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Border interceptions of forest insects established in Australia: intercepted invaders travel early and often

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Abstract

Invasive forest insects continue to accumulate in Australia (and worldwide) and cause significant impacts through costs of prevention, eradication and management, and through productivity losses and environmental and biodiversity decline. We used our recent non-native Australian forest insect species inventory to analyse border interception rates (2003–2016) of established species, and link interception frequencies with biological traits, historical establishment patterns, commodities and countries of origin. The strongest predictor of interception frequency was year of establishment. Polyphagous species were more likely to be intercepted, as were more concealed species, although this latter likely reflects the higher interceptions of bostrichid borers and other wood-boring Coleoptera relative to other taxa. Interceptions occurred more often for species native to Asia; in contrast, interceptions from other regions were more likely to be of species invasive there. While interception frequencies did not provide a good overall indicator of contemporaneous species establishments, wood and bark borers were more closely linked for establishments and interceptions. The first fifty forest insect species to establish comprised 85% of all border interceptions of established species between 2003 and 2016, while the most-recent fifty species represented just 6% of interceptions. We suggest that early-establishing species are among the "super-invaders" that continue to move globally, while more recent invasive species may be exploiting new trade pathways, new commodity associations, or changes in dynamics in their countries of origin.

Keywords

Biosecurity, exotic, nonindigenous species, non-native, quarantine

Introduction

International trade and travel pose an increasing risk of the movement of non-native species. Forest insect invasions are among the most wide-ranging and high-impact unintended outcomes of this globalised economy (Brockerhoff et al. 2006), causing significant impacts to planted and native forests via costs associated with their prevention, detection (Mayo et al. 2003), eradication (Brockerhoff et al. 2010) and management (Cameron et al. 2018), and severe impacts on forest productivity (Moser et al. 2009), ecosystem functions (Clark et al. 2010), ecosystem services (Boyd et al. 2013) and biodiversity (Liebhold et al. 2017), as well as negatively influencing property prices and trade (Holmes et al. 2009; Aukema et al. 2011; Lovett et al. 2016).

Australia has recorded an average of one new non-native forest insect (those associated with plantation, amenity and native trees, and timber) establishment per year over the last 135 years (Nahrung and Carnegie 2020), with one species (*Sirex noctilio*) costing AUD$35M in losses and control (Cameron et al. 2018), while another two (*Hylotrupes bajulus* and *Marchalina hellenica*) cost AUD$45M in eradication/containment since 2003 (Carnegie and Nahrung 2019). There are increased costs associated with post-border detections compared with the prevention of arrival (Epanchin-Niell et al. 2015; Reaser et al. 2020), and hence, it is important to identify high-risk invasion pathways with a view to reducing risk (Byers et al. 2005; McGeoch et al. 2016). Given conflicting reports on the utility of border interceptions to predict invasion risk (e.g. Brockerhoff et al. 2006; Haack 2006; Caley et al. 2014; Lee et al. 2016), the recent initiation of a National Forest Biosecurity Surveillance Strategy in Australia (Department of Agriculture and Water Resources 2018), and the ongoing risk of invasive insects to Australia's forests, we sought to examine potential relationships between border interceptions and established forest and timber insects in Australia. To this end, we used historical and contemporaneous data to identify patterns that may help to understand invasions and potentially reduce future incursions. For example, a better understanding of pathway-commodity-taxa relationships can assist with designing surveillance tools for early detection within areas of high risk (Poland and Rassati 2019).

Biological invasions are generally considered in three distinct phases: arrival, establishment and spread (Liebhold and Tobin 2008). We have previously explored non-native forest insect establishment and spread (Nahrung and Carnegie 2020) and post-border detections and responses to recent incursions of forest insects in Australia (Carnegie and Nahrung 2019); here we add contemporaneous arrival of these established non-native insects to our examination of Australian non-native insect invasion processes. We used our recently compiled database (Nahrung and Carnegie 2020) to examine border interception patterns for recent and historical established insect species in relation to biological traits, invasion history and phylogeny. Interceptions are defined as by ISPM 5 (FAO 2019): the detection of a pest during inspection – in this case at the border. We use our results to identify – at least among those already established – taxa that are more likely to be intercepted, pathways that are likely to be used, and origins that represent higher likelihood of interceptions occurring to inform emerging forest biosecurity arrangements in Australia.

Materials and methods

Insects of forest-relevance (amenity, plantation and native trees, and timber-in-service pests) that established in Australia over the last 135 years were taken from Nahrung and Carnegie (2020), a database that includes the year of first recorded occurrence host range, distribution and impact collated from records and literature. The number of interceptions of each insect species was extracted from the Australia-wide Department of Agriculture, Water and Environment (DAWE) border interception database (2003–2016), accessed under a formal data-sharing deed with HFN. These interception data comprise air, sea and mail border detections made during inspection by phytosanitary personnel at ports of entry associated with international cargo, travellers and mail. Available details included country of origin, and commodity-association, which were categorised to geographic region and broad commodity (dried (including woven plant material, dried fruit, seeds, nuts and grains) and fresh plant material (including nursery stock, fresh flowers, fruit and vegetables), wood packaging (pallets, dunnage, and crates) and wood products (logs, timber, furniture and artefacts), non-host commodity (hitch-hiking)). Within these commodity classes, the data were further partitioned as to whether they comprised commercial (cargo) or non-commercial (baggage, mail and personal effects) pathways. The Australian state/territory in which the interception occurred was recorded and included in some analyses.

Descriptive summaries of interception frequencies at Order and Family levels were prepared, as well as by native range and shipment origin. Frequencies were compared using goodness of fit two-way Chi-square tests where required and where sample sizes were high enough to allow comparison. Family-level analyses only considered families for which at least three species were established, or more than ten interceptions were recorded.

Traits previously noted to be important in forest invasions (body size, concealment, host-associated lifestages (Nahrung and Swain 2014) and parthenogenetic reproduction (Niemelä and Mattson 1996)) were determined for each established species from literature. Polyphagy, impact, year of establishment and number of Australian states and global regions where each insect is also invasive were taken from Nahrung and Carnegie (2020) and further used in trait analyses. Non-multidimensional scaling (nMDS) and analysis of similarity (ANOSIM) based on an index of association matrix (Clarke and Gorley 2015) of these traits was used to compare intercepted and non-intercepted species groups, with similarity percentage (SIMPER) analysis subsequently used to identify the traits that contributed the most to group separation (Clarke 1993). The software used for these multivariate analyses was Primer 7 (V 7.0.13, PRIMER-e). Spearman rank correlation was used to examine relationships between the number of interceptions and numerical trait scores. These were further examined using Mann-Whitney U-tests testing comparing trait ranks between binary groups "intercepted" and "not-intercepted". For intercepted species, geographic origin and commodity associations were also examined. These analyses were performed using IBM SPSS V26.

