

Ips grandicollis and other bark beetles: Biosecurity readiness for New Zealand's plantation forestry

Stephanie Sopow, Mike Davy, and Nicolas Meurisse



Image: Pest and Diseases Image Library, Bugwood.org. Licensed under CC BY 3.0 US.

Close-up image of Ips grandicollis adult on the end of a pin.

Report information sheet

Report title	<i>IPS GRANDICOLLIS AND OTHER BARK BEETLES: BIOSECURITY READINESS FOR NEW ZEALAND'S PLANTATION FORESTRY</i>
Authors	<i>STEPHANIE SOPOW, MIKE DAVY AND NICOLAS MEURISSE</i> <i>SCION</i>
Client	NEW ZEALAND FOREST OWNERS ASSOCIATION, FOREST BIOSECURITY COMMITTEE
Client contract number	CN012700
MBIE contract number	NA
PAD output number	92410502
Signed off by	ANDREW CRIDGE, PORTFOLIO LEADER, TREES TO HIGH-VOLUME WOOD PRODUCTS
Date	April 2025
Confidentiality requirement	Confidential (for client use only)
Intellectual property	© New Zealand Forest Research Institute Limited. All rights reserved. Unless permitted by contract or law, no part of this work may be reproduced, stored or copied in any form or by any means without the express permission of the New Zealand Forest Research Institute Limited (trading as Scion).
Disclaimer	The information and opinions provided in the Report have been prepared for the Client and its specified purposes. Accordingly, any person other than the Client uses the information and opinions in this report entirely at its own risk. The Report has been provided in good faith and on the basis that reasonable endeavours have been made to be accurate and not misleading and to

exercise reasonable care, skill and judgment in providing such information and opinions.

Neither Scion, nor any of its employees, officers, contractors, agents or other persons acting on its behalf or under its control accepts any responsibility or liability in respect of any information or opinions provided in this Report.

Published by: Scion, Private Bag 3020, Rotorua 3046, New Zealand. www.scionresearch.com

Executive summary

Overview

Bark beetles in the genera *Ips* and *Dendroctonus* are among the most serious insect pests of coniferous forests in the Northern Hemisphere. *Dendroctonus* spp. are generally more aggressive, while *Ips* spp. typically colonise stressed, declining, or recently felled trees. However, high *Ips* populations can overcome healthy trees' defences by attacking in large numbers. Additional damage arises from associated blue stain fungi, contributing to tree mortality and timber discolouration. Unlike *Dendroctonus*, *Ips* has successfully invaded the Southern Hemisphere, with *Ips grandicollis* (five-spined bark beetle), native to North America, established in Australia since the 1940s. This review assesses the threat *I. grandicollis* poses to New Zealand and identifies knowledge gaps and opportunities for improved preparedness for *Ips* and bark beetles generally.

Key results

A literature review of *I. grandicollis* in Australia and the United States suggests that if introduced to New Zealand, it could pose a considerable risk to the forest estate, particularly under climate change-induced drought, fires, and windthrow events. In Australia, *I. grandicollis* has caused widespread mortality of *Pinus radiata*, with major outbreaks in the 1970s and 1980s exacerbated by drought. Further damage to other pine species followed the 1994 bushfires due to blue stain fungi vectored by the beetle. Large populations of *I. grandicollis* developed in fire-damaged material, enabling attacks on apparently healthy trees. In its native North America, *I. grandicollis* remains damaging despite control by a range of natural enemies. Along with *I. avulsus* and *I. calligraphus*, it causes annual losses in the tens of millions of dollars, including tree mortality and log degradation from blue stain fungi. The European and Mediterranean Plant Protection Organization lists *I. grandicollis* as an A1 quarantine pest with quarantine regulations enforced by Japan, Taiwan, South Korea, and Turkey. Biosecurity New Zealand also classifies it as an Unwanted and Regulated pest.

Implications for New Zealand

Pinus radiata is highly susceptible to *I. grandicollis*, and its likelihood of introduction in New Zealand is estimated to be higher than other bark beetles with similar life history traits (e.g., in the genera *Ips* and *Dendroctonus*). This is due to its invasiveness, including establishment in Australia, China, and Jamaica. Proximity to Australia increases biosecurity risk, and *I. grandicollis* is frequently intercepted at New Zealand's borders, with 49 records in Scion's BUGS database (1950-2000), primarily recorded in dunnage, casewood, and pallets from North America and Australia.

Recommendations and further work

A readiness plan for *I. grandicollis* and other threatening bark beetles is advised, starting with enhanced consideration of risk pathways and border vigilance. As part of this plan, a national surveillance programme targeting bark beetles and wood borers is strongly recommended to improve early detection and provide evidence of pest-free areas for export markets. Readiness measures, including surveillance, should include:

- Establishing survey protocols and diagnostic methods targeted towards the most at-risk bark beetle species or groups of species
- Mapping *Pinus* spp. near points of entry to support surveillance and delimitation
- Raising sectoral, government, and public awareness for incursion response.

If eradication is unfeasible, a "slow-the-spread" programme should be implemented, including monitoring the movement of felled trees and forest material to predict pest spread. Further research should include predictive spread and outbreak risk modelling for industry resilience to new invasions, considering cumulative pest pressures, global warming and extreme climate events. Additionally, pre-emptive investigations into biological control options and a reassessment of forest sanitation protocols are recommended. Details on these recommendations are provided in the final section of the review.

New Zealand biosecurity readiness: *Ips grandicollis* and other bark beetles

Table of contents

Executive summary.....	4
1. Introduction.....	7
2. An overview of bark beetles and <i>Ips grandicollis</i>.....	7
2.1 Bark beetles	7
2.1 History of <i>Ips grandicollis</i> in academic literature	10
3. <i>Ips grandicollis</i>	10
3.1 Taxonomy	10
3.2 Morphology	12
3.3 Biology	13
3.4 Host range and susceptibility	16
4. Impact and risk factors	17
4.1 Bark beetle attacks and associated tree responses	17
4.2 Risk factors	17
4.3 Blue staining	19
4.4 Relationship to <i>Sirex noctilio</i> biological control.....	20
5. Diagnostics	21
5.1 Attack symptoms.....	21
5.2 Trap-based sampling	21
5.3 Collections on infested wood material	23
5.4 Morphological and molecular identification.....	23
6. Risk of <i>Ips grandicollis</i> to New Zealand	23
6.1 Global spread and current distribution.....	23
6.2 Potential entry pathways for <i>Ips grandicollis</i> into New Zealand	24
6.3 Spread pathways for <i>Ips grandicollis</i> within New Zealand	25
7. Control methods and risk management options	25
7.1. Import health standards	25
7.2 Surveillance	26
7.2 Eradication programmes.....	28
7.3 “Slow the spread” programmes	29
7.4 Silvicultural practices	29
7.5 Chemical control	30
7.6 Biological control.....	31
7.7 RNA interference	33

