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Environmental impact classification for alien insects: a review of mechanisms and their biodiversity outcomes

Melodie A. McGeoch, Morgan J. Lythe, Marie V. Henriksen, Chris M. McGrannachan

There is strong incentive to identify and prioritize invasive alien species according to their biodiversity and ecosystem impacts. Invasive alien insects and their environmental impacts are poorly represented in much invasion biology literature and many invasive species databases, and the appropriateness of proposed impact classification has not been assessed for insects. We examine standardized impact mechanisms and their outcomes for their relevance and sufficiency to describe the environmental impacts of alien insects. Mechanisms of direct impact, such as competition and herbivory, are well represented. Indirect and higher-order interactions and their impacts are less so. We recommend specific interpretation of mechanisms of impact for insects, and explicit consideration of indirect interactions as key mechanisms by which alien insects impact the environment.

Addresses
School of Biological Sciences, Monash University, Clayton 3800, Victoria, Australia

Corresponding author: McGeoch, Melodie A. (melodie.mcgeoch@monash.edu)

Highlights

- Individual alien insect species impact the environment by multiple mechanisms.
- Classification of alien insect impacts is needed to better understand their consequences.
- Novel interactions and indirect impacts of alien insects are significant and underestimated.
- These are not adequately captured in the proposed alien impact classification scheme.
- An evidence-based list of invasive alien insects is needed to prioritize management effort.

Introduction

The impacts of alien species on native biodiversity and ecosystems are significant [1]. Understanding the form and size of these impacts is essential for prioritizing species for prevention, early warning and control efforts (McGeoch et al. in review). This is recognised by global targets for reducing the pressure on biodiversity, specifically Aichi Target 9 of the Strategic Plan for Biodiversity 2011-2020, which includes that by 2020 "*Invasive alien species … are identified and prioritized, priority species are controlled or eradicated …*" [2]. The range of ways in which invasive alien species impact biodiversity are well appreciated [1]. However, until recently there has been no widely accepted approach for assessing the impacts of a broad suite of alien taxa that enables the comparison and prioritisation of the size of their impacts [3]. A common approach to assessing impact is essential for evaluating and tracking biological invasion and the success of intervention efforts.

Invasive alien insects, like other taxa, have a range of ecological impacts, although comparatively few invasive insect species have been studied, particularly under field conditions [4]. The literature is also strongly biased to a handful of species, a narrow range of ecological mechanisms of impact and those with socio-economic consequences; ecosystem structural changes and its consequences have, for example, received little attention [4]. Although invasive insects impact biodiversity in multiple ways, their impacts on native insect biodiversity, particularly closely related insect families, are often especially significant [5,6,7**]. A standardised approach for classifying alien insect species is needed. This should be based on the nature and size of their environmental impacts, and be able to accommodate data rich and data poor species. It would improve rapid decision-support schemes for policy and management, contribute to achieving Aichi Target 9, and accelerate efforts to fill some of the important information gaps on alien insect species and the consequences of their invasion [8,9].

Recently, a standardised system was proposed that classifies alien species, based on a suite of impact mechanisms, according to the size of their environmental impacts [3]. This system is being advocated for adoption as the standard scheme by which the IUCN classifies the negative impacts of species of all taxa that have become invasive (Hawkins et al. submitted). The approach relies heavily on a standard set of impact mechanisms, and their environmental and socio-economic outcomes. The relevance and sufficiency of this scheme has yet to be reviewed for alien insects. Such a review is essential prior to application and widespread adoption of the system; to ensure that the outcomes are equally robust and comparable across the higher level taxa for which its adoption is intended, including the Insecta.

In this review we examine the appropriateness and relevance, for alien and invasive insects, of the impact mechanisms and their environmental outcomes that underpin this proposed method for classifying the environmental impact of alien taxa. The review more broadly outlines and assesses a scheme for describing the direct and indirect impacts of invasive alien insects, upon which the magnitude of these impacts and their relative importance can be classified.

Which alien insect species are invasive?

Identifying which alien insects are invasive forms the first task specified by Aichi Target 9. The number of alien insects known to be invasive, i.e. to have negative impacts on biodiversity and ecosystems, is considered to be significantly underestimated [10]. Kenis [4] found published evidence of ecological impacts for only 72 insect species, and found strong bias in the literature towards North America and ants (Table S2). As a contribution to Aichi Target 9, and more specifically to the management of invasive alien insects, the development of an evidence-based list (following McGeoch et al. [11]) of alien insects with environmental impacts is a priority.

In the absence of such a list, we used the Global Invasive Species Database (GISD) (http://www.issg.org/database). The database is managed by the Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission, and focuses on invasive alien species that threaten native biodiversity and natural ecosystems. It was therefore considered appropriate for our purpose. All invasive alien insect species were extracted from the database (n=85, accessed April-May 2015). Each of these species was scored (yes/no) for relevance against each of the 10 mechanisms (Table 1) [3,8] and the associated outcomes of these impacts for the environment (biodiversity and ecosystems), society and the economy (Table S1). We scored species against environmental and socio-economic impact outcomes, to assess the extent to which species with environmental impacts also have socio-economic ones.