Finally, to test the hypothesis that interception frequency can be used as a predictor of establishment as a surrogate of propagule pressure (*sensu* Caley et al. 2014;

Eschen et al. 2014), we compared interceptions and establishments over the same period for which our interception data were available (2003–2016).

We acknowledge the limitations of the border interception data including a lack of information on relative inspection rates and import volumes, difficulties in accurately identifying different insect lifestages and potential differences in inspection rates and methods between jurisdictions. The insects were destroyed as part of usual biosecurity processes.

Results

A total of 4,013 interceptions were made of 74 of the 135 forest insect species established in Australia (Suppl. material 1). There were 1,954 interceptions of the established Coleoptera, 1,815 interceptions of established Hemiptera, and 244 of established species in other Orders (Hymenoptera (4), Lepidoptera (179), Thysanoptera (61)). Significantly fewer of the established species that primarily impact forestry (28/70) were intercepted than species that affect other industries as well as forestry (46/65) (χ^2_1 = 12.9, P = 0.0003). Most established species were never (41%) or rarely (1–5 times) (35%) intercepted (Figure 1), with significantly more species of established Coleoptera intercepted (27/33) than species of Hemiptera (43/93) (χ^2_1 = 12.5, P<0.001).

For families represented by three or more species, there were no interceptions of any of the three established species in each of the Adelgidae, Cicadellidae and Tenthredinidae (Figure 2, Table 1). The Bostrichidae was the most-intercepted family, with all six established species intercepted – five in at least six Australian states/territories – and an average of 262 interceptions per species (Table 1). In contrast, the Aphididae had high numbers of interceptions representing the lowest proportion of established species, with 77% of established species never intercepted (Table 1). Within the Hemiptera, a significantly higher proportion of scale insects (Diaspididae, Coccidae, Pseudococcidae) were intercepted than aphids (72%) (χ^2_1 = 17.1, P<0.001) (Table 1).

Interception frequencies varied by native range, with higher intercepted: unintercepted ratios for species that originated from Asia-Pacific and South America than for species whose native range was Europe or North America (Figure 3).

Based on the similarity (index of association) of trait scores (body size, concealment, host-associated lifestages, sexual/asexual or partial asexual reproduction, polyphagy, impact, year established, distribution within Australia and global distribution), ANOSIM showed a significant difference between established species that were intercepted and those that were not intercepted (R = 0.17, P = 0.001) with nMDS showing a slight separation between groups (Figure 4a) and SIMPER analysis revealing that 'year established' contributed 79% of the dissimilarity between groups. Group separation was maintained (R = 0.19, P = 0.001) when 'other' taxa were removed (Figure 4b), with 'year established' contributing 80% to dissimilarity between intercepted and non-intercepted taxa.

The number of border interceptions per established species was negatively correlated with their year of establishment (rho = -0.4, P < 0.001), with intercepted species hav-

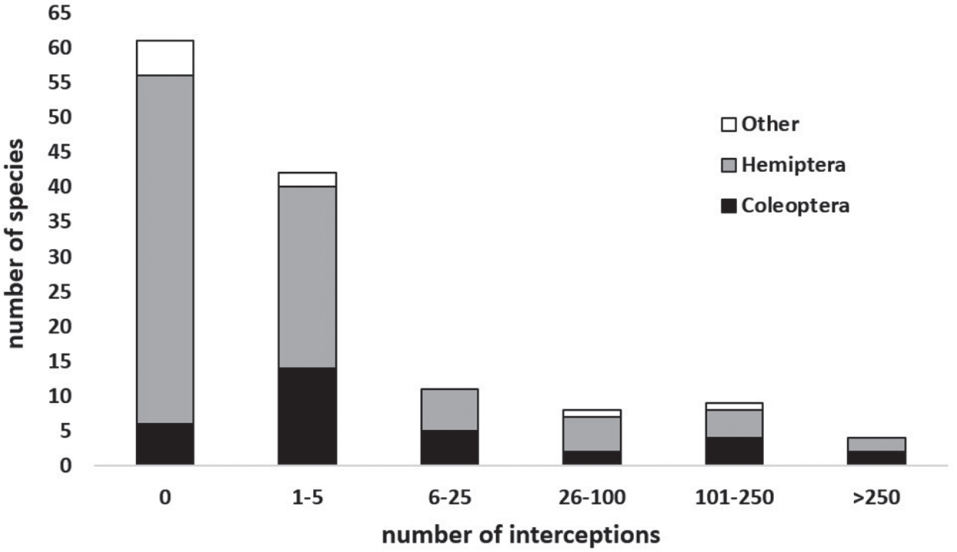

Figure 1. Frequency histogram showing the number of times established forest insects were intercepted at the Australian border between 2003 and 2016. Total number of interceptions = 4,013. "Other" orders include species of Lepidoptera (2), Thysanoptera (2) and Hymenoptera (5).

Table 1. Number of established species, intercepted species and total number of interceptions (2003–2016) per family for forest insect species established in Australia. Only families with >3 established species or >10 interceptions were tabled. COL=Coleoptera; HEM=Hemiptera; OTH=other orders (Lepidoptera, Thysanoptera).

Order	Family	N species established	N species intercepted (%)	N interceptions	Interceptions/established sp
COL	Anobiidae	1	1	15	15.0
	Bostrichidae	6	6 (100)	1573	262.2
	Cerambycidae	3	3 (100)	16	5.3
	Curculionidae	19	14 (73.6)	224	11.8
	Dynastidae	1	1	55	55.0
	Ptinidae	1	1	68	68.0
HEM	Aphididae	30	7 (23)	813	27.1
	Coccidae	15	10 (66.7)	60	4.0
	Diaspididae	24	17 (70.8)	796	33.2
	Pseudococcidae	7	6 (85.7)	139	19.9
OTH	Noctuidae	1	1	179	179.0
	Thripidae	1	1	61	61.0

ing established in Australia significantly earlier (median establishment year 1926) than those that were not intercepted (median 1952) (Mann-Whitney U-test, U = 1387.5, P < 0.001) (Figure 5); similarly, a significantly higher proportion of the species that established prior to 1900 was intercepted than for the species that established since the 1940s (χ^2_1 = 0.02–8.5, P = 0.004–0.9). The first fifty forest insect species to establish comprised 85% of all border interceptions between 2003 and 2016, while the most-recent fifty species represented just 6%.