8. Recommendations for further readiness work	33
8.1. Preparedness.....	33
8.2. Research.....	35
8.3. Future proofing.....	36
Acknowledgements.....	37
References	38
Appendix A.....	49
Appendix B.....	51
Appendix C.....	52
Appendix D.....	53

1. Introduction

The forestry and wood products industry are a vital component of New Zealand's economy, generating around \$6.6 billion in annual export earnings. It ranks as the country's fourth-largest export sector, just behind horticulture (Ministry for Primary Industries, 2024a). Dominating the plantation estate is the introduced Californian radiata pine, *Pinus radiata*, which comprises 91% of New Zealand's commercial forests (Forest Owners Association, 2023).

Monoculture plantations, while sometimes viewed as more vulnerable to biotic and abiotic disturbances (Field et al., 2025; Jactel & Marini, 2021), offer several significant advantages, including ease of management and uniformity in production (Bauhus et al. 2017). This is especially true for radiata pine, New Zealand's most studied and well-understood tree species (Mead, 2013). *Pinus radiata* is highly productive across much of New Zealand's plantation estates, now ranking among the most productive timber forests in the temperate zone with an average national yield of 27 m³ ha⁻¹ year⁻¹ (Palmer et al., 2010) and only experiencing occasional impacts from extreme weather events. The country's geographic isolation and robust biosecurity measures have also played a crucial role in preventing the establishment of many damaging forest insect pests that have successfully invaded elsewhere (Mead & Burdon, 2023). However, global trade and climate change increase the risk of new biotic threats to all forests, including plantations. Continued vigilance and preparedness remain essential to safeguarding plantation forestry from emerging threats.

Among the exotic pests established in New Zealand, the simultaneous introduction of the siren wood wasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) and its symbiotic fungus, *Amylostereum areolatum* Fr. (Boidin, 1958), has been the most damaging to *P. radiata* (Bain et al., 2012). Eleven species of exotic bark and ambrosia beetles are also established in New Zealand, with two introduced bark beetles (*Hylurgus ligniperda* Fabricius and *Hylastes ater* Paykull) and one introduced ambrosia beetle (*Xyleborinus saxesenii* Ratzeburg) capable of developing on dead or dying branches, stems, or stumps of *P. radiata*. These species, however, are not capable of colonising live trees, though adult *Hylastes ater* feed on the root collar of pine seedlings and occasionally cause mortality (Sopow et al., 2015). Because these beetles also frequently infest freshly felled logs in pine plantations, they can be a concern as quarantine pests for New Zealand's international trade partners (Pawson et al. 2014). As a result, exported logs must undergo phytosanitary treatments, including debarking and fumigation, before departing New Zealand. The establishment of *Ips grandicollis* or a similarly aggressive bark beetle in New Zealand's pine plantations, along with potential disturbance-related outbreaks, could cost the forestry industry millions of dollars a year in control measures and lost revenue, as it has done in Australia (Wylie et al., 1999).

2. An overview of bark beetles and *Ips grandicollis*

2.1 Bark beetles

Ecologically, the term 'bark beetle' refers to a group of beetles that typically breed subcortically (i.e., just under the bark of trees), within the family Curculionidae and subfamily Scolytinae (Vega & Hofstetter, 2014). Bark beetles differ from ambrosia beetles, which also have many species in Scolytinae but live within the wood. Bark and ambrosia beetles can be differentiated by their feeding habits: ambrosia beetles vector and cultivate symbiotic fungi for consumption in the tree's xylem tissue, as opposed to bark beetles, which consume phloem tissue directly (Vega & Hofstetter, 2014). This review addresses bark beetles, which also often vector fungal species, but do not cultivate them for food (Six, 2012).

Bark beetles can be further categorised by their aggressiveness, describing the tendency of a species to attack living trees. The vast majority of bark beetles exhibit low aggressiveness and tend to colonise recently felled trees, injured trees, or trees experiencing significant stress, such as from wind damage, drought, or following severe defoliation from herbivory. A small number of species,

however, have evolved strategies allowing them to exploit healthy trees (Table 1). Opportunistic aggressiveness tends to be the most common strategy, whereby the species is generally restricted to dead and dying trees but, when conditions are favourable, can build up in such large populations that rates of attacks increase significantly and host defences get overwhelmed (Weed et al., 2015).

Table 1: Bark beetle species and species traits categorised by aggressiveness. Reproduced and paraphrased from Weed et al. (2015).

Aggression Category	Synonyms	Capacity for Adult Aggregation	Tolerance to Host Defenses	Capacity to Overwhelm Host Defense	Kill Healthy Trees	Examples
Aggressive	Primary, near-obligate parasites	High	High	High	Yes	<i>Dendroctonus frontalis</i> (Zimmermann), <i>Dendroctonus rufipennis</i> (Kirby), <i>Dendroctonus ponderosae</i> Hopkins, <i>Ips typographus</i> (L.)
Opportunistically aggressive	Secondary, moderately aggressive, facultative parasites	High	Low	Moderate	Yes	<i>Dendroctonus pseudotsugae</i> Hopkins, <i>Ips confusus</i> (LeConte), <i>Ips pini</i> (Say), <i>Scolytus ventralis</i> LeConte, <i>Tomicus piniperda</i> (L.)
Non-aggressive	Near-obligate parasites	Low	High	High	No	<i>Dendroctonus micans</i> (Kugelann)*, <i>Dendroctonus terebrans</i> (Olivier), <i>Dendroctonus valens</i> LeConte*
	Saprophytic, obligate scavengers	Low	Low	Low	No	<i>Hylastes</i> sp., <i>Hylurgops</i> sp., <i>Pityogenes</i> sp., <i>Pityophthorus</i> sp.

*May aggregate as adults and/or kill trees in regions outside of coevolved community.

Epidemic episodes are usually geographically restricted and short-lasting, following a drought, fire, or windthrow event (Figure 1). In certain circumstances, however, large forest areas can become more vulnerable to attacks, and epidemics can affect entire regions or countries. It is expected that such large epidemics will become increasingly common under the combined effects of climate change, drought, storm-induced damage, and other abiotic and biotic stressors (Kausrud et al. 2012; Gandhi & Hofstetter, 2021).

