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The ecological transformation of Aotearoa/New Zealand

Impacts of exotic invertebrates on New Zealand's indigenous species and ecosystems

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Abstract: Biological invasions have significantly affected New Zealand's native species and ecosystems. Most prominent are the effects of exotic mammals and plants, whereas few invertebrate invasions are known to have major effects on native ecosystems. Exceptions are the well-known cases of *Vespula* wasps in *Nothofagus* forest ecosystems and *Eriococcus* scale insects in *Leptospermum* shrublands. This limited impact is surprising because over 2000 exotic invertebrates have become established in New Zealand, among them many pests of exotic crop plants. The low impact of exotic invertebrates that invaded forests and other native ecosystems in New Zealand is in contrast to the situation in other parts of the world where many invertebrates have become important pests. We provide an overview of known invasions by exotic invertebrates in New Zealand, and explore in more detail several examples of invasive species, including herbivores, predators, parasitoids, decomposers and other groups in forests, grasslands, and other terrestrial ecosystems. Several hypotheses have been proposed to explain the comparative scarcity of such invasions that affect New Zealand's indigenous ecosystems. There is a common view that New Zealand's native species and ecosystems are inherently resistant to exotic invertebrate invaders, and there is some evidence to support this view. As a result of the high level of endemism in New Zealand's flora, many native plants are phylogenetically distant from the host plants of many plant-feeding invaders. This provides some protection. Less host-specific plant-feeding insects, generalist predators, parasitoids and decomposers are less affected by such constraints, and these groups are perhaps more represented among the successful invaders of natural ecosystems. However, the shortage of studies on invader impacts on native species and ecosystems, compared with studies on economically important crops and production ecosystems, means that an unbiased comparison is not possible at this time. Furthermore, many invaders go through extended lag phases where their impacts are not easily noticed until they become more abundant and create more damage. Likewise, indirect effects of invaders, through more complex interactions in food webs, as well as impacts on ecosystem functions such as decomposition and pollination, are more subtle and difficult to detect without careful study. There is clearly a need for more research to determine more accurately which exotic invertebrates are already present, what their direct and indirect impacts are, and what generalisations and predictions about threats to native species and ecosystems are possible.

Keywords: biological invasions; herbivores; hypotheses; invasibility; parasitoids; predators; resistance

Introduction

Invasions by exotic species have played a major role in the decline of New Zealand's biodiversity, along with the loss of natural habitat. Most attention has focused on exotic vertebrates and plants, so here we examine the impact of exotic invertebrates. There has been some confusion in the terminology used to describe biological invasions (Colautti & MacIsaac 2004; Falk-Petersen et al. 2006); 'invasive' has been used either for species (native and exotic) with expanding ranges, or as a synonym for exotic (Colautti & MacIsaac 2004). Here we refer to species as invasive only if they are exotic *and* expanding their range, and we use the term 'exotic' as a shorter synonym for non-indigenous, i.e. a species outside its native range.

Collectively, the impact of intentionally and unintentionally

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introduced animals and plants has led to range restriction, population decline, or extinction of numerous terrestrial species, especially birds, invertebrates, and plants (e.g. Atkinson & Cameron 1993; DOC/MfE 2000; Allen & Lee 2006; Gibbs 2010; Innes et al. 2010; Tennyson 2010). Some of these invasions have also disrupted various aspects of the functioning of natural ecosystems (Fukami et al. 2006; Kelly et al. 2010). Such biological invasions are now recognised world-wide as some of the most significant threats to the ecology of natural and production ecosystems (Liebhold et al. 1995; Mack et al. 2000; Clavero & García-Berthou 2005; Traveset & Richardson 2006), with the potential to cause huge economic and environmental impacts. In New Zealand, the deleterious effects of exotic mammals, such as possums, rats, deer and mustelids, are well documented (e.g. Atkinson & Cameron 1993; Allen & Lee 2006; Forsyth et al. 2010), but over 2000 exotic insects and other invertebrate species have also become established (MfE 1997; Emberson 2000). Among these are many important 'pests' (Scott 1984). The potential seriousness of unwanted insect introductions was recognised soon after the European colonisation of New Zealand had begun. Fereday (1872) suggested that the damage caused by the currant clearwing, *Synanthedon tipuliformis* (Lepidoptera: Sesiidae), may prevent the cultivation of redcurrant in New Zealand, and that this "shows how careful we ought to be when introducing anything useful that we bring not with it a grievous pest". The actual and potential impact of exotic invertebrate 'pests' can be gauged by the quantity of insecticides used in New Zealand's agriculture and horticulture. For example, in 1998, this amounted to c. 268 tonnes of insecticide active ingredients (Holland & Rahman 1999). But despite our increased awareness and efforts to prevent biological invasions (Anonymous 2003), new species continue to arrive at a steady rate (Charles 1998; Brockerhoff & Bain 2000; Ridley et al. 2000; Withers 2001; Kriticos et al. 2005; Kay 2005; Ward et al. 2006; Kelly & Sullivan 2010).

The impact of exotic invertebrates on New Zealand's natural ecosystems appears to be relatively minor (i.e. not causing a decline in host or prey populations and not being readily noticeable, e.g. through conspicuous defoliation or mortality), but has also received little attention compared with the impacts of exotic mammals and plants, with the exception of a few high-profile invaders (see below). This special issue's predecessor (NZ. J. Ecol. 12s, 1989) did not cover invertebrates and their role in past changes to New Zealand's fauna and flora. However, some 10 years earlier, Lowe (1973) stated "Many common pest insects have arrived here with man's assistance […] yet there is only one instance of an exotic insect doing widespread and continued damage to native plants" (referring to the scale insect *Eriococcus orariensis* which causes 'manuka blight'). He also mentioned the exotic wasp *Vespula germanica*, as a "nuisance insect." A review by Atkinson and Cameron (1993) similarly indicates that the "effects [of exotic invertebrates] on native biota and communities are less evident than those on crops or orchards", but they cite several examples of exotic predators (*Vespula* spp., *Steatoda capensis*) and parasitoids (*Trigonospila brevifacies*) that affect indigenous species. By the 1990s, the ecological impact of *Vespula* wasps in *Nothofagus* forests was much better understood, both in terms of their removal of honeydew, an important food source for birds and invertebrates (Moller et al. 1991), and as direct predators of insects (Harris 1991; Beggs 2001).

Although our incomplete knowledge of the invertebrate fauna of New Zealand must be taken into account, and especially the occasional difficulty in determining whether a species is in fact indigenous or exotic, the prevailing view remains that relatively few exotic invertebrates appear to have invaded our natural ecosystems (Ridley et al. 2000). This is reinforced by the comparison with exotic insect 'pests' which cause significant damage to New Zealand's agriculture and horticulture (e.g. Scott 1984). Does this indicate, therefore, that New Zealand's natural ecosystems are 'resistant' to invasion by such insects and other invertebrates, particularly those feeding on plants?

This is in stark contrast to insect invasions in other parts of the world which clearly show that significant impacts on indigenous species and ecosystems are now very common (Vitousek et al. 1997; Simberloff 2005; Lockwood et al. 2007). For example, in North America numerous exotic forest insects, including gypsy moth (*Lymantria dispar*), emerald ash borer (*Agrilus planipennis*) and several weevils damage indigenous plants and alter forest ecosystems (Liebhold et al. 1995; Pinski et al. 2005; Poland & McCullough 2006). Similarly, in many countries several exotic ant species, including Argentine ant (*Linepithema humile*) and red imported fire ant (*Solenopsis invicta*) are known to invade natural habitats, reducing native ant diversity and disrupting ecosystem processes (Holway et al. 2002; Ness & Bronstein 2004; Rowles & O'Dowd 2007; Langkilde 2009). In the northern United Kingdom, the New Zealand flatworm *Arthurdendyus triangulates* (Turbellaria: Geoplanidae) has become an important predator of native lumbricid earthworms (Boag et al. 1997). In some locations, it has apparently led to serious decline and even local extinctions of earthworms, with flow-on effects on soil fertility.

Some ecosystems or habitats appear to be more prone to invasion than others, and there is a large body of literature on the factors that may explain this. Elton (1958) proposed that "the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones…" and that simple communities (such as agricultural systems) are "more vulnerable to invasions." This notion has gained support from several recent studies that found a negative relationship between diversity and biological invasions (e.g. Kennedy et al. 2002; Levine & D'Antonio 1999; Jactel & Brockerhoff 2007), although some studies concluded, conversely, that species-poor systems were more resistant to invasion than diverse ecosystems (Levine & D'Antonio 1999; Kay 2006). Disturbance is another factor widely recognised as an important factor in invasion of ecosystems (e.g. Hobbs & Huenneke 1992, Lockwood et al. 2007). The hypothesis that the higher biodiversity and comparative lack of disturbance in New Zealand's natural ecosystems, compared with modified ecosystems, would convey some level of protection from invertebrate invaders appears compelling. However, this seems to be inconsistent with observations on invasions by other taxa. It appears that broad generalisations may be inappropriate and that it is important to be aware of various context-specific issues. There is no published, comprehensive review of the comparative susceptibility to invertebrate invasions of New Zealand's natural ecosystems, except for the work by Ridley et al. (2000) on tree-feeding insects, the only published review to date.