We adopted a conservative approach and only evidence of impact was scored positively across species and mechanisms; using the CABI Invasive Species Compendium (an encyclopaedic resource that draws together scientific information on all aspects of invasive species; http://www.cabi.org/isc/) and additional primary literature where required. Eleven species were excluded based on no evidence of impact outcomes or where two species in the same family had identical scores (to prevent representational bias); 74 species were therefore assessed that include a representative range of insect orders and families known to be invasive (Table S2). Note, we make no inferences about the relative magnitude of any impact, but rather focus on the relevance and frequency of mechanisms of impact and their outcomes across orders and families of invasive alien insects.

First we reviewed evidence for the relevance of each of the 10 general mechanisms of impact (Table 1) for alien insects specifically using previous reviews on the subject and the literature cited here, as well as evidence scored against the species listed in Table S1. Based on this review process for each mechanism we assigned one of three environmental relevance categories: highly relevant, relevant but likely to be underestimated, or of low relevance (Table 1). The frequency with which a mechanism was found to apply across the species examined (percentages in Table 1) is not directly related to the relevance category in some cases, because the outcomes were either mostly socio-economic rather than environmental, or because we evaluated the evidence available to underestimate the likely prevalence of the mechanism.

What impacts do invasive insects have?

Mechanisms of impact

Four of the 10 impact mechanisms, i.e. competition, predation, disease transmission and herbivory, are well-known, relevant and direct mechanisms by which alien insects impact biodiversity (scoring positively for between 15-61% of the invasive alien insects examined; HIGH, Table 1).

There is clear evidence for three other mechanisms, although evidence of their relevance is limited to a more narrow range of orders, families or cases than the above mechanisms, and may also be underestimated (RELEVANT, Table 1). Hybridisation is rare between alien and native insects (although may simply be understudied) [4,12]. Similarly there are comparatively few published examples of alien insect parasites, although the term parasitism as it applies to insects includes parasites and parasitoids (Table 1); a mechanism pervasive in the Hymenoptera and Diptera. Thousands of parasitoids have been introduced as biological control agents, and there are several examples of the impact of alien parasitoids on non-target insect species [4]. However, these impacts have not been adequately studied and are likely to be underestimated [13,14]. Last, there is evidence of interactions between alien insects and other alien species, including alien insect-insect and alien insect-plant interactions (Table 1) [4]. Such interactions may be more common than currently documented and deserve closer attention.

Three other mechanisms are either uncommon, unlikely to impact native species significantly, or in some cases the definition of the impact requires modification for insect-specific impacts (LOW, Table 1). For alien insects, poisoning or toxicity is more of a human health problem than an environmental concern; it has not been found to impact native species independently of predation as the primary mechanism (e.g. the Harlequin ladybird) [7**]. However, this mechanism could potentially impact threatened native insect species. Bio-fouling is rarely caused by insects, though occasionally swarms damage infrastructure [16]. Bio-fouling as an indirect mechanism of impact has not been considered, but may be relevant in some instances. For example, the invasive yellow crazy ant *Anoplolepis gracilipes* tends the honeydew-producing scale insect *Tachardina aurantiaca* on Christmas Island, leading to a population increase of *T. aurantiaca* and an increased level of honeydew residue on tree surfaces. This in turn causes the increased colonisation of sooty mould on honeydew-covered trees, resulting in canopy dieback and tree death [17]. Chemical, physical or structural ecosystem impacts are caused by alien insects in some cases, such as ant nest building that affects soil chemical and physical properties [4]. Large changes to habitat structure and associated ecosystem impacts via changes in flammability occurring as a result of herbivory-induced forest dieback is one example by which this mechanism can incorporate insect activity [15**].

Diversity and frequency of mechanisms

Invasive insect species tend individually to impact biodiversity through more than a single mechanism (1.78 ± 1.02 (s.d.) impact mechanisms per species), with a maximum of five mechanisms for a single species (i.e. the Africanized honeybee, *Apis mellifera scutellata,* and the red imported fire ant, *Solenopsis invicta*).

The most frequent impact mechanism was herbivory (Figure 1a,b) and the two main orders contributing to this impact are Coleoptera and Hemiptera (Figure 1a). However, the Hymenoptera have more mechanisms by which they impact native biodiversity than other orders. Hymenopteran contribution to herbivory is minor, but because the order has a wide range of impact mechanisms (including disease spread, competition, and poisoning/toxicity (due to allergic reactions to stinging)) it dominates the order-mechanism association network (Figure 1a). The distribution of impact mechanisms across insect families is highly influenced by Formicidae, which has both the widest range of mechanisms and most frequently recorded individual mechanisms (Figure 1b). By contrast, herbivory achieves its dominance as an impact mechanism (Figure 1b) by being represented across a wide range of families without any major contribution from any one family. Thus, the link between the dominant family (Formicidae) and the dominant impact mechanism (herbivory) is weak (Figure 1b). This highlights the importance of looking beyond the most prominent invaders to fully understand the range of impacts of invasive insects.

