumonidae (Orthocentrinae), Megaspilidae (*Lagynodes, Megaspilus*), Platygastridae (*Platygastoides*), Scelionidae (*Baeus*, *Ceratobaeus*, *Idris, Mirobaeoides, Odontacolus Anteromorpha*, *Probaryconus*, *Duta*, *Teleas*, *Trimorus*), Diapriidae, Proctotrupidae, Monomachidae (*Monomachus*)
7	Parasitoid of solitary, and more rarely social, Vespoidea and Apidae in nests	Mutillidae, Eulophidae (*Melittobia*), Gasterupiidae, Ichneumonidae (*Labium*)
8	Parasitoid (or hyperparasitoid) of arthropods found in a wide spectrum of plant-associated niches, but also some litter-associated arthropods (herbivores, predators or detritivores)	Ceraphronidae (*Ceraphron*), Megaspilidae (*Conostigmus*), Chalcididae (*Brachymeria*, *Antrocephalus*, *Proconura*), Eucoilidae, Eulophidae (*Euderus*), Perilampidae (*Chrysolampus*), Trichogrammatidae, Bethylidae (Bethylinae), Braconidae (Agathidinae, Braconinae, Cheloninae, Meteorinae, Microgastrinae), Ichneumonidae (Ichneumoninae, *Mesochorus*, Pimplinae, Tryphoninae), Pompilidae