In this paper we review the presence and impact of exotic invertebrates on native species and natural ecosystems in New Zealand, covering herbivores, predators, parasitoids, decomposers and other groups, in forests, grasslands and other terrestrial ecosystems. We also address whether our indigenous species and ecosystems are indeed less susceptible to invasion than crop species or modified ecosystems and, if so, why such differences in 'invasibility' exist. We also note knowledge gaps in New Zealand regarding the prevention or reduction of future invasions into natural ecosystems and some research suggestions.

Overview of exotic invertebrates in New Zealand

There are far too many exotic invertebrates present in New Zealand to provide an exhaustive list of such species in this paper. A representative list of some of the better known exotic species covering the major groups of invertebrates present in New Zealand is presented in Table 1. In the following sections these and other exotic species are described in more detail, grouped by trophic levels of food webs and, where practical, by habitat (i.e., forest vs. open habitats). This is followed by sections exploring some of the ecological considerations that are relevant to invertebrate invasions in New Zealand and elsewhere. Insects are perhaps over-represented, compared with other invertebrates, in this paper but this is probably a reflection of the greater importance of insect impacts and a correspondingly larger research effort.

Herbivores of forests and shrublands

Between 1950 and 1997, 70 exotic insect species that affect trees or shrubs were newly recorded in New Zealand (Ridley et al. 2000), and several more have become established in the last 10 years. Together with pre-1950 records, the total number of exotic insects that affect woody plants is about 200 (Ridley et al. 2000). These include 51 beetles (Brockerhoff & Bain 2000), approximately 62 moths (E.G. Brockerhoff et al. unpubl.; Hoare 2001) (excluding a few species that were introduced intentionally as biological control agents), a number of Hemiptera and several species from other orders. Although there are relatively few publications on exotic plant-feeding insects affecting native plants and ecosystems, compared with the literature on exotic crop plants, there is in fact a substantial amount of information in Spiller and Wise's (1982) catalogue and in several databases. For example, there are almost 3300 records of insect attack on native plants in Scion's Forest Health Database, but only 212 of these concern exotic insects (and most were associated with minor damage) (John Bain pers. comm.). Other plant-feeding exotic invertebrates include snails (gastropods) and nematodes, but, to our knowledge, no review of those specifically associated with woody plants has been undertaken.

By far the majority of these exotic plant-feeding invertebrates are typically found on exotic plants, and surprisingly few of these have been recorded as feeding on indigenous plants. Among the 51 beetle species, nine have been found as borers in dead wood of indigenous (and exotic) plants (Brockerhoff & Bain 2000; Brockerhoff et al. 2003). Because these beetles do not attack live plants, their impact on indigenous plants is negligible. For example, the European house borer (*Anobium punctatum*), attacks wood of indigenous podocarp trees but only dead wood, particularly dry timber (Table 1). Furthermore, most of the species were recorded from native plants occurring in modified habitats, whereas infestations in less disturbed indigenous ecosystems appear to be relatively rare (Brockerhoff & Bain 2000), so these species are unlikely to have an impact on native species through competition for dead wood resources. The South American weevil *Asynonychus cervinus* (Table 1) is a polyphagous root feeder which has been recorded from live plants, from at least two native woody plants, *Corynocarpus laevigatus* and *Entelea arborescens*, but it is not known to cause any significant damage (Brockerhoff & Bain 2000). However, indirect impacts through fungal pathogens that could potentially be associated with such beetles have rarely been examined in much detail in New Zealand. For example, the European elm bark beetle (*Scolytus multistriatus*) is an important vector of the pathogen *Ophiostoma novo-ulmi* which causes Dutch elm disease in North America, Europe and New Zealand (Gadgil et al. 2000). There was a concern the pathogen could hybridise with a closely related endemic pathogen that is associated with *Nothofagus* spp., *Sporothrix nothofagi*, and that this could lead to a more virulent strain that could be spread by a native ambrosia beetle, *Platypus apicalis*, which readily attacks dead elms and was found to carry spores of *O. novo-ulmi*. However, mating experiments have shown that *O. novo-ulmi* and *S. nothofagi* did not hybridise in any of the crosses tested, suggesting that the risk of this scenario eventuating is low (Gadgil et al. 2000).

Most of the exotic Lepidoptera are specialists of exotic plants, but 14 species are polyphagous (across two or more plant families) (Hoare 2001), and some of these represent a threat to indigenous plants. For example, the light brown apple moth (*Epiphyas postvittana*) is extremely polyphagous – in New Zealand alone over 250 host plants are known – and it can be found feeding on indigenous plants such as *Pittosporum* spp., *Kunzea ericoides*, *Weinmannia racemosa* and *Metrosideros excelsa* (Suckling & Brockerhoff 2010; Brockerhoff et al. 2009). However, these attacks are not known to have any major impact. Other polyphagous defoliators that may pose a threat to native woody plants and natural ecosystems are in the family Lymantriidae, such as the painted apple moth (*Teia anartoides*) (Table 2) (Hoare 2001). Painted apple moth established in New Zealand in 1999 and fed on a wide range of species, including native *Corynocarpus laevigatus* (karaka) and *Avicennia marina* (grey mangrove); however, the moth was declared eradicated in 2006 (Stephens et al. 2007). The oak leafminer (*Phyllonorycter messaniella*) occasionally mines the leaves of the indigenous *Pittosporum crassifolium*, *Griselinia lucida* and *Nothofagus fusca*, but has little impact on these plants. A more recent arrival, the Australian gum leaf skeletoniser (*Uraba lugens*), has caused noticeable defoliation of *Metrosideros*, but concerns have been alleviated by the finding that this appears to occur only as spill-over from *Eucalyptus* trees, when these grow beside *Metrosideros* (Withers & Jones 2003). Overall, many native woody plants appear to be largely resistant to exotic defoliating insects, as bioassays with several exotic tussock moths (Lymantriidae) on a range of native tree species suggest (see section on 'Resistance' of native trees to invasive herbivores below).

A comparatively greater number of exotic sapsuckers (i.e. sap sucking insects) have been found to be capable of attacking native woody plants, probably because their mode of feeding allows them to bypass plant defences (Ridley et al. 2000). Exotic sapsuckers recorded from native woody plants include both oligophagous and polyphagous species, but their impact appears to be mostly minor (Ridley et al. 2000). For example, the Australian passionvine hopper (*Scolypopa australis*) attacks native plants in several unrelated plant genera (Table 1), and although it is occasionally very abundant, its direct impact on native plants appears to be minor (Ridley et al. 2000). However, *S. australis* could potentially act as the vector of a phytoplasma candidate that may be involved with sudden decline of cabbage tree (Beever et al. 1996; Andersen et al. 2001). An Australian scale insect, *Eriococcus orariensis*, infesting manuka (*Leptospermum scoparium*) caused significant damage; this is generally referred to as 'manuka blight' (Hoy 1961; Ridley et al. 2000). Initially, heavy attack often resulted in the death of manuka, but later *E. orariensis*

Table 1. Examples of exotic invertebrates present in New Zealand, with representatives of the principal guilds or trophic groups, and comments about their impact on native (and exotic) species and ecosystems (see also text).