Outcomes of impacts

Eleven environmental impact outcomes and ten socio-economic impact outcomes were identified for this group of species selected specifically for their known environmental impacts (from 37 possible mechanisms, Table S1). The relative numbers of environmental (2.04 ± 1.57) versus socio-economic (2.01± 1.37) impact outcomes per species were similar. Most species with environmental impacts also had socio-economic impacts (91%). Even though GISD focuses on alien species with biodiversity impacts, evidence for only socio-economic impacts was found for 22% of the insect species listed (supporting the interpretation of bias in knowledge of which species have environmental impacts towards those principally identified for their socio-economic impacts). The most frequently scored environmental impact outcomes were native population size decline, native biodiversity, reduction or inhibition of the growth of other species and impacts on native plant or animal health (90.7 % of all links, Fig. 1c,d). The distribution of impacts across outcomes was higher on average and more evenly distributed across socio-economic outcomes (including damage to forestry, agriculture and ornamentals, as well as human health and nuisance and alteration of recreational use and tourism) than environmental ones, again most likely reflecting the knowledge bias towards socio-economic impacts (Fig. S1).

The dominant insect orders contributing to the four dominant environmental outcomes are Hymenoptera, Hemiptera and Coleoptera (Figure 1c). Hymenoptera have most impact outcomes and the Formicidae is the main contributor to the most common outcome (population size decline) (Figure 1c). The Formicidae thus dominate both impact mechanisms and impact outcomes. However, a large contribution to an impact mechanism does not always correspond to a large contribution to impact outcomes, exemplified by Cerambycidae. This family has a minor influence on impact mechanisms with a relatively small contribution to herbivory (Figure 1b), while it is one of three main contributors to the impact outcomes (Figure 1d). Thus, the relevance and occurrence of a particular impact mechanism within an insect family is not necessarily a good predictor of its contribution to the realised outcomes of that impact mechanism. This supports the need for the assessment and classification of invasive alien insects (along with other taxa) according to the magnitude of their impacts (against these mechanisms and outcomes), as proposed by Blackburn et al. [3].

Research to better represent invasive alien insect impacts

There are multiple biases likely to affect the strength of the associations that we have identified here between insect orders and families and impact mechanisms and their outcomes. First, the number of invasive alien species is likely a significant underestimate [4,10] and as a result the distribution of mechanisms and outcomes across orders and families may be biased. Alien insect impacts have only been the focus of research attention since the 1990's [4]. Nonetheless, because the impacts of serious invasive species tend to be conspicuous and comparatively well documented [18], the degree to which our analysis represents the mechanisms and outcomes of more serious invaders is accurate. Furthermore, invasive alien species and their impacts on biodiversity may receive attention because these species also have socio-economic impacts (Fig. S1; Kumschick et al. [19] found a strong correlation between the environmental and socio-economic impact scores of arthropods from Europe). This may also be part of the reason why the more direct effects of competition, herbivory, predation and disease transmission are better studied and better represented in the associations (see Fig. 1) [4] than the more indirect and more difficult to study mechanisms and their negative outcomes, such as interactions between alien species, impacts on pollination and food webs.

Future directions

Adequacy of ten impact mechanisms

We have shown that the proposed standard mechanisms by which invasive species impact the environment are largely appropriate for application to insects, with a range in their relevance from high, relevant but probably underestimated, to low relevance. In some instances a more narrow definition of the mechanism applies (herbivory), and in others an expanded definition would better capture the nature of the mechanism (parasitism) for insects. In these cases we have suggested some refinement to the interpretation of the ten mechanisms (Table 1) when applied to categorising alien insects based on the magnitude of their impacts [3].

Sufficiency of ten impact mechanisms: importance of interactions and indirect impacts

Although the 10 proposed mechanisms of impact are largely relevant, are they sufficient and inclusive for adequately describing the range of ways in which alien insects may impact the environment? Most of the examples in Table 1 concern direct impacts on the environment, whereas alien insects also impact the environment indirectly in multiple ways. This includes indirect effects on native plants and animals, indirect effects through herbivory and apparent competition that alter community structure and ecosystem processes, and the evolutionary consequences of these [15**, 19]. For example, 59% of 27 different ecosystem services provided or mediated by ants impact ecosystems indirectly [20]. Some of these indirect impacts may be adequately captured by the current mechanisms, but others are more diffuse and difficult to classify (see below). Although some of these indirect impacts become apparent when considering the range of impact outcomes (listed in Table S1, such as modification of foodwebs), the potential pervasiveness and significant consequences of indirect mechanisms of impact mean that they deserve more explicit consideration.

We suggest that by not defining indirect mechanisms of impact explicitly, they run the risk of being underestimated in impact assessment and prioritisation schemes, particularly because they are often understudied and less well-understood by comparison with direct effects [12]. For example, pollination is a critically important ecosystem process that is severely impacted by alien invasive pollinators [21]. Pollination falls under two mechanisms: competition (with native pollinators for flower resources) and interaction with other invasive species (for example alien plants). However, generalist alien pollinators may also facilitate the pollination of native species resulting in significant modification of plant community structure [22]. In this way a positive novel interaction between an alien pollinator and a native plant species (an interaction not captured by mechanism no. 10), may have a negative indirect impact on both insect and plant community structure [15**].