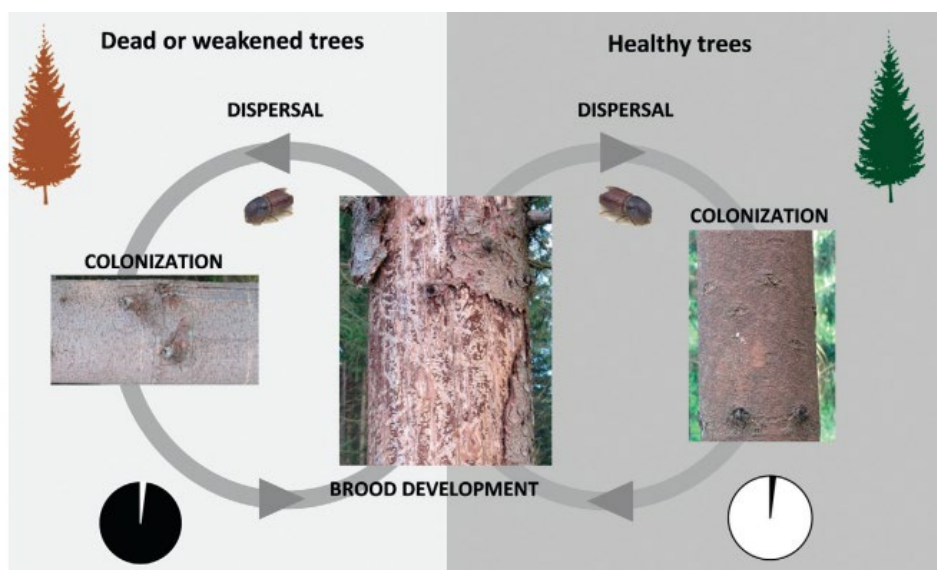


Figure 1: The typical alternation of endemic breeding conditions (most of the time) and intermittent epidemics (usually triggered by extreme weather events) in opportunistically aggressive bark beetle species like *Ips grandicollis*. Figure reproduced from (Krokene, 2015).

A very small number of bark beetles can tolerate conifer resin defences even at low attack densities. These are categorised either as highly aggressive “tree killers” (e.g., *Dendroctonus frontalis*) or as “near-parasite” species able to cope with host tree resin defences for long periods and complete their life cycle without killing their hosts (e.g., *D. terebrans*). Tree mortality caused by aggressive bark beetles is typically much more significant in areas of new introduction or range expansion. In these regions, natural enemies may be absent or unable to control outbreak bark beetle populations, allowing them to reach higher levels.

Infestations of bark beetles in plantation forests often result in reduced growth rates of the trees as the flow of sap is restricted or tree mortality if the phloem is sufficiently girdled (Neumann, 1987). Even when a tree survives to harvest, fungi vectored by the bark beetles cause blue staining, rendering it unsuitable for pulping, while the changes to the timber’s aesthetics reduce its marketability (Safranyik & Wilson, 2007). Bark beetle hosts include a broad range of coniferous and broadleaf tree species (Figure 2). Among conifers, species in the genus *Pinus* are commonly attacked (Lantschner et al., 2017).

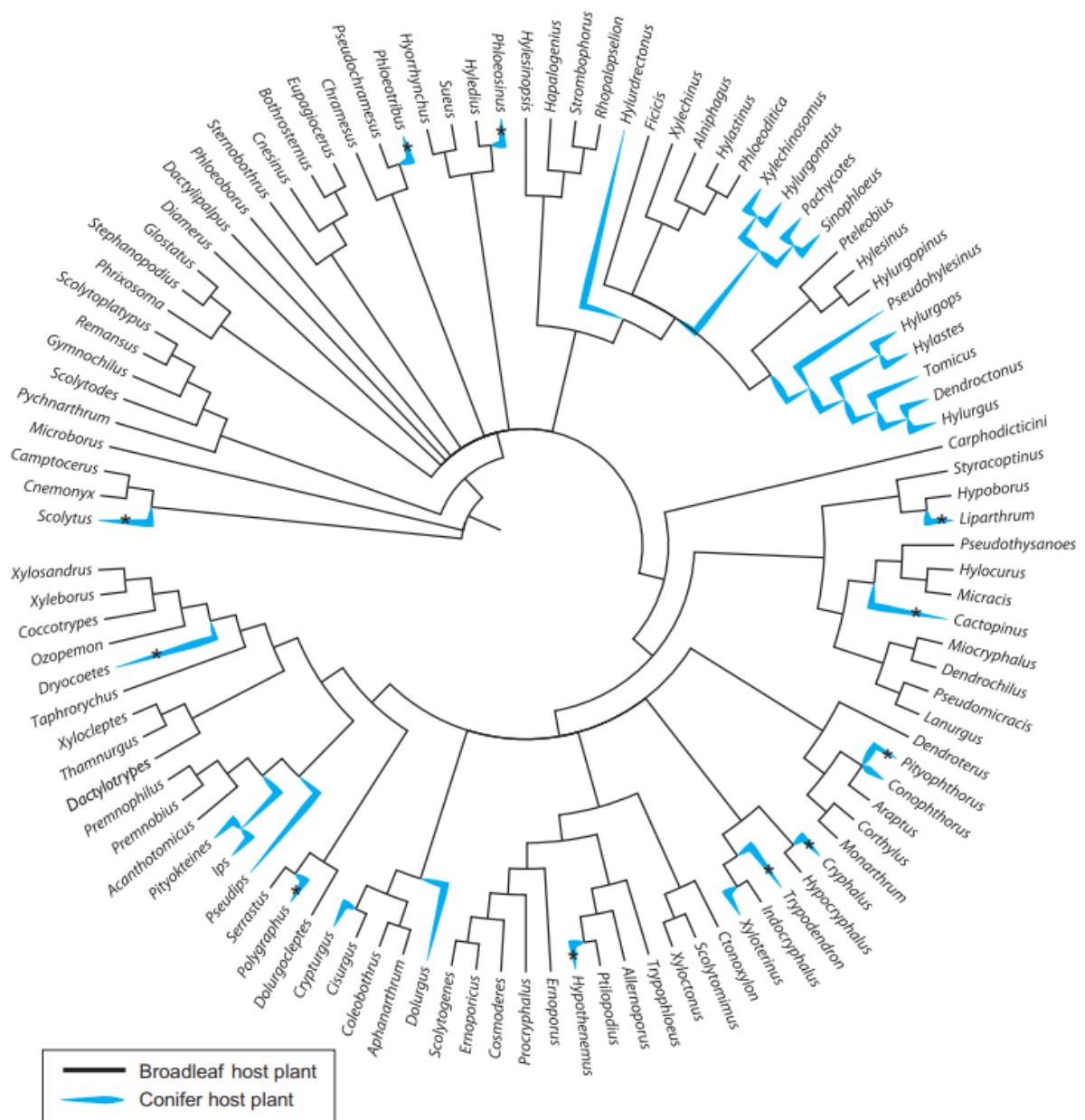


Figure 2: A phylogenetic tree of bark beetle genera, including associations with broadleaf and conifer hosts. Figure reproduced from (Kirkendall et al., 2015).