Species	Order*: Family	Guild	Habitat[§]	Detected	Native range	Host or prey and impact[#] on species and ecosystems
Epiphyas postvittana	Lep.: Tortricidae	Defoliator	Not NF	1891	Australia	Polyphagous, direct impact on a wide range of exotic and native woody and other plants, indirect impacts on native moths via shared natural enemies (+) (1)
Uraba lugens	Lep.: Nolidae	Defoliator	UP, EF	2001	Australia	*Eucalyptus* spp., minor direct impact from spill-over to *Metrosideros* if adjacent to infested eucalypts (+ ?) (2)
Cantareus aspersus	Gastropoda: Helicidae	Defoliator	All (?)	1860s	Europe	Polyphagous, minor direct impact on a wide range of plants (+ ?) (3)
Eriococcus orariensis	Hem.: Eriococcidae	Sapsucker	NF	1937	Australia	Direct impact on *Leptospermum*, *Kunzea* (as in Australia) (++) (4)
Scolypopa australis	Hem.: Ricaniidae	Sapsucker	NF	c. 1875	Australia	Minor direct impact on *Coriaria*, *Leptospermum*, *Muehlenbeckia* (+ ?) (5)
Listronotus bonariensis	Col.: Curculionidae	Stem borer / defoliator	EG, NG	1927	South America	Unknown direct impact of adult feeding on native *Chionochloa*, *Poa* and *Festuca*, and oviposition on the latter two (+ ?) (6)
Anobium punctatum	Col.: Anobiidae	Wood borer	Not NF	1875	Europe	Borer in exotic & native dead wood (e.g. *Dacrydium cupressinum*), minor if any direct or indirect impact on native species (+ ?) (7)
Hylastes ater	Col.: Curculionidae	Bark beetle	EF	1929	Europe, N. Asia	*Pinus* spp., no direct impact on native species or ecosystems (–) (8)
Scolytus multistriatus	Col.: Curculionidae	Bark beetle	UP	1989	Europe, N. Asia	*Ulmus* spp., no direct impact on native species or ecosystems (–) (9)
Asynonychus cervinus	Col.: Curculionidae	Root feeder	Not NF (?)	1937	S. America	Polyphagous on exotic and native plants (*Corynocarpus*, *Entelea*), minor if any direct or indirect impact on native species (+ ?) (10)
Hypharpax australis	Col.: Carabidae	Omnivore	Not NF	1916	Australia	Probably seeds and invertebrates (?), rare in native forest, unknown but probably minor direct or indirect impact on native species (+ ?) (11)
Laemostenus complanatus	Col.: Carabidae	Predator	Not NF	1870s	Europe (?), now cosmopolitan	Native and exotic isopods and amphipods, minor if any direct or indirect impact on native species (+ ?) (12)
Vespula germanica	Hym.: Vespidae	Predator	All	1945	Europe	Direct and indirect impacts on wide range of native species (e.g. invertebrates, nestling birds) and potentially indirect impacts on nutrient cycling and pollination (++) (13)
Vespula vulgaris	Hym.: Vespidae	Predator	All	1984	Europe	As *V. germanica*, but more abundant in natural ecosystems (++) (14)
Linepithema humile	Hym.: Formicidae	Predator	Not NF (?)	1990	South America	Potentially major impact on native invertebrates, also honeydew (+) (15)
Podalonia tydei	Hym: Sphecidae	Predator	Sand dunes	1975	Australia	Native and exotic Lepidoptera larvae, probably minor impact (+) (16)
Miomantis caffra	Man.: Mantidae	Predator	Not NF (?)	1978	Southern Africa	Invertebrates, apparently displaces native mantis (++) (17)
Steatoda capensis	Ara.: Theridiidae	Predator	Not NF	1942	South Africa	Invertebrates, impact mostly minor, apparently major on katipo (++) (18)
Trigonospila brevifacies	Diptera: Tachinidae	Parasitoid	All (?)	1967, intr.	Australia	Introduced (biocontrol), polyphagous on native and exotic Tortricidae, other Lepidoptera, potentially major direct/indirect impact (++) (19)
Echthromorpha intricatoria	Hym.: Ichneumonidae	Parasitoid	Not NF (?)	1900	Australia	Self-introduced, potentially major direct and indirect impact on red admirals and potentially other native Lepidoptera (++) (20)
Microctonus aethiopoides	Hym: Braconidae	Parasitoid	EG, NG	1982, intr.	Palaearctic	Introduced (biocontrol), recorded attacking 14 native non-target weevils in the field, direct impact probably minor (+) (21)
Oxidus gracilis	Polydesmida: Paradoxosomatidae	Decomposer	All (?)	1920	East Asia	Cosmopolitan hothouse species; dead plant matter, unknown impact on decomposition and nutrient cycling (+ ?) (22)
Cylindroiulus britannicus	Polydesmida: Julidae	Decomposer	All (?)	1919	Northwest Europe	Dead plant matter, impact as above (+ ?) (23)
Ophyiulus pilosus	Polydesmida: Julidae	Decomposer	All (?)	1922	Western Europe	Dead plant matter, impact as above (+ ?) (24)
Opogona omoscopa	Lep: Tineidae	Decomposer	All (?)	1914	Australia	Dead plant matter, impact as above (+ ?) (25)
Lumbricus rubellus	Annelida: Lumbricidae	Decomposer	Not NF (but remnants)	Mid-1800s (?)	Europe	Dead plant matter, potentially a competitor of native earthworms, direct and indirect impact unknown (+ ?) (26)

* Order: Ara., Araneae; Col., Coleoptera; Hem., Hemiptera; Hym., Hymenoptera; Lep., Lepidoptera; Man., Mantodea. [§] EF, exotic forest/scrub; NF, native forest/scrub; HA, Horticulture/agriculture; EG, exotic grassland; NG, native grassland; UP, Urban and parks; Not NF, not in native forest or shrubland. [#] Definition of known or likely impact on native species and ecosystems: (-), no known impact; (+ ?), some but probably low impact; (+), minor impact; (++), moderate or major impact (for details see text and cited references). References: 1 Suckling & Brockerhoff (2010), Munro & Henderson (2002); 2 Withers & Jones (2003); 3 Barker (1999); 4 Hoy (1961), Ridley et al. (2000); 5 Ridley et al. (2000); 6 Derraik et al. (2001), Murray et al. (2003), Lister (2006), Barratt et al. (2007); 7 Brockerhoff & Bain (2000); 8-9 Brockerhoff & Bain (2000), Gadgil et al. (2000), Brockerhoff et al. (2003); 10 Brockerhoff & Bain (2000); 11-12 Larochelle & Larivière (2001), Berndt et al. (2008), Pawson et al. (2008); 13-14 Moller & Tilley (1989), Moller (1990), Harris (1991), Moller et al. (1991), Toft & Rees (1998), Beggs & Rees (1999), Beggs (2001), Beggs & Wardle (2006); 15 Ward & Harris (2005), Ward et al. (2005), Harris & Barker (2007); 16 Faulds (1977), Callan (1979), Harris (2001); 17 Ramsay (1990); 18 Hann (1990); 19 Munro & Henderson (2002); 20 Barron et al. (2003); 21 Barlow et al. (2004), Barratt et al. (2007); 22-25 Tomlinson (2007); 26 Lee (1961).

suffered from an entomopathogenic fungus, *Angatia thwaitesii*, probably also introduced, and its impact became less serious (Ridley et al. 2000). Among the 28 exotic species of armoured scale insects (Hemiptera: Diaspididae) found in New Zealand, only four have been recorded from native plants (Charles & Henderson 2002). For example, *Lindingaspis rossi* has been recorded from at least 17 native plant species in 13 families. All records from native plants are for polyphagous species which are "occasionally found in isolated patches of native bush" (Charles & Henderson 2002), but apparently not in undisturbed forest.

Numerous snails have been introduced to New Zealand, and many of these are plant-feeding. For example, the brown garden snail (*Cantareus aspersus*, formerly *Helix aspersa*), is common in modified vegetation and can also be found in disturbed indigenous shrubland and forest; however, it is absent from closed-canopy indigenous forest (Barker 1999). To our knowledge, few studies investigated the impact of snails on indigenous vegetation in New Zealand. Naturalised slugs were found to damage the native fern, *Botrychium australe*, and this was facilitated by the expansion of the introduced grass *Agrostis capillaris* (Sessions & Kelly 2002). *Cantareus aspersus* and other exotic snails feed on a wide range of plants and could affect forest regeneration.

Herbivores of grasslands and other open habitats

Several exotic weevil species have been collected from New Zealand native grasslands, but the weevil species involved have usually not been recorded feeding or breeding on New Zealand native plants, and their presence in native grasslands often appears to be simply a case of vagrance, with no direct relationship with any indigenous species or ecosystem. Examples include *Rhinocyllus conicus* and *Trichosirocalus horridus*, and *Exapion ulicis*, that have been intentionally introduced to New Zealand for biological control of thistles and gorse, respectively. All three species have been recovered from tussock grassland in Central Otago (Dickinson et al. 1998; Murray et al. 2003; Barratt et al. 2009). Similarly, the accidentally introduced species *Gymnetron pascuorum* can be found in New Zealand native habitats, but it is restricted to feeding on plantain (*Plantago lanceolata*) (Kuschel, 1990). *Sitona discoideus*, another species that is a strong flyer and is highly dispersive, has been collected at 1300 m altitude in the Waikaia Ecological Region (Dickinson et al. 1998), and at 2800 m altitude on the Inland Kaikoura Ranges (C.B. Phillips, unpubl.). However, its hosts are restricted to species of *Medicago* and *Trifolium* (Vink & Phillips 2007) and it is unlikely to have host plants in New Zealand's native flora.