More generally, facilitation of native species by aliens that results in ecosystem impacts through negative trophic cascades is evident in many other examples, such as alien invasive ant impacts on plants through mutualistic interactions and seed dispersal [8]. Alien herbivores can disrupt chemically-mediated interactions between native plants, their natural enemies and pollinators [23**]. This disruption can negatively impact native populations, multiple trophic levels and native ecosystems. Another example is the multiple indirect and non-target impacts of management strategies against invasive alien insect pests, including the use of insecticide, biological control and even genetically engineered insects [14,24]. This has variably positive or negative direct effects on native insects depending on the specificity of the treatment [25], and the indirect ecological and evolutionary effects of these pest management strategies are little understood [12,26].

Novel and indirect interactions such as those described above do either not clearly, or not explicitly, fall under any of the 10 existing mechanisms. We suggest that a mechanism is needed that encompasses, for example, "facilitation of native species", where the first order impact may be positive on the native species, but where the higher order interactions have negative impacts on food webs or ecosystems. Impact on ecosystems is in fact an impact category applied to assessing environmental and economic impacts of arthropods in Europe; and emerged as one of the more important categories of impacts [8]. An eleventh mechanism that represents indirect interactions and ecosystem or food web impacts may be warranted.

Conclusion

This assessment provides a basis for future adoption of the environmental impact classification scheme for alien taxa. Well known, direct mechanisms of alien insect impacts are well captured by the proposed standard alien classification scheme. Novel and indirect interactions, and their ecosystem outcomes, are critical mechanisms by which alien invasive insects impact the environment, supported by a growing body of evidence. A scheme that does not explicitly consider these often higher-order mechanisms is likely to underestimate the magnitude and consequences of the impacts of invasive alien insects on the environment.

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Table 1

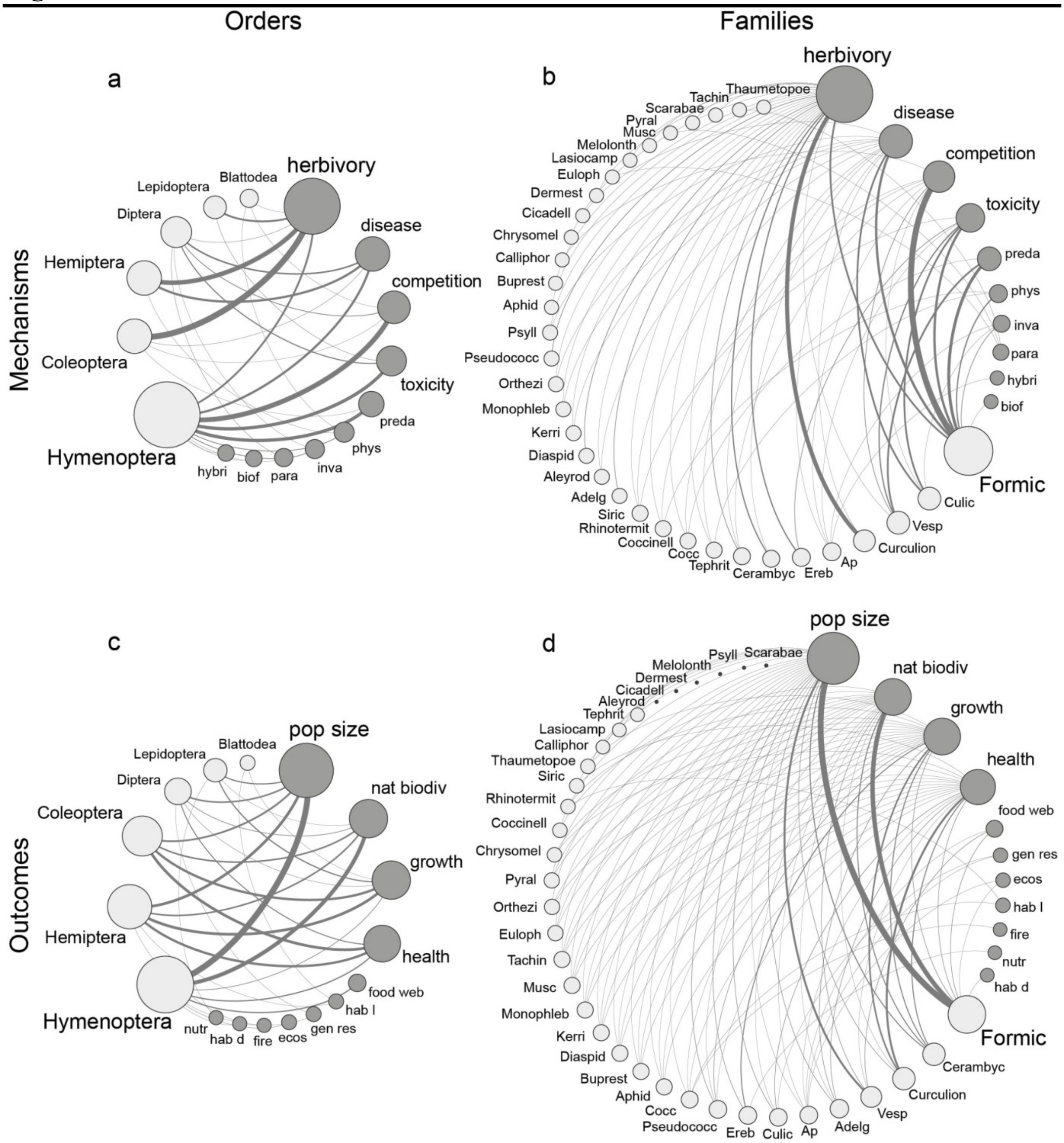
Mechanisms by which alien insects may impact insect diversity and broader biodiversity (environmental impact outcomes). Percentages are estimates of the number of invasive alien insects (n=74) associated with each mechanism.