The most notorious bark beetles include a mixture of species problematic in their native range (e.g., the southern pine beetle *D. frontalis*, the six-spined engraver beetle *I. calligraphus*, the pine engraver *I. pini* and the small southern pine engraver *I. avulsus*), in “expansion” areas (e.g., the eastward expansion of the mountain pine beetle *D. ponderosae* and the progressive colonisation of Europe by the European spruce bark beetle *I. typographus*), or associated with introduction to new continents (e.g., the red turpentine beetle *D. valens* in China, the common pine shoot beetle *Tomicus piniperda* in North America and the eastern five-spined bark beetle *I. grandicollis* in Australia). Many of these species are from the genus *Ips*, commonly referred to as ‘engraver beetles’ for the branching galleries they excavate on the surface of the sapwood, under the bark.

Only three species in the problematic bark beetle genera *Ips* and *Dendroctonus* have successfully established on continents outside their native ones: *I. grandicollis*, *I. calligraphus*, and *D. valens*. *Ips calligraphus*, invasive in the Philippines and China, has been classified as a high-risk invader for the southern hemisphere (Lantschner et al., 2017). *Ips grandicollis*, already present in Australia and impacting *P. radiata* plantations, can be used as a case study on the risk of bark beetles to New Zealand forestry.

2.1 History of *Ips grandicollis* in academic literature

Early records of *I. grandicollis* predominantly concern the beetle’s taxonomy or biogeographic distribution within its native range in North America. However, it gained attention in the 1950s after becoming an issue in pine plantations in Australia (Stoate, 1953). By the late 1980s, *I. grandicollis* and the wood wasp *Sirex noctilio* were widely considered the most damaging forest insects introduced into the Southern hemisphere (Morgan, 1989). The subsequent years saw a huge body of academic research on the aggregation pheromones of *I. grandicollis*, as well as related bark beetle species, and the impact these pheromones had on aggregation behaviour. This work facilitated trapping research and remains the most prevalent area of study for *I. grandicollis*.

The nematode *Deladenus* (= *Beddingia*) *siricidicola* was introduced to control *S. noctilio* in Australia from 1970 but had variable success (Bedding, 1993). Researchers later found a link between *I. grandicollis* attack and a reduction in the success of the *S. noctilio* biological control programme, which initiated an influx of studies in the 2010s to investigate this relationship (see section 4.4). Other modern studies (over the past 20 years) on *I. grandicollis* are diverse and cover a range of topics, including but not limited to invasion biology, the impact of disturbances on bark beetle outbreaks, the associated fungi *Ophiostoma ips*, associated mites, and tree defences, with most of the research conducted primarily in North America or Australia.

3. *Ips grandicollis*

3.1 Taxonomy

Scientific name: *Ips grandicollis* (Eichhoff)

Synonyms: *Tomicus grandicollis* (Eichhoff, 1867), *Tomicus cacographus* (Zimmermann, 1868), *Tomicus cribricollis* (Eichhoff, 1868), *Ips chagnoni* (Swaine, 1916), *Ips cloudcrofti* (Swaine, 1924)

Common names: Eastern five-spined bark beetle, eastern five-spined engraver, southern pine engraver

Phylum: Arthropoda

Class: Insecta

Order: Coleoptera

Family: Curculionidae

Subfamily: Scolytinae

The genus *Ips* (Figure 3) contains roughly 40 described species (IPPC, 2024), all of which feed on the phloem tissue of conifers in the genera *Pinus*, *Picea*, *Larix*, *Abies*, and *Cedrus* (Vega & Hofstetter, 2014). These host genera all originate from the Northern Hemisphere. Native *Ips* species are therefore only represented from North and Central America, Europe, Asia, and North Africa. A few species have become pests outside their natural range, including continental range expansions and introductions in peripheral islands (e.g., *I. apache* in Central America, *I. calligraphus* in the Caribbean, *I. subelongatus* and *I. typographus* in Europe), as well as human-mediated long-range introductions (*I. calligraphus* in the Philippines and China, *I. grandicollis* in Australia and China) (Lantschner et al., 2020). In many cases, the extension of host conifer forests has contributed to these range expansions and remote introductions, notably the large-scale plantation of *Picea* spp. in Western Europe, or *Pinus* spp. in the Southern hemisphere (Lantschner et al., 2020).