A flightless European weevil, *Otiorhynchus ovatus*, occurs in tussock grasslands in Central Otago (Barratt et al. 2009). It has been suggested this species might be sufficiently polyphagous to feed on New Zealand native plants (Brockerhoff & Bain 2000), but as yet there are no published records. It is noteworthy that this species, and the other three species of *Otiorhynchus* that are established in New Zealand, were not found on the native plants sampled by Kuschel (1990). The species that is perhaps most likely to have host plants in New Zealand's native grassland flora is the 'Argentine stem weevil' (*Listronotus bonariensis*), a South American species that has a wide host range within grasses (Poaceae). It is abundant throughout New Zealand, is a strong flier, and is by far the most frequent exotic species found in tussock grassland (Barratt et al. 2007). It has been collected in Otago from remnant native shrubland (Derraik et al. 2001), tussock grasslands (Murray et al. 2003), and even at 1640 m on Coronet Peak (Barratt et al. 2007). A laboratory trial found that *L. bonariensis* adults would feed on several native grasses including narrow-leaved snow tussock (*Chionochloa rigida*), hard tussock (*Festuca novae-zelandiae*) and silver tussock (*Poa cita*), although not to the same extent as on the exotic ryegrass, *Lolium perenne* (Lister 2006).

Although at least seven species of exotic weevils are sometimes found in New Zealand native grasslands, several studies have noted a more general pattern of exotic weevil species being largely restricted to modified habitats. White (1975) examined insect damage affecting *Chionochloa* seed production in 22 alpine tussock grassland sites in the South Island, but did not record any exotic species as causing damage. This is perhaps not surprising given that many seed insects are highly host specific (see also Sullivan et al. (1995) for seed feeders of woody plants). Similarly, exotic beetles are generally much more abundant in New Zealand's modified habitats than in indigenous habitats nearby (Kuschel 1990; Harris & Burns 2000; Pawson et al. 2008). Barratt et al. (1998) recorded 21 exotic Curculionoidea in pasture, lucerne and modified native grassland across three regions in New Zealand, but these species are not normally found in native habitats. Together, these observations indicate that any impacts of exotic weevils on New Zealand native grasslands are likely to be restricted to the effects of just a few species, and evidence to date suggests these impacts are minor. However, it should be noted that damage from root-feeding species is cryptic, and species of *Otiorhynchus* and *Naupactus*, for example, may be having as yet unrecognised impacts.

Exotic herbivores can also have intra-guild impacts on other, native herbivore species. This has been demonstrated for the Australian moth *Nyctemera amica* which is established in New Zealand and readily hybridises with the native magpie moth (*Nyctemera annulata*) (Kay 1980; Sullivan et al. 2008). Both species are specialists of *Senecio* herbs, and there are several native and exotic *Senecio* species in New Zealand. At least in the Auckland region, the native *N. annulata* appears to be largely displaced by the hybrid (Sullivan et al. 2008; Jon Sullivan pers. comm.). A similar case of hybridisation between an exotic and a native species apparently leading to displacement of the latter has been reported for the lycaenid butterfly *Zizina labradus*, an Australian species, and the native *Zizina oxleyi* (Gibbs 1980; Barlow & Goldson 2002). However, Kenis et al. (2009) point out that it is difficult to prove displacement by hybridisation unless it is confirmed by adequate genetic analysis.

Predators of invertebrates of forests, shrublands and open habitats

Predators often have strong, readily observable effects on prey survival, so not surprisingly the impact of invasive predators is frequently highlighted in invasion ecology (Lockwood et al. 2007). The impact of generalist invasive predators can be particularly devastating on the native fauna of island systems, but most of the well-studied New Zealand examples are of mammalian predators, such as stoats and rats. Nevertheless, some arthropod generalist predators (AGPs) have also invaded New Zealand's native forests and shrublands, and their impacts are potentially just as devastating. The impacts of many AGPs that have invaded native ecosystems have not been evaluated, but here we examine two species of *Vespula* wasp, Argentine ants (*L. humile*), ground beetles (Carabidae) and several others (Table 1).

The potential for significant impacts of AGPs is exemplified by the extremely high densities of *Vespula vulgaris* found in some *Nothofagus* beech forests (Thomas et al. 1990). The ecological impacts of *Vespula* are multifarious; reduction in native invertebrate prey species (Beggs 2001), predation of nestling birds (Moller 1990), competition with native species for honeydew, and potentially flow-on effects to nutrient cycling (Beggs & Wardle 2006). Predation rates on some vulnerable native insects are so high that it is estimated *Vespula* wasp density would need to be reduced by more than 90% to achieve conservation gains (Toft & Rees 1998; Beggs & Rees 1999). Similarly, in high density years, *Vespula* consume so much honeydew that there is little left for the native fauna that feed on it (Moller & Tilley 1989). Honeydew is such an abundant source of bioavailable energy in these forests that the domination of this resource by an invasive species is likely to have an impact at all trophic levels (Beggs & Wardle 2006).

Social insects are of particular interest as invasive AGPs since flexible individual and colony responses allow many to become invasive (Moller 1996). Ant diversity is surprisingly low in New Zealand, with only 11 native species (Don 2007), but generalist exotic ant species continue to arrive and 28 exotic species are thought to be established (Lester 2005; Ward 2005; Ward et al. 2006; Don 2007). For at least six of these exotic ant species there is a relationship between the length of time they have been present in New Zealand and their geographic range (Ward 2007). Apparently, it takes many decades for some species to reach all environmentally suitable habitat. Since many species are still spreading and there are currently no studies on their impact in New Zealand, it is impossible to draw general conclusions about exotic ants in natural habitats at this time. Furthermore, generalist exotic ant species are continually intercepted at New Zealand ports (Lester 2005; Ward et al. 2006). Although it is predicted New Zealand is too cool for many invasive ants to become widespread, species such as red imported fire ant (*Solenopsis invicta*) have the potential to establish in warmer areas (Harris & Barker 2007, Ward 2007). Argentine ant (*Linepithema humile*) is one exotic species which has established and is still spreading in New Zealand. Potentially, its distribution will be relatively widespread and will include some indigenous ecosystems, but probably not intact indigenous forest (Ward & Harris 2005; Ward et al. 2005; Harris & Barker 2007). Although the impact of Argentine ants has not been studied in New Zealand, there have been numerous international studies (e.g. Suarez & Case 2002; Sanders et al. 2003; Walters 2006) which demonstrate this invasive AGP species can have diverse impacts in various systems.

Two exotic sphecid wasps (Hymenoptera: Sphecidae) occur in New Zealand, *Podalonia tydei* and *Pison spinolae* (Callan 1979), both of Australian origin. The presence of *P. tydei* in New Zealand was detected in 1975, although it had already been collected in 1967 (Faulds 1977). This species inhabits sand dunes and its main prey species in New Zealand appears to be the native cutworm *Agrotis innominata* (Lepidoptera: Noctuidae) (Faulds 1977; Harris 2001). Apparently *P. tydei* can be abundant, but to our knowledge it has not been determined whether it affects populations of its native prey species. *Pison spinolae* preys on spiders, and it is assumed to have been introduced some time around 1880 (Callan 1979). It appears to be relatively common but probably not sufficiently abundant to have a significant effect on its prey populations.

Ground beetles (Carabidae) are generally among the most well studied insects, and the 395 native and 29 exotic species are relatively well known in New Zealand (Larochelle & Larivière 2001). Most carabids are predators but some are omnivores. Exotic species such as *Hypharpax australis* and *Laemostenus complanatus* are among the most abundant carabid species in disturbed habitats such as urban gardens, farmland and clearfelled plantation forests, but they are rare or absent in native forests (Berndt et al. 2008; Pawson et al. 2008). For example, in the central North Island in a mixed landscape of native forest remnants, plantation forests and exotic grassland, not a single exotic carabid was trapped in native forest, not even near the edge adjacent to exotic forest or grassland (Pawson et al. 2008). Consequently, the impact of exotic carabids in native habitats is probably low, although effects on native species occurring in exotic habitats are possible.

A southern African mantis, *Miomantis caffra*, has been spreading from Auckland where it was first found in 1978 (Ramsay 1990). There is some evidence it is displacing the native mantis *Orthodera novaezealandiae*, possibly because *M. caffra* is more aggressive, has more offspring and may also live longer than *O. novaezealandiae* (Ramsay 1990). Although *M. caffra* appears to be able to live in a wide variety of habitats, it seems to prefer open habitats and may not be able to colonise native forests.