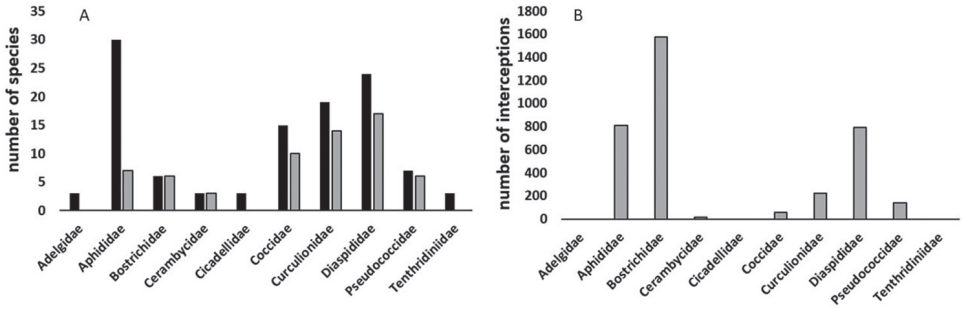

Figure 2. Number of established (black) and intercepted (grey) species (**A**), and number of interceptions (**B**) between 2003 and 2016 of invasive forest species in families with >3 species established in Australia.

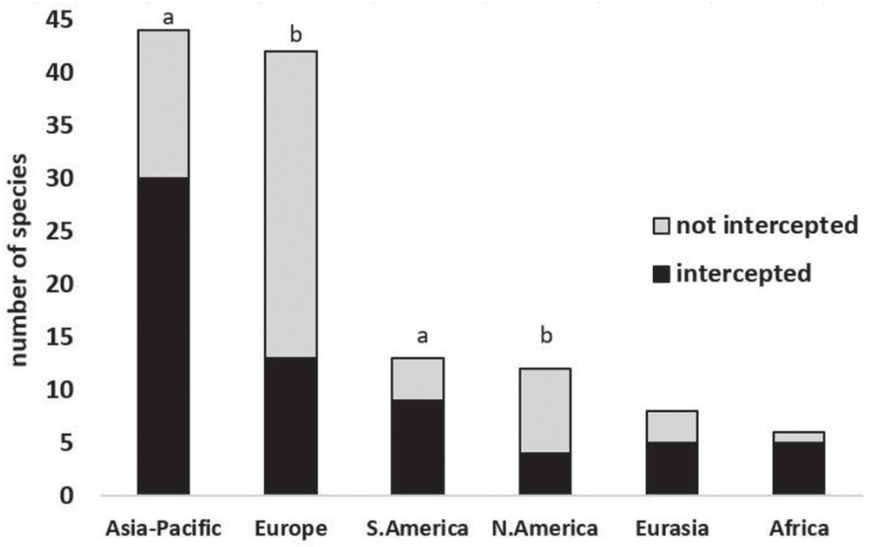

Figure 3. Relative number of species intercepted and not intercepted between 2003 and 2016 of forest-related insect species established in Australia according to their native range. Letters above bars designate significant differences between frequencies of intercepted/not intercepted taxa for regions with sufficient data to enable comparison.

As well as interception probability being associated with time since establishment, it was also significantly related to polyphagy (Spearman rank correlation, rho = 0.49, $P < 0.001$), with those species that were intercepted having significantly broader host ranges than those that were not intercepted (Mann-Whitney U-test, U = 3394.5, $P < 0.001$). Similarly, insects with a broader geographic distribution within Australia (Spearman rank correlation, rho=0.49, $P<0.001$) and globally (rho = 0.37, $P < 0.001$) were more likely to be intercepted than those with smaller distributions.

This relationship with prior distribution may be reflected in the number of interceptions where shipment origin was recorded (n = 3,821), where insects detected from North

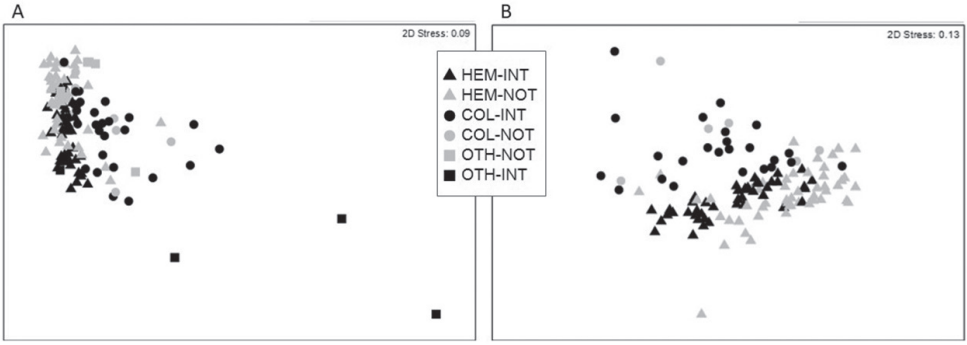

Figure 4. nMDS plots based on the index of association of traits of non-native Hemiptera (triangles), Coleoptera (circles) and insects from other orders (squares) (**A**) and Hemiptera and Coleoptera only (**B**) established in Australia and whether they were intercepted (INT) (black) or not intercepted (NOT) (grey) at the border between 2003 and 2016.

Table 2. Most frequently intercepted (>100 times between 2003 and 2016) established non-native forest-related insects in Australia. Forest-specific species are marked with an asterisk, with those causing moderate impact marked with two asterisks. N is the number of times each species was intercepted, and year is the first recorded establishment in Australia.