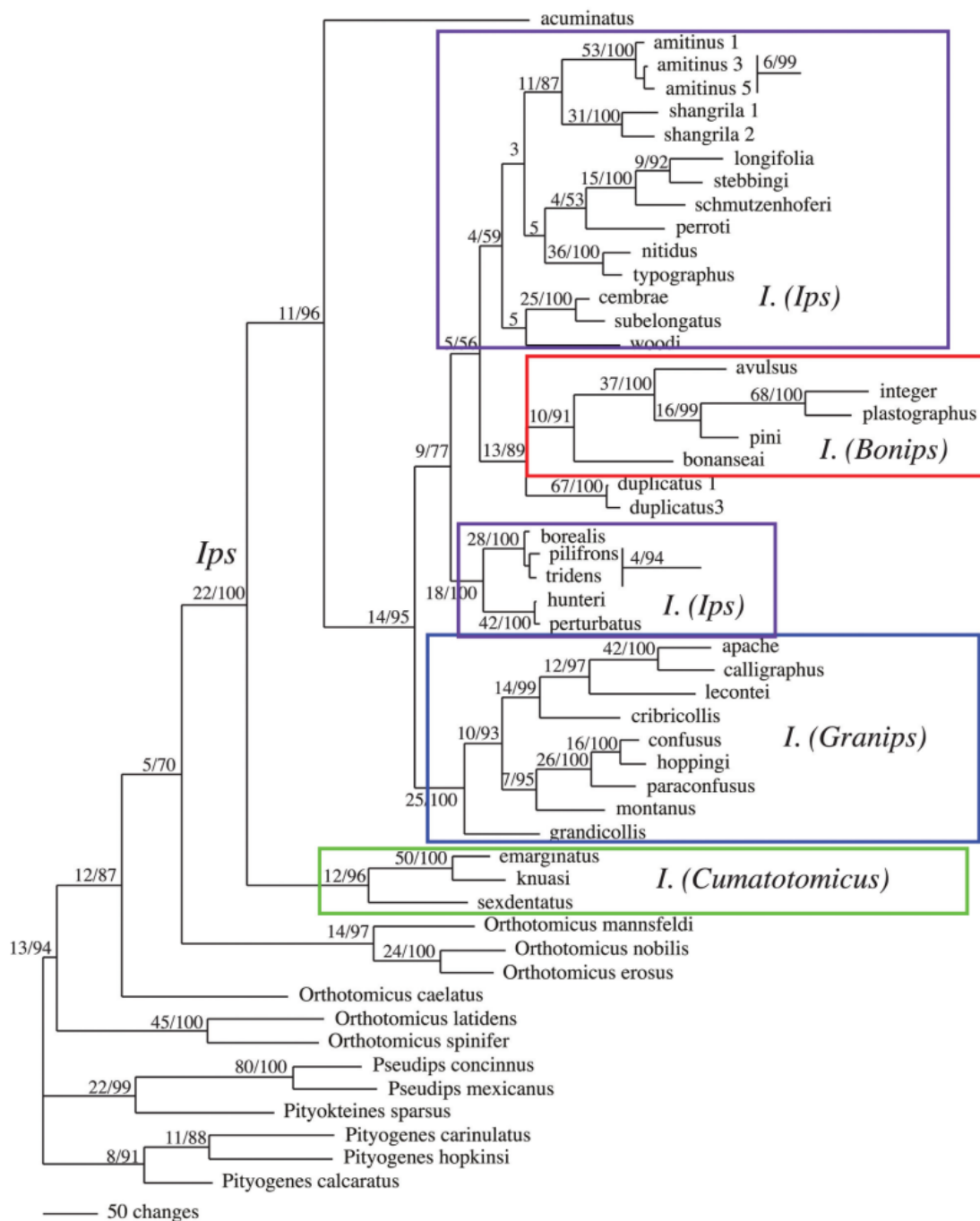


Figure 3: Phylogenetic tree of the *Ips* genus, Reproduced from Cognato (2015).

Ips grandicollis was first described by Eichhoff in 1867 and was first placed in the genus *Tomicus* (Eichhoff, 1867), before being moved to *Ips*. *Ips grandicollis* has historically been grouped within the 'grandicollis' subgroup based on morphological features along with six other *Ips* species, including *I. confusus*, *I. cribricollis*, *I. hoppingi*, *I. lecontei*, *I. montanus*, and *I. paraconfusus*. Parsimony analysis has verified this grouping using molecular and morphological data, and in addition includes *I. apache* and *I. calligraphus* to this monophyletic subgenus 'Ips (Granips)' Cognato. These nine species have highly similar morphology, making them difficult to differentiate using traditional techniques. *Ips grandicollis* is very closely related to *I. cribricollis* (Page et al., 1997) and some authors have considered these a single species (Wood, 1982). However, it is now widely accepted that they are distinct (Cognato, 2015).

3.2 Morphology

Ips grandicollis and other *Ips* species share the general features of most bark beetles. They have a cylindrical and compact body shape, with short legs adapted for burrowing. Their antennae are clubbed, and their head is downward facing, largely hidden from above by the thorax. Adult *I. grandicollis* are reddish-brown. They range from 2.5 to 5 mm in size, comparable to most other *Ips* species. However, individuals in certain species can reach up to 8 mm (IPPC, 2024).

The most useful diagnostic characteristics to distinguish *Ips* from other bark beetles include features of the antennae and the elytra (the hardened forewings of beetles). Other specific characters of the elytra and the frons (the part of the head between the eyes) are also used to distinguish between *Ips* at the species level. The number of prominent spines on the elytral declivity, for instance, is a key characteristic to support identification. The number of these spines is related to the common name of several species (Figure 4). A morphological key to *Ips* species is provided in the ISPM 27 Annex 27 (IPPC, 2024).

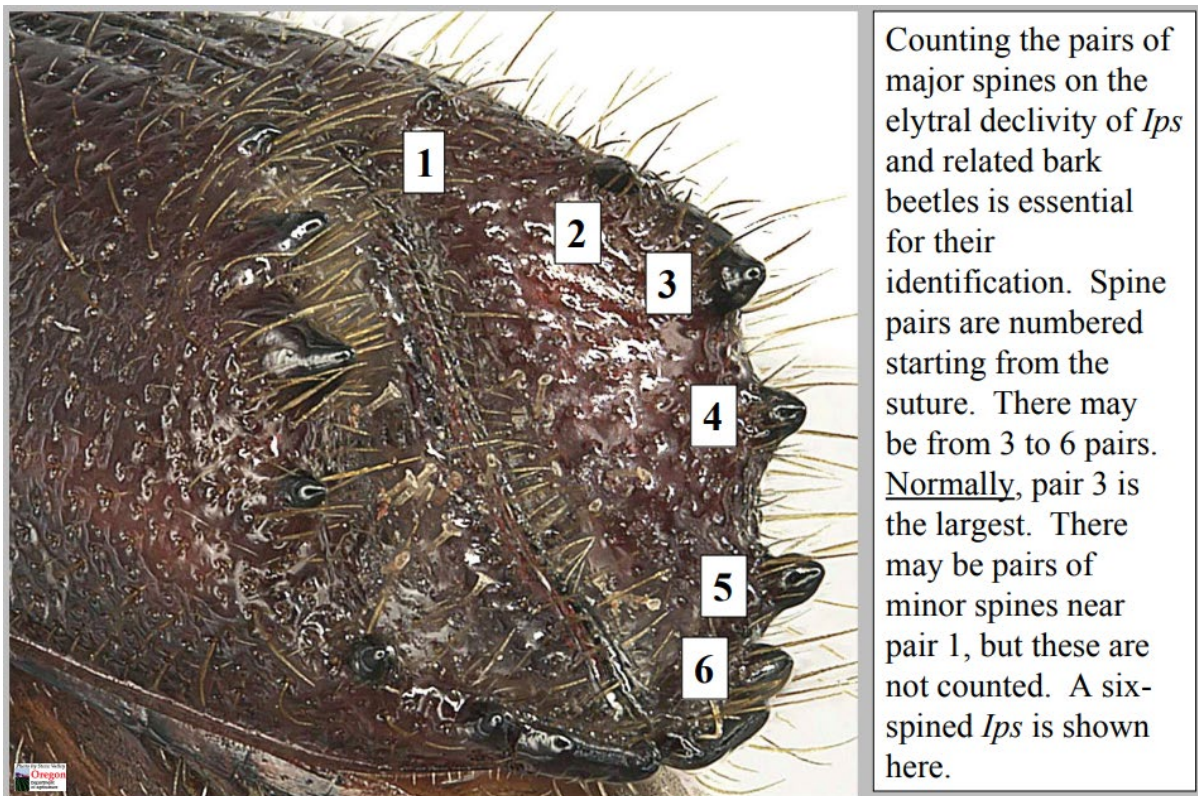


Figure 4: Diagram of spines on the elytral declivity of *Ips* spp. Image borrowed from LaBonte and Valley (2011).