Approximately 60 introduced spiders are found in New Zealand. Most arrived with human assistance, but about one third are likely to be self-introduced. Many of these exotic spiders occur only in urban environments, or in modified or disturbed habitats, such as exotic grassland where *Tenuiphantes tenuis* and other introduced Linyphiidae are common (e.g. Vink et al. 2004). Although exotic spider species have been found in native grasslands, they are certainly not as common as they are in exotic grasslands. Topping and Lövei (1997) surveyed spiders in native tussockland on the Volcanic Plateau and found only endemic species. In low-altitude shrublands in Otago, only two of the 33 spider species found were exotic (Derraik et al. 2001). The European linyphiid, *Diplocephalus cristatus*, is one of very few exotic spiders that are occasionally found in native forest (e.g. Ward et al. 1999), but possibly not in undisturbed forest interiors. It is not known whether any of these spiders seriously impact native species or natural ecosystems. However, there is evidence that the native katipō (*Latrodectus katipo*) (Theridiidae), which lives in coastal dunes among driftwood and low vegetation, is displaced by the exotic *Steatoda capensis*, a South African spider, which is common in modified habitats throughout New Zealand. Modified habitats frequently abut the coastal habitat *S. capensis* shares with *L. katipo*, therefore, *S. capensis* has a greater population reservoir, which, combined with its greater fecundity, allows it to recolonise vacant habitat more rapidly than *L. katipo* (Hann 1990). The decline in *L. katipo* numbers in recent years has certainly coincided with the spread south of *S. capensis*. However, other factors, especially the loss and deterioration of habitat, could have also contributed to the decline in abundance of *L. katipo*.

Parasitoids of forest and shrubland insects

Introduced biological control agents that attack an invasive species in an indigenous ecosystem would be considered to be beneficial and to have a positive impact. An ichneumonid parasitoid, *Sphecophaga vesparum vesparum*, was introduced in an attempt to reduce the abundance of *Vespula* wasps (Donovan & Read 1987). However, although the parasitoid established and spread in indigenous forest, it has so far failed to build up to sufficient numbers to significantly reduce the abundance of *Vespula* wasps (Beggs et al. 2008). *Sphecophaga vesparum vesparum* is highly specialised to attack social wasps and since New Zealand lacks any native social wasps, it is highly unlikely it will attack any native species.

In contrast, some introduced parasitoids attack native non-target species. Red admiral (*Bassaris gonerilla* (F.) Lepidoptera: Nymphalidae) is an iconic New Zealand butterfly. Circumstantial evidence that populations have declined over the last century (Gibbs 1980) prompted a study of population impacts of the pupal parasitoid, *Pteromalus puparum* (L.) (Hymenoptera: Pteromalidae). This parasitoid was introduced to New Zealand in the 1930s for biocontrol of the cabbage white butterfly (*Pieris rapae* (L.) Lepidoptera: Nymphalidae). It proved to be a partially successful control agent of the target species (Ferguson 1989), but has also been observed attacking non-target species such as *B. gonerilla* and the yellow admiral (*B. itea* (F.)). The observations of non-target attack on *B. gonerilla* led to speculation that the decline in numbers was partly attributable to *P. puparum* (Gibbs 1980). However, Barron et al. (2003) found that on average 14% of *B. gonerilla* pupae were parasitised by *P. puparum*, but a self-introduced ichneumonid, *Echthromorpha intricatoria* (F.), was having a greater impact on parasitism, with average parasitism levels of about 26%. However, pupal parasitism was over-shadowed by 95% mortality of eggs of *B. gonerilla*, caused by an unidentified egg parasitoid, *Telenomus* sp. (Hymenoptera: Scelionidae) for which native/exotic status has not been determined (Barron et al. 2003). Population modelling has indicated that non-target attack by *P. puparum* has been minimal (Barron 2007).

Another introduced parasitoid that may have a negative impact in indigenous systems is the tachinid *Trigonospila brevifacies* (Table 1) which was introduced to control light brown apple moth (*Epiphyas postvittana* (Walker) Lepidoptera: Tortricidae). This biological control agent has been recorded attacking eight non-target Lepidoptera species in broadleaf/podocarp forests, and has become dominant in the tortricid parasitoid guild (Munro & Henderson 2002). Its host range was found to overlap with 12 native and one exotic parasitoid species and so it competes with native parasitoids in the field, comprising up to 80% of the parasitoid load per species. The impact of *T. brevifacies* is therefore two-fold: it attacks non-target Lepidoptera, and competes for hosts with native parasitoids in the field. *Xanthopimpla rhopaloceros* (Hymenoptera: Ichneumonidae) was also introduced for the biological control of *E. postvittana* and it has been recorded from the gregarious tineid *Hierodorus atychioides* (Valentine & Walker 1991).

Parasitoids used for biological control are often selected because they have invasive characteristics, and they are expected to establish and spread. Since 1998, a comprehensive risk assessment must be carried out by the applicant for a biocontrol introduction before the regulatory agency (ERMA New Zealand) will make a decision under the Hazardous Substances and New Organisms Act 1996 to approve or reject importation into quarantine, or for release.

Parasitoids of grassland insects

Although there is no evidence of any major direct impact of exotic weevils in native tussock grassland habitats in New Zealand, introduced parasitoids of pest weevils have been found in native grassland environments, generating concern about impacts on native biodiversity. A retrospective (post-release) case study involving two species of *Microctonus* (Hymenoptera: Braconidae: Euphorinae) that were introduced as biocontrol agents has been undertaken over a number of years (e.g. Barratt et al. 1997; Barratt et al. 2000; Barratt 2004; Barratt et al. 2007). *Microctonus aethiopoides* Loan was introduced into New Zealand in 1982 to control the exotic lucerne weevil, *Sitona discoideus* Gyllenhal. *Microctonus aethiopoides* is a solitary endoparasitoid of the adult stage of the target weevil. Another species, *Microctonus hyperodae*, was introduced in 1991 to control Argentine stem weevil (*Listronotus bonariensis*), a pest of grass species. Both parasitoids have become well established and both have suppressed populations of their respective hosts (Goldson et al. 1993, 1994). *Microctonus aethiopoides* was, however, released with only limited host range testing in quarantine, which revealed no evidence of attack on non-target species (Marlon Stufkens pers. comm.). Subsequently, laboratory host range tests have shown that 14 non-target species were attacked, some at a level similar to that of the target host *S. discoideus.* Since its release, *M. aethiopoides* has been found to be relatively polyphagous compared with *M. hyperodae.* In the field, *M. aethiopoides* has been found to parasitise 14 native and five exotic species of weevils (Barratt 2004). The native weevil species which appeared to be most at risk from non-target attack by *M. aethiopoides* were in the subfamily Entiminae, although Curculioninae with ecological affinities to the target host have also been parasitised in the field. This finding has led to concern in New Zealand about the impacts of biological control agents on non-target species (e.g. Barratt et al. 2000), particularly given the 90% endemism at the species level of indigenous Coleoptera found in New Zealand (Klimaszewski & Watt 1997).

Non-target attack by *M. aethiopoides* occurs in native grassland environments, as well as in the target host environment (lucerne) and in developed pasture (Barratt et al. 2007). Although attack rates are generally low (<10%), in some instances up to 24% parasitism of a non-target weevil species has been recorded. Modelling suggests, however, that population impact is likely to be greater at higher altitudes, where the intrinsic rate of increase is lower than at lower altitudes (Barlow et al. 2004). As an invasive species, *M. aethiopoides* has successfully established in grassland environments beyond the target host habitat. Its host has a good dispersal flight ability and earlier assumptions that the target host (adult stage) would not survive outside of the lucerne environment have recently been dismissed, since it has been shown in the laboratory that weevils can survive successfully on a diet of white clover (*Trifolium repens*), with no adverse effects on *M. aethiopoides* development (Diane Barton unpubl.). However, as yet there is no evidence that any native weevil population has been placed at risk as a result of *M. aethiopoides* establishment.

Many attempts have been made to introduce parasitoids for biological control of two other indigenous pasture pests, grass grub (*Costelytra zealandica* Coleoptera: Scarabaeidae) and porina, a group of species in the genus *Wiseana* (Lepidoptera: Hepialidae). Eighteen parasitoids species, mainly Tachinidae, were released for grass grub, but only three of these were recovered subsequently (Cameron & Wigley 1989) and it is assumed all failed to establish. For porina, two tachinids from Argentina have been considered for biological control, but no releases have occurred. Clearly, if indeed none of these parasitoids are established in New Zealand, there have been no opportunities for negative impacts in grassland ecosystems.