Impact mechanisms - leading to deleterious impacts on native taxa*	RELEVANCE Impact by invasive alien insects	Insect example
1. Competition - the alien taxon competes with native taxa for resources (e.g. food, water, space).	HIGH (26%) Competition between alien and native insects is common.	Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae), displace native ant species through interference competition, potentially reducing native biodiversity and indirectly altering food web structure and ecosystem processes. [5]
2. Predation - the alien taxon predates on native taxa, either directly or indirectly (e.g. via mesopredator release).	HIGH (15%) Many alien insects are predatory.	Ladybeetles, including the Harlequin ladybird*, Harmonia axyridis* (Coleoptera: Coccinellidae), preys upon larvae of intra-guild native *Coleomegilla maculata* (Coleoptera: Coccinellidae). [7,27]
3. Hybridisation - the alien taxon hybridises with native taxa.	RELEVANT, POSSIBLY UNDERESTIMATED (1%) Hybridisation between alien and native insect species is known to occur.	Invasive Cape honeybee (*Apis mellifera capensis*) hybridises with African honeybee (*Apis mellifera scutellata*) (Hymenoptera: Apidae) reducing colony fitness. [28]
4. Transmission of disease - the alien taxon transmits diseases to native taxa.	HIGH (26%) Many alien insects are capable of disease transmission; often this is by spreading fungal or bacterial spores while feeding.	Dutch Elm Disease is spread to North American elm (*Ulmus* spp.) by the invasive banded elm bark beetle, *Scolytus schevyrewi* (Coleoptera: Curculionidae), causing high tree mortality. [29]
5. Parasitism - the alien taxon parasitizes native taxa. ***In insects this includes the impact of parasitoids and hyperparasitoids (that result in death of the host), as well as parasites (that may not kill the host)*.	RELEVANT, PROBABLY UNDERESTIMATED (4%) Parasitism of native insects by alien insects has been documented.	*Compsilura concinnata,* (Diptera: Tachinidae) introduced as a biocontrol agent for Gypsy Moth in North America switches to non-target native Giant Silk Moth, *Hyalophora cecropia* (Lepidoptera: Saturniidae) after its first generation, causing high larval mortality. [30]
6. Poisoning/toxicity - the alien taxon is toxic, or allergenic by ingestion, inhalation or contact to wildlife, or allelopathic to plants. ***Plant allelopathy is not relevant to insects*.	LOW ENVIRONMENTAL RELEVANCE (22%) Some alien insects have toxic stings or urticating hairs that may be a nuisance to humans and vertebrates. No significant impacts on other taxa are known, and broader impacts on biodiversity are unlikely.	Glassy-winged sharpshooter, *Homalodisca vitripennis* (Hemipitera: Cicadellidae) poisons predatory spiders [31]
7. Bio-fouling - the accumulation of individuals of the alien taxon on wetted surfaces leads to deleterious impact on native taxa.	LOW (1%) Bio-fouling by alien insects is very rare and is unlikely to cause much impact. Although possible impacts of	Chironomid fly, *Telmatogeton japonicas* (Diptera: Chironomidae), larvae build tubes on hard surfaces in intertidal zone which can alter microhabitat, however

	indirect interactions have not been considered.	no negative environmental impacts have been reported. [32]
8. Grazing/ herbivory/ browsing - grazing, herbivory or browsing by the alien taxon. ***Herbivory rather than grazing or browsing is insect-relevant.*	HIGH (61%) Many alien insects negatively impact plants through herbivory and while there is no direct impact on native insect biodiversity, there may be indirect effects, for example, via displacement of native insect habitat.	Emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae), feeding has resulted in millions of ash trees being killed in North America. Impacts include changes to the understorey environment, successional changes and reduction in food sources for other arthropod herbivores. [33]
9. Chemical, physical or structural impact on ecosystem - the alien taxon causes changes to either: chemical, physical, and/or structural characteristics of the native environment; nutrient and/or water cycling; disturbance regimes; or natural succession.	LOW (7%) These impacts are unlikely to be caused directly by alien insects, or impact on native insects, however there are indirect means by which these impacts may be caused by insects.	Displacement of native *Messor* and *Pogonomyrmex* ants (Hymenoptera: Formicidae) that create deep nests by shallow nesting invasive *Linepithema humile* could alter soil characteristics. [34]
10. Interaction with other alien species - The alien taxon interacts with other alien taxa, (e.g., by pollination, seed dispersal, habitat modification), facilitating a deleterious impact. ** *Facilitation of natives is highly relevant for alien insects, with higher order deleterious impacts, but is currently not captured by this mechanism.*	RELEVANT, PROBABLY UNDERESTIMATED (5%) Mutually beneficial interactions between two or more alien insect species are known to occur.	Red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), protects an invasive mealybug, *Phenacoccus solenopsis* (Hemiptera: Pseudococcidae), from predators in return for honeydew, facilitating the population growth and fitness of both species. [35]