The elytra of *I. grandicollis* have five spines each on the lateral edge of the declivity (posterior slope of the elytra), with the second spine being the largest and bluntest. The declivity is concave, and the bottom edge is produced into a flattened ledge. An identification typically requires an examination of specimens under a microscope and comparisons with specimens in a well-curated reference collection. *Ips grandicollis* can be distinguished from *I. cribricollis* by the relative distances between the first and second spines, which are roughly equal to the distance between the second and third spines in *I. grandicollis*, but distinctly wider in *I. cribricollis*.

3.3 Biology

3.3.1 Attack

In its native range in North America, *I. grandicollis* typically behaves as a secondary coloniser in a bark beetle complex where it usually follows mass attacks on the lower part of pine stems by the much more aggressive southern pine beetle *D. frontalis* (Paine et al., 1981). *Ips grandicollis* typically infests the trunk within the first 3 m above ground level, but may colonise higher regions, particularly after disturbances such as wind damage or pruning (Abbott, 1993; Fettig et al., 2007). Two other species in the complex, *I. calligraphus* Germar and *I. avulsus* Eichhoff can colonise both the main stem and the lateral branches. A fifth species, *D. terebrans*, is a more solitary or quasi-solitary coloniser of live trees, where its ability to cope with host defences allows complete brood development without killing the host. It is suggested that initial attacks of healthy trees by *D. terebrans* may facilitate the initial establishment of *D. frontalis* and subsequent *Ips* species (Sullivan et al., 2024).

In Georgia (USA), attacks of pine billets by *I. grandicollis* have been shown to peak 3-4 weeks after the early-colonising bark beetles (e.g., *D. terebrans*) arrive, with a pronounced decline in attractiveness after eight weeks (Flechtmann et al., 1999). Another study, in North Carolina (USA), showed a marked decline in *I. grandicollis* attack rates once 27 attacks per square foot of bark have been reached (Hertel et al., 1969). In pine plantations in Australia, attacks on host trees by *I. grandicollis* occur shortly after host trees are felled. Logs have shown to be attacked up to 64 days after felling, with attacks occurring more quickly during periods of increased temperatures (Abbott, 1993). Two different types of attack by *I. grandicollis* have been observed in Australia: breeding attacks and feeding attacks (Yousuf et al., 2014).

Breeding attacks occur in both endemic and epidemic situations, initiated by males with adequate fat reserves. Once a suitable host is located, the male bores into the tree's outer bark to reach the phloem, where it constructs a nuptial chamber. At this point, the male also starts producing aggregation pheromones to attract females. In a related species, *I. pini*, aggregation pheromone production starts 16-20 hours after feeding, which is thought to be similar for *I. grandicollis* (Tillman et al., 2004). Adult females are likely capable of detecting localised concentrations of aggregation pheromones, as dispersing females distribute evenly across colonising males early on in the colonisation process, reducing intra-specific competition (Latty et al., 2009). As population density increases, females begin to distribute randomly across males.

Feeding attacks typically occur during outbreak scenarios when densities of pre-emergent young adults become sufficiently high in their natal galleries that they are unable to complete maturation feeding (Yousuf et al., 2014). Unlike breeding attacks, either males or females may initiate these attacks (Witanachchi, 1986; Yousuf et al., 2014). Both types of attack may simultaneously occur during outbreaks, however, feeding attacks are not observed in the beetles' native range in North America, where outbreaks are less common.

To locate suitable hosts, males use chemical cues from stressed trees, which produce a different composition of volatiles than healthy trees (Chénier & Philogène, 1989; Werner, 1972b). The aggregation pheromone ipsenol is produced by colonising *I. grandicollis* adults (usually males) to attract conspecifics to the host (Vité & Renwick, 1971). Other bark beetles use different aggregation pheromones, and these semiochemicals can have attractant and repellent effects across species. For example, *I. grandicollis* is attracted to ipsenol, cis-verbenol, and (-) α -pinene,

but is repelled or interrupted by ipsdienol and lanierone used by other bark beetles, including *I. pini*, *I. confusus*, *I. avulsus*, and *I. calligraphus* (Allison et al., 2012; Aukema & Raffa, 2005; Birgersson et al., 2012; Kohnle et al., 1994; Vité & Renwick, 1971). Interruptants and repellents can be advantageous to both the coloniser and the established species by reducing resource competition (Ayres et al., 2001). Due to their influence on insect behaviour, aggregation pheromones may be used in bark beetle management strategies, such as baiting traps with attractive pheromones and/or using others to deter their spread (e.g. Birgersson et al., 2012).

3.3.2 Mating and larval development

Like most *Ips* species, *I. grandicollis* has a female-biased sex ratio. It is also characterised by a mating system called polygyny, where one male mates exclusively with multiple females during a single breeding season (Griffin et al., 2020). As part of the polygynous mating strategy, the male establishing the nuptial chamber usually stays with the females, ensuring that he is the primary mate, and may defend them from other competing males. This constitutes a harem, which can comprise up to six females per male (Cognato, 2015). The size of the harem is positively related to population density, with greater harem sizes occurring in areas with recently felled logs (Griffin & Symonds, 2021). Once they have mated, the females dig their maternal tunnels in the phloem, where they typically lay 20–30 eggs in small niches along the walls (Figure 5). In *I. grandicollis*, high egg output (23 eggs per gallery or more) can be observed in harems of four or more females, which is predicted to approach or exceed carrying capacity, with a potential increase of larval competition (Latty et al., 2009).



Figure 5: Inner bark gallery characteristic of *Ips grandicollis*. The lower “H”-shaped gallery comprises one male nuptial chamber and four radiating maternal galleries created by four females. Photo credit: Jeffrey M. Eickwort, Florida Department of Agriculture & Consumer Services.

Ips larvae develop as they eat phloem tissue, constructing their own radiating galleries outwards from their mothers' galleries (Wood, 1982) (Figure 5). Consequently, the length of these larval galleries is strongly correlated to gallery age and can be used to determine the establishment order (Reid, 1999).