A self-introduced, solitary parasitic wasp, *Radumeris tasmaniensis* (Hymenoptera: Scolyiidae), was discovered in Northland in 2000 (Barratt et al. 2002). It is known as the yellow flower wasp and occurs naturally in Australia and Papua New Guinea. An ectoparasitoid of scarab beetles, it is able to detect and locate scarab larvae in the soil. The female wasp oviposits externally on the host and the emerging wasp larva feeds on the scarab larva. The host range of the species seems to be determined by host larval size, the requirement being third instar larvae in the weight range of 1–5 g. There are records of 3 subfamilies of Scarabaeidae being attacked in Australia. The arrival of this species has raised concerns that New Zealand native scarabs such as species of *Pericoptus*, *Stethaspis* and *Odontria* might be at risk from yellow flower wasp (Willoughby et al. 2001). It was also considered that the introduced African black beetle (*Heteronychus orator* (F.)) present in abundance in Northland pastures could become a host allowing yellow flower wasp populations to increase. However, there is no evidence this has occurred, or that the wasp has spread inland from the dune system where it has established. Monitoring of yellow flower wasp distribution and potential host species was carried out until the stage when eradication was no longer considered a viable option. Little research has been carried out since then to assess risk or impacts from this species, although monitoring by the Department of Conservation suggests that the wasp has had an impact on populations of two undescribed species of *Pericoptus* in coastal dune environments (Tony Beauchamp pers. comm.).

Decomposers of forests and shrublands

Invertebrate decomposers can have an important influence on decomposition rates and hence a flow-on effect on nutrient cycling and plant growth (Swift et al. 1979; Bonkowski & Scheu 2004). Hence, an invasive invertebrate decomposer may impact on key ecosystem processes, with potentially far-reaching effects on an ecosystem. Exotic earthworms are a well-studied invader in a number of ecosystems, particularly northern temperate forests (Bohlen et al. 2004; Frelich et al. 2006; Hendrix 2006; Eisenhauer et al. 2007; Holdsworth et al. 2007), but the impact of exotic invertebrates on decomposition has received comparatively little attention in New Zealand. However, earlier studies have documented changes of the earthworm fauna that occurred with land use change. Native megascolecid earthworms, which are common in indigenous forest, declined markedly following conversion to exotic pasture, and were eventually mostly replaced by exotic lumbricid earthworms (Lee 1961). This change in the earthworm fauna had already been observed in the late 1800s (e.g. Smith 1894). Despite their dominance in modified, open vegetation, these exotic earthworms appear to be rare or absent in indigenous forests, although some species have been recorded in forest remnants. For example, *Lumbricus rubellus* has been found in Riccarton Bush (Johns 1995) (Table 1). Nevertheless, some exotic decomposers are relatively abundant and widespread in New Zealand forests. For example, the exotic moth *Opogona omoscopa* and exotic millipedes, such as *Oxidus gracilis*, *Cylindroiulus britannicus* and *Ophyiulus pilosus*, are often abundant in litter of broadleaf tree species including puriri (*Vitex lucens*) and karaka (*Corynocarpus laevigatus*) (Tomlinson 2007). The exotic decomposer species may compete with native invertebrate fauna for litter resources, as well as influence nutrient cycling in forest habitats where they are abundant, thereby affecting plant growth (Tomlinson 2007). Amongst exotic Lepidoptera, detritivores are the dominant group, particularly in the families Tineidae and Oecophoridae (Hoare 2001). This latter family is already represented in New Zealand with an impressive endemic radiation (Hoare 2005), so the establishment of closely related adventive species is of concern if they compete with native species for detritus, as well as having a possible impact on nutrient cycling.

Parasites and pollinators

Apart from the herbivores, predators, parasitoids and decomposers (as discussed above), there are other trophic groups or 'guilds' which deserve mention, if only briefly here. There is a rich diversity of invertebrates with parasitic lifestyles as ectoparasites or endoparasites. Parasites of New Zealand's native animals are not well known, and recent studies of these groups resulted in the discovery of numerous undescribed species. For example, Mironov and Galloway (2002) described five new species of feather mite from native and exotic birds in New Zealand. Several trematodes and nematodes infest native and exotic birds in New Zealand, but it is not known whether these parasites are all native or whether they include exotic species (Tompkins & Poulin 2006). The impact of exotic parasites on native animals has generally received even less attention, but several cases with serious impacts are known from other countries (Tompkins & Poulin 2006). For example, an exotic nematode is thought to be responsible for the decline of the native grey partridge in the UK (Tompkins et al. 2000).

Eight bee species that were purposely released have become established in New Zealand to aid crop pollination and, in the case of the honey bee (*Apis mellifera*), honey production (Donovan 1980; Brad Howlett pers. comm.). Introductions of the honey bee began in 1839 and it is now thought to be among the most common insects in New Zealand (Donovan 1980). Two bumble bees, *Bombus terrestris* and *B. hortorum*, and the lucerne leafcutting bee (*Megachile rotundata*), are also common and widespread while other introduced bees have a more restricted distribution and are less common. Numerous other exotic Hymenoptera and other exotic insects also visit flowers of introduced and native plants. These species could affect New Zealand's biota by altering the reproductive success of native plants, pollination of weeds, and through competition with, or displacement of, native pollinators.

A recent review of native and exotic flower visitors of New Zealand's native plants explored whether exotic insects have any negative effects on pollination (Kelly et al. 2006). Several mechanisms are possible that could have such effects, for example, exotic pollinators might compete with native species or they could be less effective as pollinators. The honey bee, bumblebees (*Bombus* spp.) and other exotic Hymenoptera represent a significant proportion of the visitors of native plants' flowers, and, in five out of 15 cases, exotic insects were responsible for more than half of the visits (and up to 98% in one case) (Kelly et al. 2006). But relative visitation rates are insufficient to assess pollination success. Some insects are known to be nectar robbers. For example, short-tongued bumblebees bite holes into the side of long-tubed flowers without facilitating pollination – but more work is needed to clarify the roles of exotic insects as antagonists or as mutualists facilitating pollination (Kelly et al. 2006).

Specific experiments to evaluate the impact of honey bees on native pollinator abundance and occurrence have been rarely conducted in New Zealand (Newstrom & Robertson 2005). Elsewhere in the world honey bees are known to affect the abundance of foraging behaviour of native fauna on flowers (Butz Huryn 1997). In New Zealand, honey bees forage on a vast number of native and introduced plant species (Butz Huryn 1995), and there is some circumstantial evidence for competition with native flower visitors for floral resources (Newstrom & Robertson 2005: 45). While acknowledging the potential effects of competition for floral resources and nesting sites (between native Hylaeinae and exotic Megachilinae), Donovan (1980) concludes that anthropogenic factors such as land disturbance through agriculture and the removal of native vegetation are more likely to influence native bee abundance than competition with exotic bees.

Synthesis

Biogeography and phylogeny as determinants of biological invasions

Most herbivorous insects exhibit some degree of host specificity. To a large extent this can be explained by plant defences, especially those based on secondary plant metabolites, chemicals that make plants unpalatable to a wide range of herbivores (Rosenthal & Berenbaum 1991). Insects, in turn, have evolved to overcome these defences and they have become adapted to exploiting certain plants. As a result there is a noticeable relationship between insect host range and plant chemistry and phylogeny (e.g. Rosenthal and Berenbaum 1991; Beccera 1997). Even polyphagous insects usually express preferences for certain host plants whereas other plants are less suitable, leading to suboptimal development. It is not surprising, therefore, that most of the serious invasive plant-feeding insects are attacking the same plants as in their native range or plants that are closely related to these. For example, most exotic insects affecting native woody plants in North America are naturally associated with congeneric plants from Europe or northern Asia (Niemelä & Mattson 1996). These Nearctic and Palaearctic regions are biogeographically and plant phylogenetically related and because of this, are considered together as the Holarctic region.

This relationship between insect herbivores and their host plants is likely to be responsible for the apparent lack of exotic herbivorous insects on New Zealand's native plants, due to their phylogenetic distinctiveness (Ridley et al. 2000). The many northern hemisphere insects that were accidentally introduced to New Zealand are largely restricted to the northern hemisphere plants that were also introduced (e.g. Brockerhoff & Bain 2000; Ridley et al. 2000). The same applies to the many plant-feeding insects from Australia of which many are associated with eucalypts and other woody plants that are native to Australia and absent from the New Zealand flora. However, Australia, other southern Australasian regions, southern Africa, and southern parts of South America share many plant families and genera with New Zealand (e.g. *Nothofagus*, *Podocarpus*, *Leptospermum*), a legacy of their shared southern, Gondwanan history. Because of this, these regions are more likely to contain invertebrates that pose a threat to New Zealand's native flora.