Species	Order	Family	N	Year
*Dinoderus minutus***	Coleoptera	Bostrichidae	564	1915
*Minthea rugicollis***	Coleoptera	Bostrichidae	529	1924
Macrosiphum euphorbiae	Hemiptera	Aphididae	373	1920
Aonidiella aurantiae	Hemiptera	Diaspididae	365	1896
Aphis gossypii	Hemiptera	Aphididae	222	1902
Pseudaulacaspis pentagona	Hemiptera	Diaspididae	195	1898
Helicoverpa armigera	Lepidoptera	Noctuidae	179	1885
*Heterobostrychus aequalis**	Coleoptera	Bostrichidae	179	2013
*Lyctus brunneus**	Coleoptera	Bostrichidae	169	1899
Myzus persicae	Hemiptera	Aphididae	161	1903
Naupactus cervinus	Coleoptera	Curculionidae	160	1934
Hemiberlesia lataniae	Hemiptera	Diaspididae	157	1897
*Sinoxylon anale***	Coleoptera	Bostrichidae	131	1924

America, Europe and New Zealand were mostly of species that were invasive in those regions (i.e. representing possible bridgehead movement) (Figure 6). However, the highest numbers of intercepted species were in shipments from Asia-Pacific, and most were of species native to that region. The highest proportion of interceptions from Africa and South America were of species that were not recorded as being established in those regions.

In parallel, the more regions from which a species was intercepted, the more interceptions of that species occurred (Spearman rank correlation, rho = 0.71, $P < 0.001$). The most commonly-intercepted species are listed in Table 2, of which five species are primarily forestry pests, with three considered of moderate impact. Primarily forest pests, including high priority pests not yet established in Australia, will be examined further in another study (Nahrung and Carnegie in prep). The median establishment

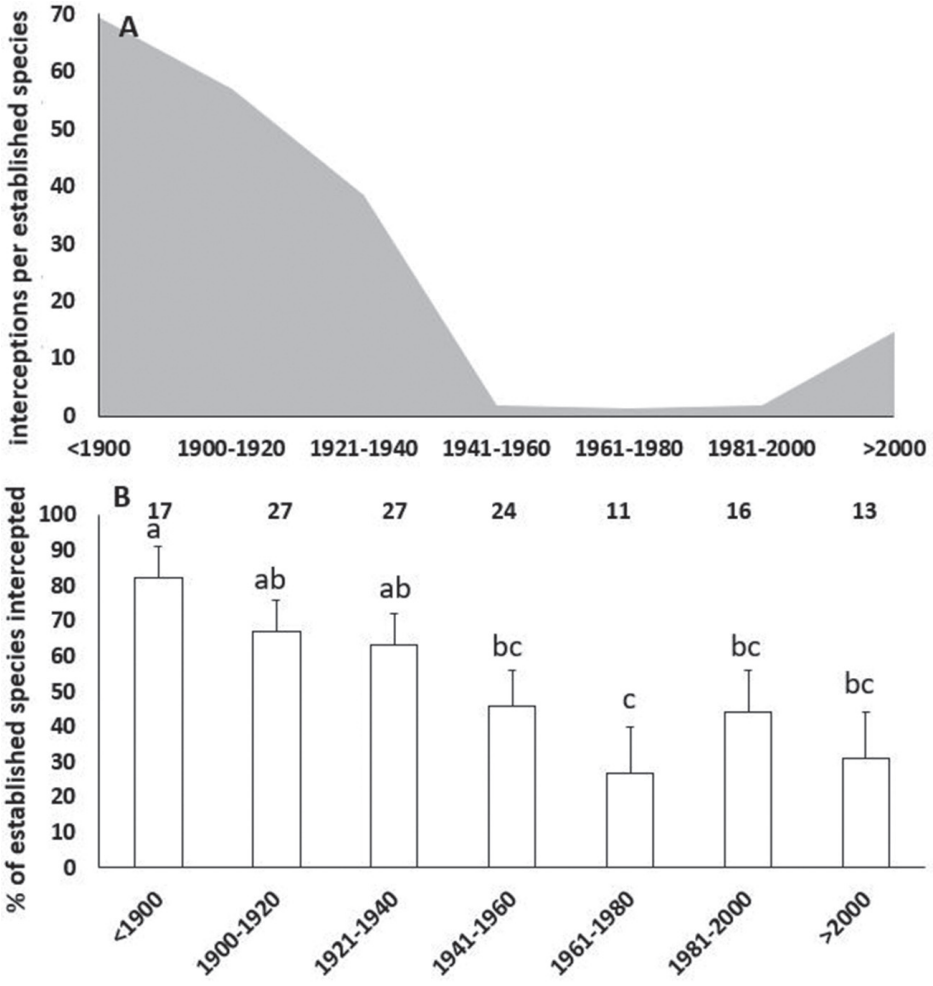

Figure 5. Number of border interceptions per non-native forest insect species that established in Australia in 20-year intervals (**A**) and the percentage (+SE) of established species that were intercepted according to when they established (**B**). Number of species that established in each time period above the bars in 5B.

year for the most highly-intercepted species was 1903, compared to 1929 for species intercepted <100 times, and 1952 for non-intercepted species (Table 2).

Of the other biological traits considered, concealed species were more likely to be intercepted (Spearman rank correlation, rho=0.29, P=0.001) and species that were more parthenogenetic were less likely to be intercepted (rho = -0.27, P = 0.002); these patterns likely reflect the very high interceptions of wood-borers (concealed, sexual) and the under-representation of intercepted aphids (free-living, parthenogenetic) among established taxa.

There were very strong commodity associations between taxa, with Hemiptera almost completely (98%) associated with fresh plant material (e.g. nursery stock, fruit,