3.3.3 Phenology

The life cycle of *Ips* beetles principally occurs beneath the tree bark, specifically within the cambium and phloem layers, where mating, oviposition, larval development, and pupation occur. Depending on the climate, there can be multiple generations per year. In cooler regions, there might be just one or two generations, while in warmer areas, there might be several overlapping generations (Eickwort & Mayfield III, 2018). As *Ips* bark beetles mostly occur in temperate regions, adults typically overwinter during the cold season and emerge in the spring when temperatures increase. In its native range in North America, *I. grandicollis* shows regional variation in its overwintering physiology. Northern populations have demonstrated slow development within logs at 0°C for 7 weeks, whereas southern populations survived under these conditions, but their development was halted (Lombardero et al., 2000).

Like many other bark beetles, *I. grandicollis* is a freeze-susceptible species, meaning individuals cannot survive temperatures below their freezing points. Lower lethal temperatures (LLTs) of -10°C have been reported for *I. grandicollis* larvae, and -20°C for adults (Lombardero et al., 2000). However, the LLTs fluctuate seasonally and are lower in winter than in summer. In Australia, adult beetles were reported to lay dormant in old galleries within felled logs or dead standing trees from late May until late August (Abbott, 1993). The average overwintering mortality in South Australia was reported to be about 71%, though this was much higher for larvae (95%) and pupae (86%), than for adults (41%) (Lawson, 1993).

Consistent with these overwintering patterns, adult beetles in Australia are reported to be most active from September to early May (Abbott, 1993). However, this period of activity may fluctuate from year to year, depending on environmental conditions. In Western Australia, *I. grandicollis* is estimated to go through roughly 6-8 generations per year (Rimes, 1959), with a maximum of nine generations per year (Abbott, 1993). This rapid reproduction rate facilitates population outbreaks under favourable conditions. In South Australia, where it is generally cooler, *I. grandicollis* is reported to have 4-5 generations per year, and only four generations are reported in Victoria (Abbott, 1993). Trees felled during summer months were shown to produce the next generation in only 15-30 days, demonstrating the fastest rates of colonisation of new material and shortest development time from eggs to new emerging adults when temperatures are high (Figure 6).

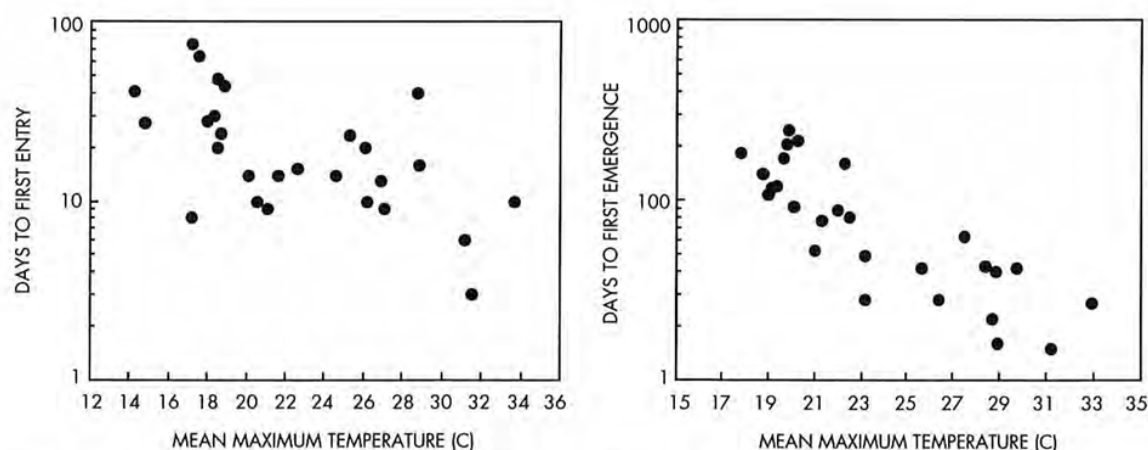


Figure 6: Relationship between mean maximum temperature (°C) and days to first entry (left) or emergence (right) of *Ips grandicollis* in *Pinus pinaster* plantations in Australia (Abbott, 1993).

3.3.4 Dispersal

Male *I. grandicollis* typically disperse earlier than females to establish a nuptial chamber on new hosts and attract mates. Compared to other bark beetle species, the dispersal ability of *I. grandicollis* is not well studied. However, long-distance dispersal has been described for other bark

beetles. Tethering devices, for instance, where insects are either attached to a fixed point or allowed to fly in a constrained circular path (flight mills), have been used to measure the distance, duration, and speed of flight of several *Ips* species in a controlled environment. This helps to quantify how far and how long an insect can fly, providing insights into its dispersal capabilities. Adult *I. confusus* have been shown to fly continuously for up to 12.6 km in a single flight using this method, with an average dispersal distance of 4.2 km (Kinn, 1971), and *I. calligraphus* have been shown to fly a maximum of 6.4 km in a single flight, with an average distance of 1.6 km (Kinn, 1986).

While trials with tethered insects or observations in wind tunnels are useful for studying insect behaviours, energetics, and dispersal capability, they do not replicate natural flight behaviours and should be complemented with field observations. Mark-release-recapture (MRR) studies are a common field-based method used to study dispersal and movement patterns in animal populations, including insects. Marked and released individuals at known locations can be recovered from the same area after some time sufficient for them to disperse, allowing scientists to analyse the distribution of actual dispersal distances across all recaptured individuals. In a MRR study by Costa et al. (2013), 95% of released *I. grandicollis* adults did not disperse further than 430 m but readily moved through fragmented landscapes, including non-forested open areas. These findings suggest that most *I. grandicollis* remain near their emergence sites, potentially due to an abundance of nearby breeding material. However, while short-distance dispersal appears limited, the species' relatively high reproductive rates may facilitate a steady range expansion over time. Additionally, dispersal potential could vary under different environmental conditions, such as strong winds, which are characteristic of New Zealand and may enhance long-distance movement.

Nonetheless, a lack of evidence of recorded long flights is typical in mark-release-recapture studies where dilution effects are large and where trap density for recaptures typically decreases as you get further from the release site. However, extrapolation models adjusted for *I. sexdentatus* and other bark beetle species indicate that a small proportion of individuals in a population may still be able to disperse over distances exceeding 1 km or more (Jactel, 1991; Meurisse & Pawson, 2017). One study examined the flight of *D. ponderosae* ~800 m above the ground where it was estimated that air currents could facilitate dispersal of 30-110 km per day (Jackson et al., 2008). A similar study estimated that *I. typographus* could disperse over 18 km also using air currents (Forsse & Solbreck, 1985). Other long-distance records have been documented for bark beetles in fragmented forest landscapes (e.g., Chase et al., 2017). More recently, *I. typographus* was shown to have reached the United Kingdom by natural long-distance dispersal from a large population reservoir in continental Europe (Inward et al., 2024).