Nevertheless, this phylogenetic distinctiveness is not an absolute, because larval feeding bioassays have revealed that elements of the southern hemisphere continental flora of Australia, such as *Corymbia* and *Eucalyptus*, are acceptable hosts for more polyphagous herbivores such as gypsy moth (*Lymantria dispar*) (Matsuki et al. 2001). Similarly, most South American *Nothofagus* species were also found to be acceptable host plants for *L. dispar ,* white-spotted tussock moth (*Orgyia thyellina*, the Australian painted apple moth (*T. anartoides*) and the North American fall web worm (*Hyphantria cunea*) (Hosking et al. 2003; Kay 2003). Furthermore, contrary to the relative host-specificity exhibited by most defoliators and other insects that feed on plant tissues, many sapsuckers are less host-specific, probably because they can circumvent some plant defences by directly accessing the vascular system (Ridley et al. 2000). Several exotic aphids, scale insects, plant hoppers, such as the passionvine hopper (*Scolypopa australis*), and others have been recorded from native plants (Spiller & Wise 1982; Ridley et al. 2000). Despite these exceptions, there is sufficient evidence that at least the more host-specific insects from regions with a flora that is phylogenetically distinct from that of New Zealand's pose a smaller risk. Similar phylogenetic relationships are likely to be important in relation to specialised predators and parasitoids that are more strictly associated with particular host insects. Therefore, this concept is also relevant for non-herbivorous invertebrates.

'Resistance' of native trees to invasive herbivores – the 'IRA' hypothesis

A number of invasive continental macrolepidoptera, Lymantriidae in particular, have established in foreign continental forest ecosystems within the Northern Hemisphere (Table 2). Lymantriidae are conspicuously absent from the New Zealand invertebrate fauna. These defoliators are generally regarded as significant threats to New Zealand's biosecurity, and one of these, gypsy moth (*Lymantria dispar*) is one of few species for which targeted surveillance efforts have been undertaken. Indeed, several incursions and establishments of lymantriids and other species with a similar biology have occurred in recent years (Table 2). However, risk assessments based on larval feeding bioassays of some of these defoliators (Matsuki et al. 2001) revealed that many of New Zealand's indigenous trees are unexpectedly resistant, or at least less palatable, than continental plants. In no-choice, randomised feeding trials undertaken in New Zealand and France, neonate larvae were fed freshly cut foliage, and parameters of development and mortality were recorded till pupation or larval death. New Zealand assays utilised foliage of local indigenous and naturalised plants while the trials in France used the foliage of New Zealand, South American and Australian endemics obtained from arboreta in the UK, Ireland and France. Representatives from at least a third of the families of the main elements of New Zealand's indigenous forest flora

Table 2. Examples of macrolepidoptera, all Lymantriidae except where noted, that successfully invaded New Zealand or other new regions. All are considered significant threats to our native forests and other ecosystems.

Species	Native range	Establishments	Host range
Lymantria dispar (gypsy moth)	Eurasia	North America 1860s	polyphagous
Lymantria umbrosa	East Asia	New Zealand 2003*	polyphagous
Euproctis chrysorrhoea	Europe	North America 1890s	polyphagous
Leucoma salicis	Eurasia	North America 1920s	oligophagous
Orgyia thyellina (white-spotted tussock moth)	East Asia	New Zealand 1996*	polyphagous
Teia anartoides (Aust. painted apple moth)	Australia	New Zealand 1999*	polyphagous
Hyphantria cunea (N. Amer. fall webworm)**	North America	Eurasia 1940s, NZ 2003*	polyphagous

* Species that were eradicated from New Zealand following extensive spray programmes using *Bt*. Note, only a single male of *L. umbrosa* (previously considered to be *L. dispar*) was found in Hamilton, and the presence of a viable population was not confirmed. ** Family Arctiidae

were on trial for each moth species (Matsuki et al. 2001; Kay 2003; Hosking et al. 2003). For the white-spotted tussock moth (*Orgyia thyellina*), all New Zealand representatives of the plant families on trial were poorer hosts than their Northern Hemisphere hosts, even those with close relatives in the New Zealand flora. For gypsy moth, New Zealand plants were poor hosts, and New Zealand *Nothofagus* species were comparatively poorer hosts than either the South American or Australian *Nothofagus* species. The Australian painted apple moth (*Teia anartoides*), which could have been expected to have some evolutionary experience with the flora of the Southern Hemisphere, followed the same trend as the Northern Hemisphere lymantriids, as did the North American fall webworm (*Hyphantria cunea*).

The notion that islands are vulnerable to invasions of continental species because of the availability of empty niches and the evolution-in-isolation of insular biota is widely accepted (Whittaker 1998; Primack 2002). However, the demonstrable resistance in the New Zealand flora to invasive polyphagous defoliators does not fit well with this paradigm. Interestingly, the resistance to invertebrates contrasts markedly with the susceptibility of the flora to alien vertebrate herbivores. The unexpected resistance of New Zealand's plants to alien invertebrate defoliators is likely to be partly explained by their distinctiveness (see above). Even polyphagous defoliators are somewhat constrained by co-evolved dietary preferences, and the unfamiliarity of the New Zealand flora may be sufficient to convey resistance to many such defoliators. However, floristic distinctiveness does not explain the comparative palatability of South American *Nothofagus* to such northern hemisphere insects (some South American *Nothofagus* were found to be more palatable than the preferred natural host plant of gypsy moth (Kay 2006)).

These observations led to the formulation of the Island Resource Allocation (IRA) hypothesis (Kay & Wratten 2006). This posits that the susceptibility of a plant species to invertebrate herbivores should be proportional to its geographic range. It reasons that plants in spatially restricted habitats such as oceanic islands, which do not support food webs that are as complex as those of continental regions, but are the continual recipients of vagile defoliators, must limit the effects of defoliator populations through bottom-up processes (e.g. plant defences affecting herbivores), to maintain a 'green world' stability. The IRA hypothesis implies that plants with large geographic ranges can rely to a greater extent on a top-down regulation of defoliators by predators and parasitoids, and such plants are expected to have comparatively poor bottom-up self-defence. This is borne out by the contrasting palatability of continental and insular *Nothofagus* found in the bioassays, but is contrary to the 'apparency hypothesis' (Feeny 1975, 1976; Forkner et al. 2004) which has previously been criticised (Edwards et al. 1986).

The need for New Zealand indigenous plants to invest in an inherent defence against invertebrate herbivores may also be reflected by other floristic traits, which have previously been more difficult to convincingly assign as a reaction to invertebrate herbivory. Dioecy, hybridism, the evergreen habit, and the presence of leaf domatia are relatively common in the New Zealand flora and are characteristics that have been implicated in the resistance to invertebrate defoliators (Coley 1988; Jing & Coley 1990; O'Dowd & Pemberton 1998; Orians 2000). Invertebrate herbivory could be a key ecosystem process in most habitats, especially those lacking native mammalian herbivores (Schowalter 2000). However, the defence against insect herbivores observed within the New Zealand flora suggests that the functioning of insular ecosystems may differ considerably in this regard from that of continental systems. The IRA hypothesis posits that indigenous plants that cannot escape herbivory in space or time must allocate resources to defend themselves in New Zealand's trophically simple environment. Nevertheless, occasional outbreaks of native defoliators, for example, *Proteodes carnifex* and *Epichorista emphanes* on *Nothofagus* (Wardle 1984), indicate that plant defences are not the sole determinant of population dynamics.