* Kumschick et al. [19]
** suggested modification to the definition or its interpretation for insects

Figure 1



The association between invasive alien insects and the mechanisms by which they impact the environment (a,b), and the outcomes of these impacts on biodiversity and ecosystems (c,d). The associations are shown at the level of Insect order (a, c) and family (b, d) (family name abbreviations with – 'idae' as suffix). The sizes of the nodes represents the total number of links a node receives, including the weight of the link (figure was produced as four quantitative bipartite networks of taxa and their impacts in Gephi using Average Weighted Degree to size nodes) [36]. Links connecting nodes indicate the presence of the impact association within the taxon and the thickness (weight) of the lines reflects the relative frequency with which the impact occurs (light grey nodes are taxa, dark grey nodes are impacts, black nodes have no impacts). Abbreviations: preda (predation), hybri (hybridization), disease (disease transmission), para (parasitism), toxicity (poisoning/toxicity), biof (bio-fouling), herbivory (grazing/herbivory/browsing), phys (chemical/physical/structural), inva (interaction with other invasive species), nutr (modification of nutrient pool), food web (modification of food web), nat biodiv (reduction in native biodiversity), ecos (unspecified ecosystem modification), hab d (habitat degradation), hab l (habitat loss), fire (modification of fire regime), pop size (population size decline), growth (reduces/inhibits growth of other species), gen res (alteration of genetic resources) and health (plant/animal health).

Supplementary material

Table S1. Environmental and socio-economic impact outcomes of alien and invasive species from Blackburn et al. [3] Outcomes with asterisks scored positively for the species we examined.

	Impact Outcomes
	Environmental – Ecosystem/Habitat
1	Modification of hydrology/water regulation or purification and quality/soil moisture
2	Primary productivity alteration
3*	Modification of nutrient pool (e.g. soil N availability) and fluxes (e.g. litter decomposition)
4	Modification of benthic communities
5*	Modification of food web (includes trophic cascades, plant-pollinator interactions, natural enemies – biocontrol)
6*	Reduction in native biodiversity
7*	Unspecified ecosystem modification
8*	Habitat degradation
9*	Habitat or refugia replacement/loss
10	Physical disturbance
11*	Modification of fire regime
12	Modification of successional patterns
13	Soil or sediment modification: erosion
14	Soil or sediment modification: accretion/bioaccumulation
15	Soil or sediment modification: modification of structure
16	Soil or sediment modification: modification of pH, salinity or organic substances
	Environmental – Species/Population
17*	Population size decline
18	Species range change (i.e. contraction, expansion, shift)
19*	Reduces/inhibits the growth of other species
20*	Alteration of genetic resources: changes in gene pool/selective loss of genotypes
21	Indirect mortality
22*	Plant/animal health
23	Interference with reproduction
	Socio-Economic
1*	Damage to agriculture (food, fuel, fibre)
2*	Damage to forestry (food, fuel, fibre)
3	Damage to aquaculture/mariculture/fishery
4	Reduce/damage livestock and products (food, fibre, labour…)
5*	Human health (diseases, allergies, injuries, toxicity)
6*	Human nuisance
7	Modification of landscape
8*	Damage to infrastructure
9*	Damage to ornamentals (gardens, golf courses…)
10*	Modification of cultural, educational, aesthetic, religious and ornamental values
11*	Alteration of recreational use and tourism
12*	Impact on trade/international relations
13	Limited access to water, land and other
14*	Other economic impact (damage to properties)

Table S2. Insect species listed in the Global Invasive Species Database (GISD, and used in our analysis). * denotes a species (n=14) that is listed on the IUCN "100 of the World's Worst Invasive Alien Species" list [37]. Paired symbols (ˣ ᶲ † •) denote species in the same Family with identical scores across mechanisms and outcomes. For such species only one was included in the analysis to avoid representational bias.