Appendix F

Species accumulation curves

(a) Bridal creeper



(b) Native

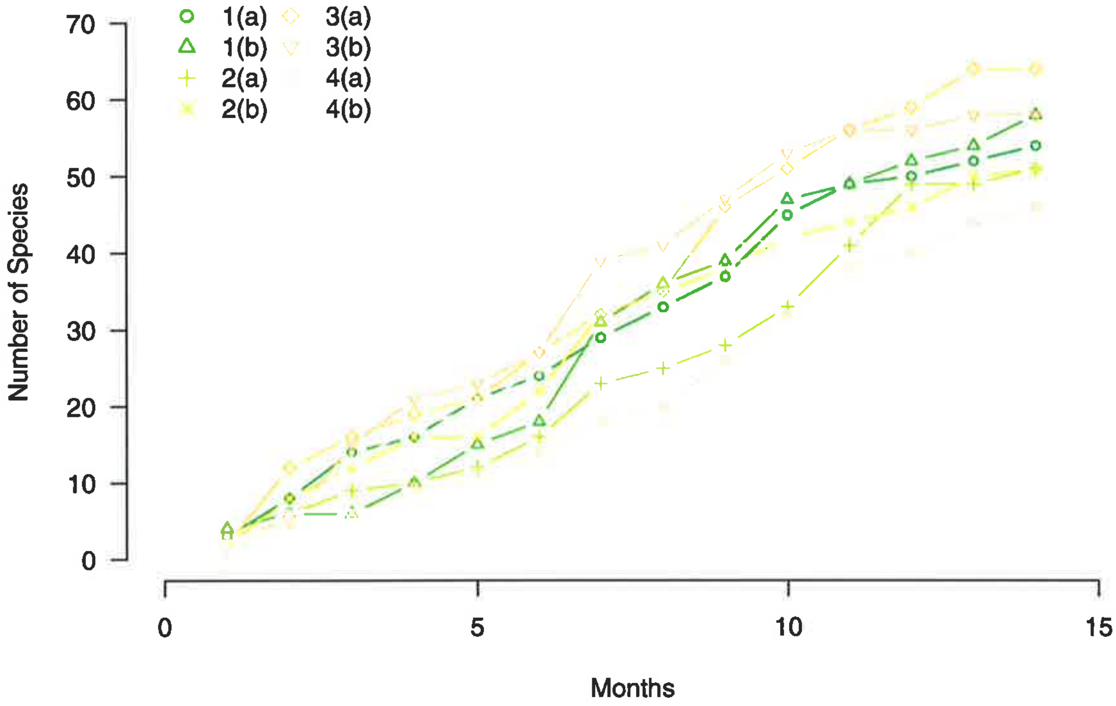
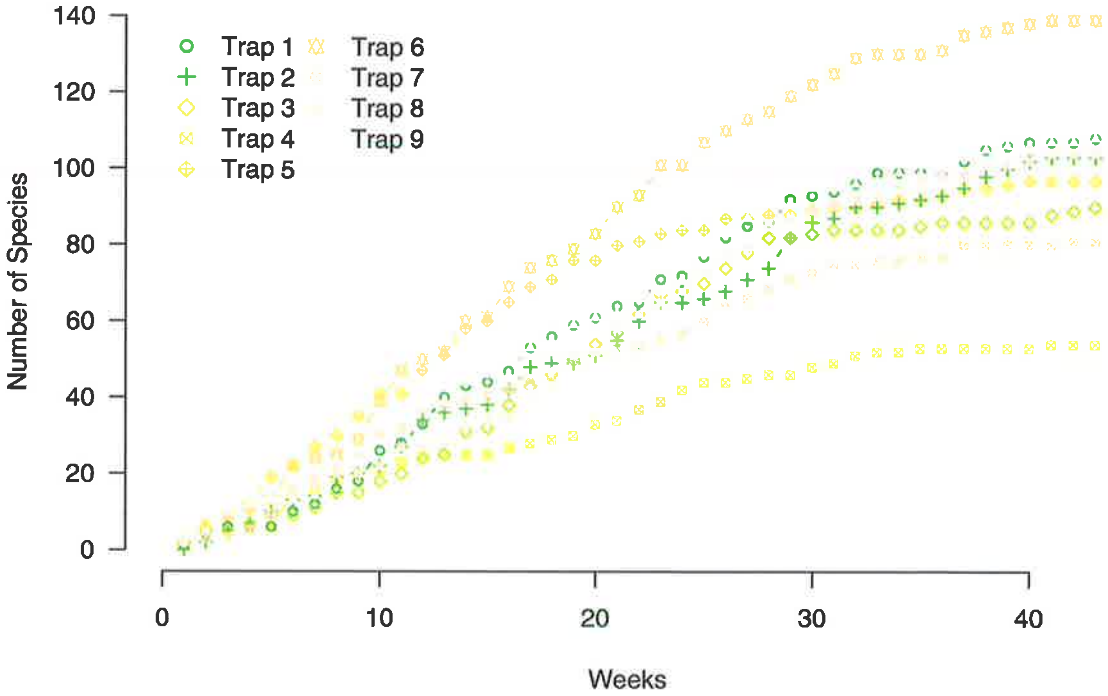
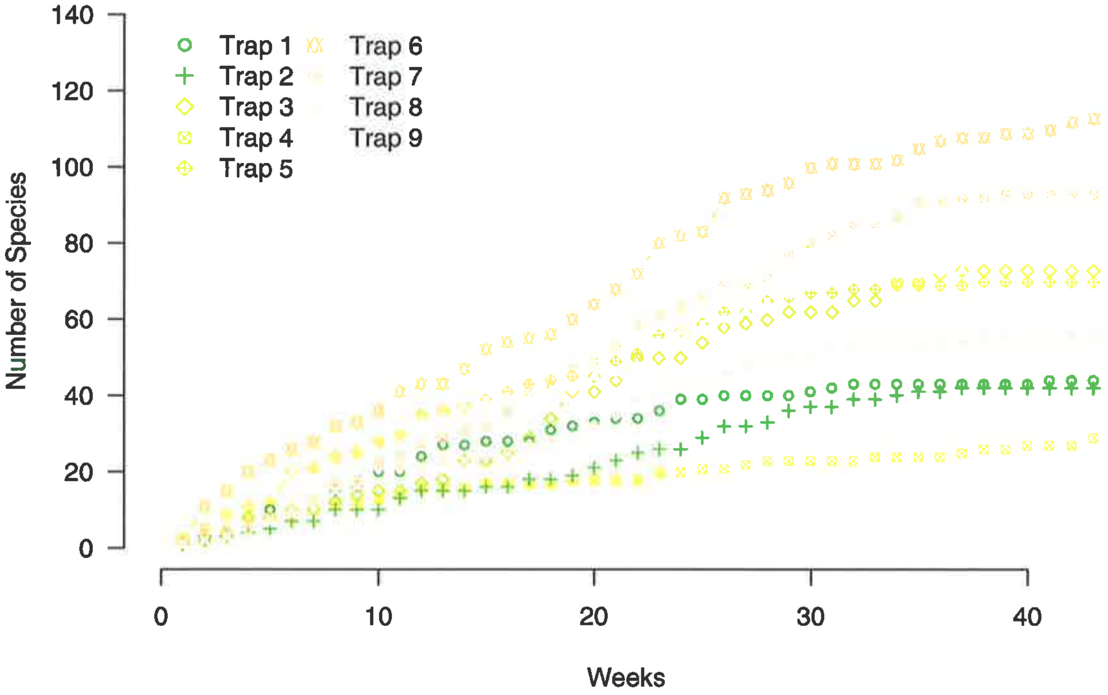


Figure A-1 Wasp species accumulation curves for **(a)** bridal creeper and **(b)** native sweep-net transects over the sampling period (monthly samples from 20 April 2001 to 26 April 2002) at Mt Billy CP.



(a) Bridal creeper



(b) Native

Figure A-2 Wasp species accumulation curves for **(a)** bridal creeper and **(b)** native emergence traps over the sampling period (weekly samples from 21 September 2001 to 12 July 2002) at Mt Billy CP.