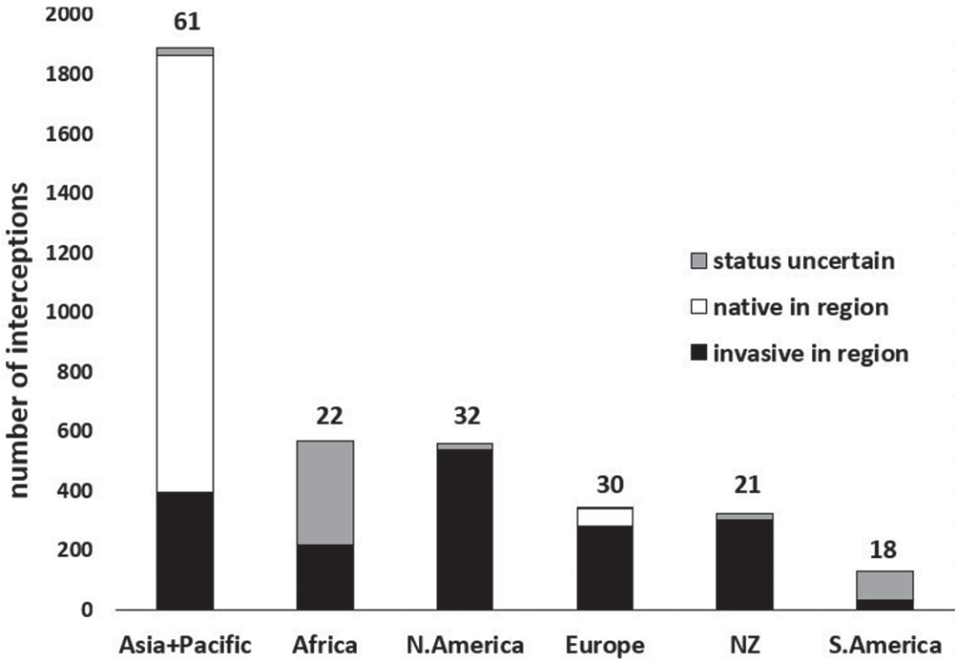

Figure 6. Number of interceptions of established forest insects in Australia from different regions, and the status of the species intercepted in that region (see Nahrung and Carnegie 2020). Numbers above bars indicate the total number of species intercepted from that source region.

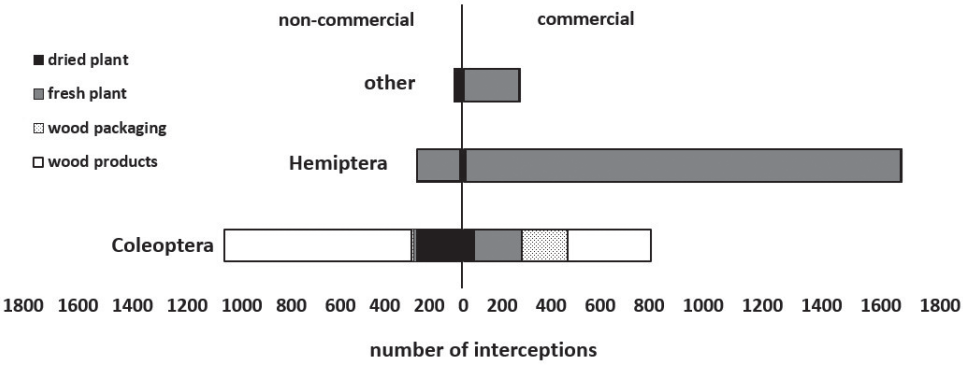

Figure 7. Number of interceptions of established forest species of Hemiptera, Coleoptera and other orders (Hymenoptera, Lepidoptera, Thysanoptera) on different commodities on non-commercial (baggage, mail, personal effects) and commercial (cargo) pathways between 2003 and 2016.

foliage) and Coleoptera largely (64%) associated with wood (e.g. packaging, timber, furniture, and artefacts) (Figure 7).

About 90% of interceptions of Hemiptera were made in commercial cargo, in contrast to Coleoptera where 60% of interceptions were associated with non-

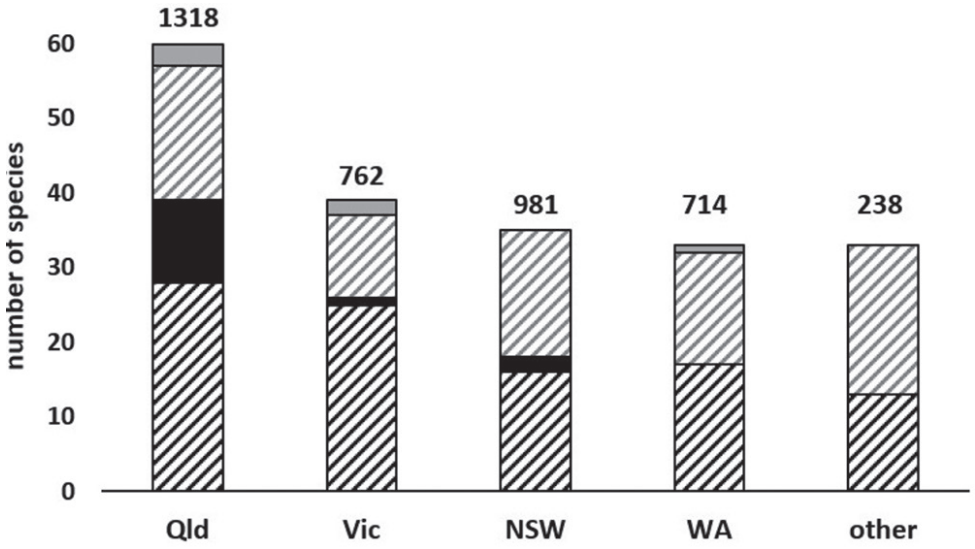

Figure 8. Number of established species of Hemiptera (black) and Coleoptera (grey) intercepted in Queensland (Qld), Victoria (Vic), New South Wales (NSW), Western Australia (WA), South Australia (SA), Northern Territory (NT), and Tasmania (Tas),with unique species in solid colour. Total number of interceptions per state is above the bars.

commercial pathways (baggage, mail, personal effects) (χ^2_1 = 988, P < 0.001); this is again likely a reflection of the high interception rate of bostrichid borers. Only about 5% of interceptions were made on non-host commodities (ie hitch-hikers).

Within Australia, one-third of all border interceptions of established species was made in Queensland. Overall, 59% of established species were intercepted at the border of the first state that they were recorded as established in, with ten species intercepted in at least six states/territories, and twenty species intercepted in only one state. Queensland had the highest number of interceptions, the highest number of species intercepted, and the highest number of unique interceptions (Figure 8).

Four of the eleven species that established during the interception data collection period (2003 to 2016) were intercepted in that timeframe, three of which were Coleoptera. Only one species was intercepted more than three times – and its establishment date is dubious (see discussion). Of the other three species, only two interceptions were made in the period prior to their discovery in Australia, such that only one interception of one of the four moderate-high impact pest species was made prior to their establishment (Table 3). Two-thirds (126) of these interceptions were made in commercial cargo.

Discussion

Just over half (55%) of the non-native forest and timber insects established in Australia since 1885 were intercepted at the border between 2003 and 2016, with one-third of

Table 3. Non-native forest insects established in Australia 2003–2016 and number of border interceptions (N) of each in this timeframe and prior to establishment in parentheses. Those causing moderate impact are marked with one asterisk, those with high impact with two.