Species	Common Name	Order	Family
***Anoplolepis gracilipes* ***	Yellow crazy ant	Hymenoptera	Formicidae
***Bemisia tabaci* ***	Silverleaf whitefly	Hemiptera	Aleyrodidae
Cactoblastis cactorum	Cactus moth	Lepidoptera	Pyralidae
Harmonia axyridis	Harlequin ladybird	Coleoptera	Coccinellidae
Icerya purchasi	Cottony cushion scale	Hemiptera	Monophlebidae
***Lymantria dispar* ***	Gypsy moth	Lepidoptera	Erebidae
***Pheidole megacephala* ***	Big-headed ant	Hymenoptera	Formicidae
Philornis downsi	-	Diptera	Muscidae
Solenopsis geminata	Fire ant	Hymenoptera	Formicidae
***Solenopsis invicta* ***	Red imported fire ant	Hymenoptera	Formicidae
***Wasmannia auropunctata* ***	Little fire ant	Hymenoptera	Formicidae
Adelges piceae	Balsam woolly adelgid	Hemiptera	Adelgidae
Adelges tsugae	Hemlock woolly adelgid	Hemiptera	Adelgidae
***Aedes albopictus* * ˣ**	Asian tiger mosquito	Diptera	Culicidae
Apis mellifera scutellata	African honey bee	Hymenoptera	Apidae
Calliphora vicina	Common blowfly	Diptera	Calliphoridae
Compsilura concinnata	-	Diptera	Tachinidae
***Coptotermes formosanus* ***	Formosan subterranean termite	Blattodea	Rhinotermitidae
Culex quinquefasciatus	Southern house mosquito	Diptera	Culicidae
***Linepithema humile* ***	Argentine ant	Hymenoptera	Formicidae
Orthezia insignis	Lantana bug	Hemiptera	Ortheziidae
Polistes chinensis antennalis	Asian paper wasp	Hymenoptera	Vespidae
Vespula germanica	European wasp	Hymenoptera	Vespidae
***Vespula vulgaris* ***	Common yellowjacket	Hymenoptera	Vespidae
Maconellicoccus hirsutus	Hibiscus mealybug	Hemiptera	Pseudococcidae
Acromyrmex octospinosus	Leaf-cutting ant	Hymenoptera	Formicidae
Aedes aegypti	Yellow fever mosquito	Diptera	Culicidae
Agrilus planipennis	Emerald ash borer	Coleoptera	Buprestidae
***Anopheles quadrimaculatus* *ˣ**	Common malaria mosquito	Diptera	Culicidae
Anoplophora chinensis	Citrus long-horned beetle	Coleoptera	Cerambycidae
***Anoplophora glabripennis* ***	Asian long-horned beetle	Coleoptera	Cerambycidae
Anthonomus grandis	Mexican cotton boll weevil	Coleoptera	Curculionidae
Aulacaspis yasumatsui	Asian cycad scale	Hemiptera	Diaspididae
Bactrocera tryoni	Queensland fruit fly	Diptera	Tephritidae
Brontispa longissima	Coconut leaf/hispine beetle	Coleoptera	Chrysomelidae
Ceratitis capitata	Mediterranean fruit fly	Diptera	Tephritidae
***Cinara cupressi* ***	Cypress aphid	Hemiptera	Aphididae
Dendroctonus valens	Red turpentine beetle	Coleoptera	Curculionidae
Dendrolimus sibiricus	Siberian moth	Lepidoptera	Lasiocampidae
Diaphorina citri	Asian citrus psyllid	Hemiptera	Psyllidae

Gonipterus scutellatus Φ	Eucalyptus snout beetle	Coleoptera	Curculionidae
Hemiberlesia pitysophila	Pine armored scale	Hemiptera	Diaspididae
Homalodisca vitripennis	Glassy-winged sharpshooter	Hemiptera	Cicadellidae
Hoplochelus marginalis	-	Coleoptera	Melolonthidae
Hylastes ater †	Black pine bark beetle	Coleoptera	Curculionidae
Ips typographus †	Eight-toothed bark beetle	Coleoptera	Curculionidae
Lasius neglectus	Invasive garden ant	Hymenoptera	Formicidae
Lymantria mathura	Rosy gypsy moth	Lepidoptera	Erebidae
Lymantria monacha	Black arches	Lepidoptera	Erebidae
Monomorium destructor (Trichomyrmex)	Singapore ant	Hymenoptera	Formicidae
Monomorium floricola	Bicoloured trailing ant	Hymenoptera	Formicidae
Monomorium pharaonis	Pharaoh ant	Hymenoptera	Formicidae
Myrmica rubra	European fire ant	Hymenoptera	Formicidae
Nylanderia pubens	Caribbean crazy ant	Hymenoptera	Formicidae
Ochlerotatus japonicus japonicus	Asian bush mosquito	Diptera	Culicidae
Oracella acuta	Loblolly pine mealybug	Hemiptera	Pseudococcidae
Orthotomicus erosus •	Mediterranean pine engraver beetle	Coleoptera	Curculionidae
Oryctes rhinoceros	Asiatic/coconut rhinoceros beetle	Coleoptera	Scarabaeidae
Pachycondyla chinensis	Asian needle ant	Hymenoptera	Formicidae
Paratachardina pseudolobata	Lobate lac scale	Hemiptera	Kerriidae
Paratrechina longicornis	Longhorn crazy ant	Hymenoptera	Formicidae
Quadrastichus erythrinae	Erythrina gall wasp	Hymenoptera	Eulophidae
Scolytus multistriatus Φ	Elm bark beetle	Coleoptera	Curculionidae
Scyphophorus acupunctatus	Agave snout weevil	Coleoptera	Curculionidae
Sirex noctilio	Sirex woodwasp	Hymenoptera	Siricidae
Solenopsis papuana	Papuan thief ant	Hymenoptera	Formicidae
Solenopsis richteri	Black imported fire ant	Hymenoptera	Formicidae
Tapinoma melanocephalum	Ghost ant	Hymenoptera	Formicidae
Technomyrmex albipes	White-footed ant	Hymenoptera	Formicidae
Tetropium fuscum	Brown spruce longhorn beetle	Coleoptera	Cerambycidae
Thaumetopoea pityocampa	Pine processionary	Lepidoptera	Thaumetopoeidae
Tomicus piniperda •	Common pine shoot beetle	Coleoptera	Curculionidae
Toumeyella parvicornis	Pine tortoise scale	Hemiptera	Coccidae
***Trogoderma granarium* ***	Khapra beetle	Coleoptera	Dermestidae
Vespa velutina (nigrithorax)	Asian black hornet	Hymenoptera	Vespidae
Vespula pensylvanica	Western yellowjacket	Hymenoptera	Vespidae
Xyleborus glabratus	Redbay ambrosia beetle	Coleoptera	Curculionidae
Xylosandrus compactus	Black twig borer/shot-hole borer	Coleoptera	Curculionidae
Number of species: 78 Number of species for analysis (excluding identical scoring pairs): 74		6 orders	34 families