Ecosystem 'resistance' to invasions and the role of disturbance

As noted earlier, habitat disturbance is thought to be an important factor facilitating biological invasions because modified habitats are often more invaded than undisturbed habitats (e.g. D'Antonio et al. 2000; Snyder & Evans 2006; Didham et al. 2007; Lockwood et al. 2007). A review of 103 animal invasions (invertebrates and other taxa) identified habitat disturbance as a factor in 28% of cases (although for plants, this percentage was much higher, at 68%) (Lozon & MacIsaac 1997). A more recent, well documented example concerns the invasive ladybird beetle *Coccinella septempunctata* which is most abundant in modified habitat (cropland), although spill-over into adjacent native habitat remnants causes significant predation of native aphids (Rand & Louda 2006). There is good evidence that habitat disturbance is an important feature of most invertebrate invasions in New Zealand (see cases mentioned above for disturbed forest and grassland ecosystems, e.g. Kuschel 1990; Barratt et al. 1998; Harris & Burns 2000). For example, in a range of habitats in the central North Island (Pawson et al. 2008), exotic beetles were largely absent in native forest remnants (less than 1% of all beetles), but they were much more common in modified habitats (c. 13% in mature closed-canopy pine plantation forest, c. 17% in clear-felled plantation forest, and c. 28% in exotic grassland pasture). (Interestingly, this appears to apply less to mammalian invaders such as rodents, possums, mustelids and deer which are often found in natural areas far from disturbance. (Kelly & Sullivan 2010)). This relationship has often been interpreted as evidence for the biotic resistance hypothesis which suggests that undisturbed natural habitats are generally less prone to invasion than disturbed habitats (Elton 1958; Kennedy et al. 2002; Levine et al. 2004). However, several alternative hypotheses may also explain this association. For example, the strong link between disturbance and human activity means that invasions in disturbed ecosystems are probably more likely to be documented than invasions in less modified systems simply because the former are more frequently studied, thus potentially creating a bias in the published literature. Moreover, this bias may be compounded by a lack of knowledge about biodiversity in unmodified systems, and related difficulties in distinguishing between native and exotic species (although our knowledge of most invertebrate taxa in New Zealand is sufficient to differentiate these). It is also possible that most of the invasive species that have been intentionally or accidentally introduced by humans to date have been a non-random sub-sample of species that has favoured disturbance-adapted species (Smith & Knapp 2001; Howard et al. 2004). This is reinforced by the strong preference of many exotic invertebrates for open habitats, whereas shady forest habitats are colonised to a much smaller degree (e.g. Berndt et al. 2008; Pawson et al. 2008). However, changes in the global pool of species being transported by humans may well lead to an increase in translocations of species capable of establishing in less-disturbed, more-natural systems, and thus to more frequent invasions into natural areas in the future (Smith & Knapp 2001; Howard et al. 2004; Levine et al. 2004; Von Holle & Simberloff 2005).

Arthropod generalist predators (AGPs)

Among the relatively small group of higher-impact invaders that were identified in our review, several are generalist predators. The ecological role of AGPs is complex because they usually have a wide host range and feed at a range of trophic levels, as well as serving as prey for larger predators (Snyder & Evans 2006). Therefore, their impact as invasive species can be unpredictable and diverse. Furthermore, AGPs can reach very high densities in their introduced ranges (Snyder & Evans 2006). Consequently, there is much potential for large negative impacts on the receiving community. Social insect predators appear particularly prone to such effects, and because New Zealand has a comparatively small social insect fauna, there are probably many unoccupied niches. In New Zealand, all these characteristics certainly apply to *Vespula* wasps, and their considerable impacts are now relatively well understood (as described above). Another, emerging threat is that of Argentine and other exotic ants which are getting an increasingly stronger foothold in New Zealand. Argentine ants are renowned for their ability to rapidly disassemble native ant communities and, as a result, to alter the community organisation among species that persist (Sanders et al. 2003; Walters 2006). This can have flow-on effects to other trophic levels. For example, in South African fynbos, Argentine ants reduce the abundance of native seed-dispersing ants, leading to a change in the composition of the plant community (Christian 2001). At the other end of the trophic scale, in California, Argentine ants have reduced the abundance of a native lizard predator higher in the food-web by displacing the native ants they feed on (Suarez & Case 2002). Given their impact in other systems overseas, it is highly likely that they represent a threat to our native biodiversity, although the nature and magnitude of any effect is not yet known and difficult to predict.

Apart from social insect invaders, there is no shortage of other invasive predators in New Zealand. They include several solitary hymenopteran predators, a South African mantis, c. 60 spiders, 29 carabid beetles (see above), c. 85 staphylinids, 18 coccinellids (Klimaszewski & Watt 1997), and many others. Impacts of invasive predators reported from other countries include displacement of native predators by various mechanisms, reduction in prey availability to native predators, and breakdown of trophic food webs through alteration of top-down or bottom-up control (Snyder & Evans 2006). Apart from the few better studied high-profile AGPs, we know little about the occurrence of such effects for most exotic predators in New Zealand, and more research is needed.

Non-target impacts of intentionally introduced biocontrol agents

Several cases of species introduced for classical biological control that led to attacks on native non-target species have raised concern about the safety of this practice (as outlined above). Clearly, future introductions of biocontrol agents should be considered more carefully, especially for entomophagous agents. Our increasing understanding of the trophic interactions between particular types of exotic invertebrates and their potential hosts in different natural and modified ecosystems can assist with assessing non-target risks and impacts. However, it is important the implications of biocontrol agent introduction are assessed in terms of population impacts, rather than simply attack rate. This has rarely been carried out for entomophagous biocontrol agents (Barlow et al. 2004). There are many examples of very high levels of attack having little impact on population dynamics and most insect populations can probably tolerate some level of attack without suffering a reduction in population density (Barlow et al. 2004). Factors that are important when considering likely impacts are the stage of development of the host that is attacked, the intrinsic rate of increase for the species (Kean & Barlow 2000) and whether continuing spill-over attack (i.e., parasitoids originating from the target host attacking native species nearby) occurs, because this is density independent (Barlow et al. 2004). *Microctonus aethiopoides* has 'established' in both developed pasture environments and native grassland. Attack rates are generally higher on non-target weevils in pasture than in native grassland (supporting the hypothesis of biotic resistance in more diverse environments). However, at the same level of attack, the impact on non-target populations might be greater in native grassland than in pasture because of the lower intrinsic rate of increase at higher altitudes (Barlow et al. 2004), where the former habitat predominates. Furthermore, unlike *T. brevifacies* mentioned above in relation to non-target impacts on native Lepidoptera, there is no evidence to suggest that *M. aethiopoides* is competing directly to the detriment of other parasitoids either in pasture or native environments, so essentially it is exploiting a largely vacant niche. However, there are numerous other parasitoids and predators (e.g. coccinellids) that were introduced as biological control agents in New Zealand (Ferguson et al. 2007), and for most of these, non-target impacts have not been well studied. However, Paynter et al. (2004) reviewed impacts of weed biocontrol agents and found only few minor (and usually anticipated) cases of non-target feeding.

Conclusions and outlook

In this review we have provided an overview of the more notable examples of the many exotic invertebrates that have become established in New Zealand and their relationships with native species and ecosystems. So far, few exotic herbivores attack native plants and fewer yet have colonised natural vegetation. There is support for the hypothesis that many of New Zealand's native plants exhibit considerable resistance to exotic herbivorous invertebrates, although species from closely related plants may represent a significant threat. Several predatory exotic invertebrates have colonised natural ecosystems and readily prey on numerous native species, especially the less host-specific predators. Detritivores such as earthworms, dermestid beetles and millipedes may be similarly unconstrained by host phylogeny and thus could also be amongst the more important biosecurity risks. Overall, closed forest ecosystems are less invaded and affected by exotic invertebrates of all trophic groups than open habitats, and habitat disturbance clearly increases the level of invasibility.

We lack assessments of the impact of exotic invertebrates on New Zealand's native species and ecosystems. Although direct impacts, such as attack of native plants and animals, have been explored, the ultimate effects on populations, communities and ecosystems are more complex and less well understood, except for a few high-profile invaders such as *Vespula* wasps. A recent review of ecological effects of invasive alien insects (Kenis et al. 2009) lists numerous cases of impacts on native flora and fauna caused by indirect effects. For example, an exotic insect can indirectly increase parasitism of related native insects because of an augmentation of the population of a shared parasitoid (known as 'apparent competition'), which may have serious consequences. Other indirect effects can be mediated by exotic invertebrates that act as vectors of plant diseases and also include effects on pollination systems, nitrogen cycling and other ecosystem processes. Although we have touched on some of these, more research is needed in New Zealand to investigate the presence and magnitude of such indirect effects.

Although our review highlights a lack of detailed knowledge of the impacts of most exotic invertebrates on New Zealand's native species and ecosystems, there is probably sufficient information to allow the detection of high-impact effects of herbivores. This cannot be said for predators, detritivores and other guilds, where effects such as species displacement and disruption of mutualisms may occur unnoticed, particularly in the case of the more obscure and less studied groups. At present, there is a perception that the limited known attack of native species and low abundance of most such exotics in natural ecosystems mean there is a low risk. However, such species may eventually become more abundant, for example because the populations of many invaders have a distinct lag phase (Mack et al. 2000). Similarly, exotic species may become more invasive when conditions become more suitable as a result of disturbance or climate change, and so far this has not received much attention in New Zealand. Finally, innovative risk assessments, such as the exploration of exotic invertebrates found on 'expatriate plant communities' (i.e., New Zealand plants growing overseas as ornamentals in gardens, etc., or as invasive plants) (e.g. Fagan et al. 2008), may also provide useful knowledge about exotic species that represent biosecurity threats to our native biota, should they arrive and become established in New Zealand.

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