Species	Order	Family	N	Year
*Nematus oligospilus**	Hymenoptera	Tenthredinidae	0	2003
Psyllopsis fraxinicola	Hemiptera	Psyllidae	0	2003
*Hylotrupes bajulus***	Coleoptera	Cerambycidae	2 (1)	2004
*Corythucha ciliata**	Hemiptera	Tingidae	3 (0)	2006
Cinara pilicornis	Hemiptera	Aphididae	0	2008
Tuberolachnus salignus	Hemiptera	Aphididae	0	2010
Chaitophorus leucomelas	Hemiptera	Aphididae	0	2011
Xylosandrus crassiusculus	Coleoptera	Curculionidae	2 (1)	2011
Heterobostrychus aequalis	Coleoptera	Bostrichidae	179 (157)	2013
Shivaphis celti	Hemiptera	Aphididae	0	2013
*Marchalina hellenica***	Hemiptera	Margarodidae	0	2014

contemporaneous establishments being intercepted in the same period. In contrast to the USA (McCullough et al. 2006), significantly more Coleoptera were intercepted than Hemiptera, although more Hemiptera were established. Bostrichid borers were the most highly intercepted family both here and in Wylie and Yule (1977)'s Australian study, and are likewise over-represented in interceptions globally (Turner et al. in review). This is reflected in our trait analyses, which indicated that concealed species were more likely to be intercepted than free-living species. Sessile concealed taxa such as wood borers are protected from desiccation and extreme temperatures and may be more likely to survive transportation (Sopow et al 2015). Frass and holes left by wood borers may provide visual cues that increase detectability that mobile insect lifestages do not, although not all borers do this (e.g. siricid wasps (Burnip et al. 2010)). Alternatively, the over-representation of concealed species in interceptions could reflect the importance of wood borers as quarantine pests (Lawson et al. 2018) and that wood products and packaging are high-risk commodities that may attract added scrutiny (Kenis et al. 2007).

Brockerhoff et al. (2006, 2014) and Haack (2006) described positive relationships between interceptions (propagule pressure) and establishments among bark and wood borers, and indeed, 88% of wood and bark borers historically established in Australia, and all three that established in our data timeframe were intercepted. Cerambycid borers comprised one-third of species in common between establishments and interceptions in Europe (Eschen et al. 2015), while Turner et al. (2020) described the Cerambycidae as having a small per arrival establishment probability relative to interception probability (and, similar to our results, that aphids had lower ratio of interception probability to establishment probability). Caley et al. (2014) also found higher interception rates of established Coleoptera in Australia, so it appears that interception rates may be more reflective of establishments for beetles (or that they are simply more detectable) – particularly wood and bark borers – compared with other taxa.

Overall, however, like Caley et al. (2014) we found that border interceptions did not provide a good predictor of incursion risk in Australia, at least during the time frames studied. Both studies also identified a similar pattern of interceptions with

historically established species, which Caley et al. (2014) attributed as a proxy of propagule pressure. We further consider this pattern as evidence for a suite of 'super-invaders' *sensu* Turner et al. (in review): species that are almost ubiquitous in global pathways with an invasive status among several world regions. Thus, although commonly used as a predictor for invasions and a proxy for propagule pressure, it may be that higher interception rates are more reflective of invasion success, than a predictor of it, at least among these species. For example, the top 5 of the 74 species intercepted here accounted for over half of all interceptions, are all invasive elsewhere (in an average of 4.4 other world regions), and established in Australia prior to 1924. Although biosecurity practices were less stringent in that timeframe with unregulated movement of live plants (the Australian federal government introduced its first Quarantine Act in 1908 (Maxwell et al. 2014)), trade and travel were also markedly lower, less diverse, and restricted to movement by sea. Over 80% of the species that could only have arrived by sea were still travelling that way between 2003 and 2016. Nahrung and Carnegie (2020) found that earlier-establishing species had broader global non-native distributions, further corroborating the notion that intercepted species have travelled 'early and often', leading to a self-accelerating process in which invasion begets invasion (Bertelsmeier and Keller 2018).

Polyphagy was also a correlate of interception frequency in our study, with insect species with a broader host range intercepted more often than those with a narrow host range – presumably a direct relationship with the more commodities on which a species feeds, the more pathways available and the more likely to be intercepted. While earlier-establishing species were more polyphagous than later-establishing species (Nahrung and Carnegie 2020), we found very strong relationships with establishment time and interception likelihood – year of establishment was the strongest contributor to group separation.

A notable exception to the patterns we found for interception frequency and establishment date and invasive distribution within Australia was *Heterobostrychus aequalis*, the lesser auger beetle, whose establishment status in Australia has been controversial, with several sources citing it as present in Australia prior to our listed establishment date of 2013 (see Wylie and Peters 2016); we therefore submit that it was in fact, elusive, rather than absent and likely established earlier. *Lyctus discedens* was unusual in its low interception rate, early establishment, and non-invasiveness in other global regions. It was also the only species established prior to 1900 that was not intercepted by sea between 2006 and 2013: we recommend its taxonomy be reviewed as its status is unclear (see Borowski 2020; R. Wylie pers. comm.).

As expected, live plants and wood products were responsible for the vast majority of interceptions, hosting mostly Hemiptera and Coleoptera, respectively, with both recognised major pathways for forest insect invasions (Liebhold et al. 2012; Lovett et al. 2016; Lawson et al. 2018; Meurisse et al. 2019) and subject to strict regulations regarding importation to Australia (Department of Agriculture and Water Resources 2015). Coleoptera were more likely to be associated with non-commercial pathways (baggage, mail and personal effects) than Hemiptera. This may reflect Australia's strict biosecurity

messaging to travellers regarding carrying fresh plant products, and a relatively lower public awareness of potential risks posed by unprocessed wooden materials.