Figure S1

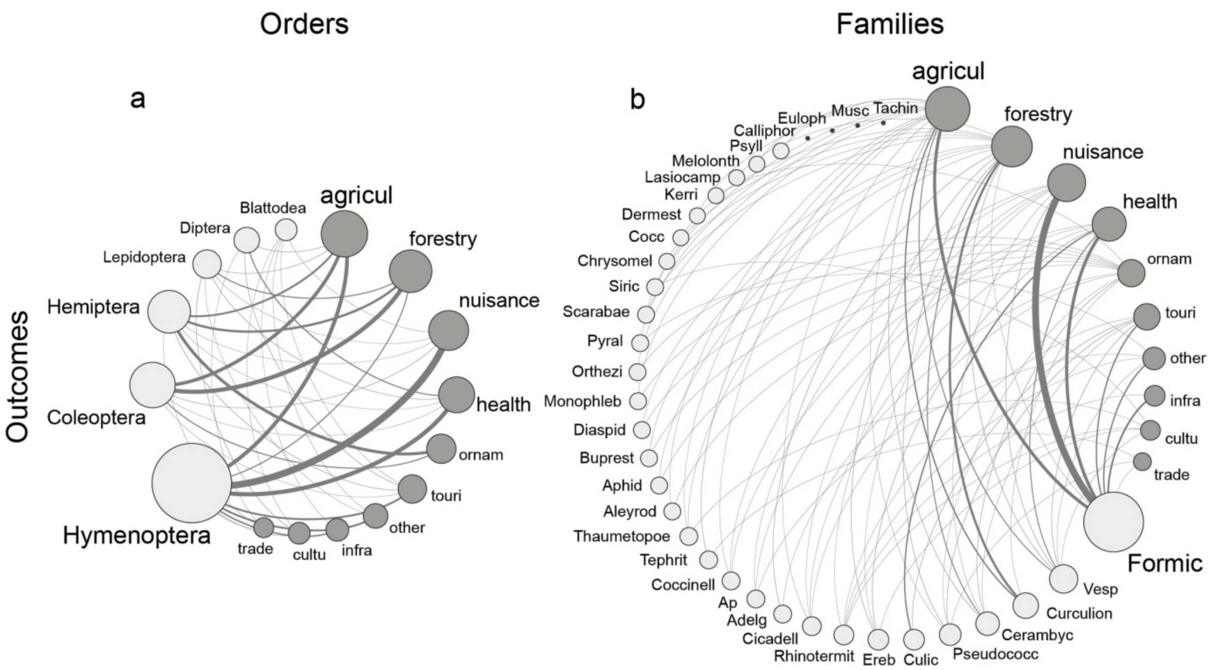


Figure S1. The association between invasive alien insects and socio-economic impact outcomes. The associations are shown at the level of Insect order (a) and family (b) (family name abbreviations with – 'idae' as suffix). The sizes of the nodes represents the total number of links a node receives, including the weight of the link (figure was produced as four quantitative bipartite networks of taxa and their impacts in Gephi using Average Weighted Degree to size nodes) [34]. Links connecting nodes indicate the presence of the impact association within the taxon and the thickness (weight) of the lines reflects the relative frequency with which the impact occurs (light grey nodes are taxa, dark grey nodes are impacts, black nodes have no impacts). Abbreviations: agricul (damage to agriculture), forestry (damage to forestry), health (human health), nuisance (human nuisance), infra (damage to infrastructure), ornam (damage to ornamentals), cultu (modification of cultural values), touri (alteration of recreational use and tourism), trade (impact on trade/international relations) and other (other economic impact).