Interceptions from Asia-Pacific accounted for over half of all interceptions of our established forest taxa and represented the highest proportion of regional native species. Wylie and Yule (1977) and Lawson et al. (2018) also reported higher numbers of border interceptions in goods originating from Asia. The number and taxonomic composition of established forest insects is similar between those originating from Europe and Asia (Nahrung and Carnegie 2020) but this similarity was not reflected in interceptions, with significantly more native Asian species intercepted than native European species. This is likely a reflection of higher trade volumes and smaller geographic distance with Asia, as found for ant invasions in Australia (Suhr et al. 2019). Further, most interceptions from all countries but Asia were apparently invasive to those regions – representing so-called bridgehead movement, increasingly recognised as a conduit to invasions globally (Bertelsmeier and Keller 2018). The patterns observed in Nahrung and Carnegie (2020) for higher establishments of Asian-origin species in northern Australia is perhaps also reflected in their interceptions, with 90% of intercepted Asian-Pacific species recorded at the Queensland border, compared with 57% or less in the other states. As trade diversifies in commodities among world regions, and as exotic plant species are planted in new regions, opportunities for new pathway associations and new arrivals arise (Brockerhoff and Liebhold 2017; Lantschner et al. 2020) – this may in part explain the 14-fold difference in numbers of interceptions between the first fifty species established and the most recent fifty species established. The lower frequency of recently-established species in interception pathways compared to long-established species could reflect a number, or a combination, of situations. It may reflect the reality that some pests arrive through non-commercial pathways (e.g. Paine et al. 2010; Essl et al. 2015), or that pathways considered 'lower risk' may attract less attention due to a risk-return principle (e.g. Kenis et al. 2007), or represent inspection 'gaps' (Bacon et al. 2012).

Conclusion

This study concentrated on species that are already established in Australia. A separate study will consider interceptions across an expanded range of species, and include the high priority pests of forest significance not yet established in Australia (Nahrung and Carnegie in prep.). However, here we have demonstrated clear relationships with interception frequency and time since establishment, polyphagy and invasiveness in other regions that provide further evidence for the notion of 'super-invaders' that established early and continue to be moved in international trade and travel, as well as the over-representation of Bostrichidae in interceptions and establishments (Turner et al. in review). Our results may be used to revise stakeholder engagement strategies, consider the role of emerging pathways in risk assessments, and to support 'over-the-horizon' surveillance and biosecurity networks in neighbouring regions.

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References

Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, McCullough DG (2011) Economic impacts of non-native forest insects in the continental United States. PLoS ONE 6(9): e24587. https://doi.org/10.1371/journal.pone.0024587

Bacon SJ, Bacher S, Aebi A (2012) Gaps in border controls are related to quarantine alien insect invasions in Europe. PLoS ONE 7(10): e47689. https://doi.org/10.1371/journal.pone.0047689

Bertelsmeier C, Keller L (2018) Bridgehead effects and role of adaptive evolution in invasive populations. Trends in Ecology and Evolution 33: 527–534. https://doi.org/10.1016/j.tree.2018.04.014

Borowski T (2020) World inventory of beetles of the family Bostrichidae (Coleoptera). Part 1. checklist from 1758 to 2012. World News of Natural Sciences 28: 155–170.

Boyd IL, Freer-Smith PH, Gilligan CA, Godfray HC (2013) The consequence of tree pests and diseases for ecosystem services. Science 342(6160): e1235773. https://doi.org/10.1126/science.1235773

Brockerhoff EG, Bain J, Kimberley M, Knížek M (2006) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Canadian Journal of Forest Research 36: 289–298. https://doi.org/10.1139/x05-250

Brockerhoff EG, Kimberley M, Liebhold AM, Haack RA, Cavey JF (2014) Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. Ecology 95: 594–601. https://doi.org/10.1890/13-0465.1

Brockerhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. Biological Invasions, 19: 3141–3159. https://doi.org/10.1007/s10530-017-1514-1

Brockerhoff EG, Liebhold AM, Jactel H (2006) The ecology of forest insect invasions and advances in their management. Canadian Journal of Forest Research 36: 263–268. https://doi.org/10.1139/x06-013

Brockerhoff EG, Liebhold AM, Richardson B, Suckling DM (2010) Eradication of invasive forest insects: concepts, methods, costs and benefits. New Zealand Journal of Forestry Science: S117–S135.

Burnip GM, Voice D, Brockerhoff EG (2010) Interceptions and incursions of exotic *Sirex* species and other siricids (Hymenoptera: Siricidae). New Zealand Journal of Forestry Science 40: 133–140.

Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IA, Seasted TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. Conservation Biology 16: 630–640. https://doi.org/10.1046/j.1523-1739.2002.01057.x

Caley P, Ingram R, De Barro P (2015) Entry of exotic insects into Australia: Does border interception count match incursion risk? Biological Invasions 17: 1087–1094. https://doi.org/10.1007/s10530-014-0777-z

Cameron NL, Carnegie AJ, Wardlaw T, Lawson S, Venn T (2018) Economic appraisal of Sirex Wood Wasp (*Sirex noctilio*) control in Australian pine plantations. Australian Forestry 81: 37–45. https://doi.org/10.1080/00049158.2018.1430436

Carnegie AJ, Nahrung HF (2019) Post-border forest biosecurity in Australia: Response to recent exotic detections, current surveillance and ongoing needs. Forests 10: e336. https://doi.org/10.3390/f10040336

Clark KL, Skowronski N, Hom J (2010) Invasive insects impact forest carbon dynamics. Global Change Biology 16: 88–101. https://doi.org/10.1111/j.1365-2486.2009.01983.x

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral Ecology 18: 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke KR, Gorley RN (2015) PRIMER v7: User Manual/Tutorial PRIMER-E: Plymouth.

Department of Agriculture and Water Resources (2015) Final Review of Policy: Importation of Phytophthora ramorum host propagative material into Australia. Canberra: Department of Agriculture and Water Resources.

Department of Agriculture and Water Resources (2018) National Plant Biosecurity Surveillance Strategy 2018–2023. Canberra: Plant Health Australia.

Epanchin-Niell RS, Liebhold AM (2015) Benefits of invasion prevention: effect of time lags, spread rates, and damage persistence. Ecological Economics 116: 146–153. https://doi.org/10.1016/j.ecolecon.2015.04.014

Eschen R, Roques A, Santini A (2015) Taxonomic dissimilarity in patterns of interception and establishment of alien arthropods, nematodes and pathogens affecting woody plants in Europe. Diversity and Distributions 21: 36–45. https://doi.org/10.1111/ddi.12267

Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, Cardoso AC, Eschen R, Gallardo B, Galil B, García-Berthou E (2015) Crossing frontiers in tackling pathways of biological invasions. BioScience 65: 769–782. https://doi.org/10.1093/biosci/biv082

FAO (2019) Glossary of phytosanitary terms. International Standard for Phytosanitary Measures No. 5. Rome. Published by FAO on behalf of the Secretariat of the International Plant Protection Convention (IPPC), 35 pp.

Haack RA (2006) Exotic bark-and wood-boring Coleoptera in the United States: recent establishments and interceptions Canadian Journal of Forest Research 36: 269–288. https://doi.org/10.1139/x05-249

Holmes TP, Aukema JE, Von Holle B, Liebhold A, Sills E (2009) Economic impacts of invasive species in forest past, present, and future. Annals of the New York Academy of Science 1162: 18–38. https://doi.org/10.1111/j.1749-6632.2009.04446.x

Kenis M, Rabitsch W, Auger-Rozenberg MA, Roques A (2007) How can alien species inventories and interception data help us prevent insect invasions? Bulletin of Entomological Research 97: 489–502. https://doi.org/10.1017/S0007485307005184

Lantschner MV, Corley JC, Liebhold AM (2020) Drivers of global Scolytinae invasion patterns. Ecological Applications 30: e02103. https://doi.org/10.1002/eap.2103

Lawson SA, Carnegie AJ, Cameron N, Wardlaw T, Venn TJ (2018) Risk of exotic pests to the Australian forest industry. Australian Forestry 81: 3–13. https://doi.org/10.1080/00049158.2018.1433119

Lee W, Lee Y, Kim S, Lee JH, Lee H, Lee S, Hong KJ (1996) Current status of exotic insect pests in Korea: comparing border interception and incursion during 1996–2014. Journal of Asia-Pacific Entomology 19: 1095–1101. https://doi.org/10.1016/j.aspen.2016.09.003

Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO (2012) Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Frontiers in Ecology and the Environment 10: 135–143. https://doi.org/10.1890/110198

Liebhold AM, Brockerhoff EG, Kalisz S, Nuñez MA, Wardle DA, Wingfield MJ (2017) Biological invasions in forest ecosystems. Biological Invasions 19: 3437–3458. https://doi.org/10.1007/s10530-017-1458-5

Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. Annual Review of Entomology 53: 387–408. https://doi.org/10.1146/annurev.ento.52.110405.091401

Lovett GM, Weiss M, Liebhold AM, Holmes TP, Leung B, Lambert KF, Orwig DA, Campbell FT, Rosenthal J, McCullough DG, Wildova R (2016) Nonnative forest insects and pathogens in the United States: Impacts and policy options. Ecological Applications 26: 1437–1455. https://doi.org/10.1890/15-1176

Mayo JH, Straka TJ, Leonard DS (2003) The cost of slowing the spread of the gypsy moth (Lepidoptera: Lymantriidae). Journal of Economic Entomology 96: 1448–1454. https://doi.org/10.1093/jee/96.5.1448

Maxwell A, Vettraino AM, Eschen R, Andjic V (2014) International plant trade and biosecurity. In Horticulture: Plants for People and Places (Vol. 3). Springer, Dordrecht, 1171–1195. https://doi.org/10.1007/978-94-017-8560-0_9

McCullough DG, Work TT, Cavey JF, Liebhold AM, Marshall D (2006) Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biological Invasions 8: e611. https://doi.org/10.1007/s10530-005-1798-4

McGeoch MA, Genovesi P, Bellingham PJ, Costello MJ, McGrannachan C, Sheppard A (2016) Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biological Invasions 18: 299–314. https://doi.org/10.1007/s10530-015-1013-1

Meurisse N, Rassati D, Hurley BP, Brockerhoff EG, Haack RA (2019) Common pathways by which non-native forest insects move internationally and domestically. Journal of Pest Science 92: 13–27. https://doi.org/10.1007/s10340-018-0990-0

Moser WK, Barnard EL, Billings RF, Crocker SJ, Dix ME, Gray AN, Ice GG, Kim MS, Reid R, Rodman SU, McWilliams WH (2009) Impacts of nonnative invasive species on US forests and recommendations for policy and management. Journal of Forestry 107: 320–327.

Nahrung HF, Carnegie AJ (2020) Non-native forest insects and pathogens in Australia: establishment, spread, and impact. Frontiers in Forests and Global Change 1(3): e37. https://doi.org/10.3389/ffgc.2020.00037

Nahrung HF, Swain AJ (2015) Strangers in a strange land: do life history traits differ for alien and native colonisers of novel environments? Biological Invasions 17: 699–709. https://doi.org/10.1007/s10530-014-0761-7

Niemelä P, Mattson WJ (1996) Invasion of North American forests by European phytophagous insects. BioScience 46: 741–753. https://doi.org/10.2307/1312850

Paine TD, Millar JG, Daane KM (2010) Accumulation of pest insects on eucalyptus in California: random process or smoking gun. Journal of Economic Entomology 103: 1943–1949. https://doi.org/10.1603/EC10214

Poland TM, Rassati D (2019) Improved biosecurity surveillance of non-native forest insects: a review of current methods. Journal of Pest Science 92: 37–49. https://doi.org/10.1007/s10340-018-1004-y

Reaser JK, Burgiel SW, Kirkey J, Brantley KA, Veatch SD, Burgos-Rodríguez J (2020) The early detection of and rapid response (EDRR) to invasive species: a conceptual framework and federal capacities assessment. Biological Invasions 22: 1–19. https://doi.org/10.1007/s10530-019-02156-w

Suhr EL, O'Dowd DJ, Suarez AV, Cassey P, Wittmann TA, Ross JV, Cope RC (2019) Ant interceptions reveal roles of transport and commodity in identifying biosecurity risk pathways into Australia. NeoBiota 53: 1–24. https://doi.org/10.3897/neobiota.53.39463

Turner R, Brockerhoff E, Bertelsmeier C, Blake R, Caton, B, James A, MacLeod A, Nahrung HF, Pawson S, Plank M, Pureswaran D, Seebens H, Yamanaka T, Liebhold A (in review) Worldwide border interceptions provide a window into human-mediated global insect movement. Ecological Applications.

Wylie FR, Peters BC (2016) Lesser auger beetle *Heterobostrychus aequalis* (Coleoptera: Bostrichidae) in Australia: absent or elusive? Austral Entomology 55: 330–333. https://doi.org/10.1111/aen.12189

Wylie FR, Yule RA (1977) Insect quarantine and the timber industry in Queensland. Australian Forestry 40: 154–166. https://doi.org/10.1080/00049158.1977.10675669

Supplementary material 1

Non-native insect species established in Australia, traits and interceptions

Authors: Helen F. Nahrung, Angus J. Carnegie

Data type: interceptions and traits of established forest species.

Explanation note: The supplementary data file contains the list of established non-native forest insects in Australia, their taxonomic placement, traits used in analyses and number of border interceptions.

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