During long distance dispersal, bark beetles may be exposed to several climatic stressors, weather events, or predators that result in mortality. Energy reserves are expended during long flights, further increasing the mortality risk if a suitable host is not found before the reserves are depleted. Mortality in *I. grandicollis* has been previously shown to be high (at least 44%) during dispersal in Jamaica, with higher mortality rates for males (77.3%) as opposed to females (35.4%). This is thought to be related to an increased amount of time spent host searching by males during early colonisation (Garraway & Freeman, 1990).

3.4 Host range and susceptibility

Ips grandicollis feeds almost exclusively on *Pinus* spp., including *P. banksiana*, *P. caribaea*, *P. caribaea* var. *hondurensis*, *P. cubensis*, *P. echinata*, *P. elliottii*, *P. kesiya*, *P. koraiensis*, *P. maestrensis*, *P. massoniana*, *P. maximinoi*, *P. merkusii*, *P. monticola*, *P. nigra*, *P. occidentalis*, *P. oocarpa*, *P. palustris*, *P. patula*, *P. pinaster*, *P. ponderosa*, *P. radiata*, *P. resinosa*, *P. rigida*, *P. strobiformis*, *P. strobilus*, *P. sylvestris*, *P. taeda*, *P. tropicalis*, *P. virginiana* and *P. wallichiana* (CABI, 2019; EPPO, 2024). It has also been recorded from *Larix laricina* (EPPO, 2024).

Principal host genera of the genus *Ips* are *Pinus*, *Picea* and *Larix*, with species of *Abies* and *Cedrus* becoming hosts during outbreaks, and it has been suggested that other conifers could be attacked when a principal host is not available (IPPC, 2024).

The native range of *I. grandicollis* in eastern North America extends from the eastern coast as far west as New Mexico and does not overlap with the natural distribution of *P. radiata* in California and Mexico in Western North America (Atkinson, 2024; Wood, 1982). A greater degree of damage is often caused when an organism meets a novel host, as is the case in Australia where both *I. grandicollis* and its pine hosts are outside of their native ranges (Brockerhoff, Gresham, et al., 2023). In Australian plantations where both *P. pinaster* (a European/Mediterranean species) and *P. radiata* are present, *I. grandicollis* adults preferentially attack *P. radiata* and typically only attack *P. pinaster* in outbreak conditions. *Radiata* pine also has a much higher mortality rate than *P. pinaster*, especially at sites experiencing overstocked stands or drought (Abbott, 1993). The congener, *I. typographus*, has been found to successfully attack non-native species of spruce at comparable densities to native ones, suggesting the potential for *I. grandicollis* to readily attack novel host species (Isitt et al., 2023).

4. Impact and risk factors

4.1 Bark beetle attacks and associated tree responses

Like other opportunistically aggressive bark beetles, *I. grandicollis* targets and successfully colonises stressed trees more frequently than healthy ones (Werner, 1972a). This is largely due to stressed trees' reduced capability to repel attacks through both preformed and induced defences (Krokene, 2015), especially the ability to increase resin flow in response to attacks (induced resinosis). An abundant induced resin flow isolates and encases the attacking beetles and is also toxic to most bark beetles and associated fungi (Denham et al., 2019; Witanachchi & Morgan, 1981). After boring into resistant trees, male *I. grandicollis* retreat and do not release their aggregation pheromone ipsenol, which reduces the likelihood of attack on these trees by other dispersing adults (Witanachchi & Morgan, 1981). Artificially stressed *P. taeda* were found to exude approximately three times less resin than healthy ones in response to bark beetle attacks (Denham et al., 2019). Similarly, defoliated trees exhibit decreased resin production, which greatly increases their susceptibility to *I. grandicollis*, even at low attack densities (Flamm et al., 1993; Wallin & Raffa, 2001).

Once established, *I. grandicollis* feeds on phloem tissue, gradually ringbarking the tree and progressively restricting sap flow (Abbott, 1993). This not only limits the tree's growth potential but also reduces its defences against further bark and woodboring insects, as carbohydrate availability hampers resin production (Denham et al., 2019). In already stressed trees, symptoms may include defoliation, often starting at the top of the crown. Mortality occurs when beetle populations are large enough to prevent the tree from transporting sufficient nutrients through the phloem tissue, but this remains uncommon in healthy trees (Mason, 1970).

4.2 Risk factors

Physiologically stressed or damaged trees between 8 and 15 years of age, with diameters ranging from 5 to 15 cm, are most vulnerable to attack by *I. grandicollis* (Neumann F. G. & Morey J. L., 1984). Abiotic disturbances are the primary causes of tree stress in plantations, and monitoring these disturbances can help predict when outbreaks are likely. *Ips grandicollis* is an opportunistic coloniser that quickly exploits trees weakened by major abiotic disturbances such as drought, fire, and storms (high winds and lightning strikes) (Neumann, 1987).

Most tree mortality attributed to *I. grandicollis* follows environmental disturbances. In the United States, fire-damaged and drought-stressed *P. resinosa* experienced mortality as high as 50% after

beetle attacks (Santoro et al., 2001), and in Australia, stands that had severe bushfires, droughts, or storms suffered up to 100% mortality (Morgan, 1989).

Fire-damaged trees' susceptibility to *I. grandicollis* has been researched extensively. While charred trees may not directly attract the beetles, longer-term induced stresses may subsequently attract the beetles (Lombardero et al., 2006; Santoro et al., 2001; Sullivan et al., 2003). In Australian pine plantations, fires have been shown to facilitate *I. grandicollis* outbreaks (Hood & Ramsden, 1997; Wylie et al., 1999). This effect is exacerbated by more frequent forest fires occurring during droughts. Furthermore, standing trees from beetle outbreaks dry out very quickly, further contributing to forest fires and spread (Hood & Ramsden, 1997). Salvaging fire-damaged trees within three months has been recommended to avoid revenue losses from blue stain (Hood & Ramsden, 1997; Wylie et al., 1999). In the aftermath of the 1994 bushfires in Australia, plantation trees were attacked by *I. grandicollis* within six weeks, with the outbreak peaking at 10 weeks (Wylie et al., 1999). Some studies suggested that the attractiveness of fire-damaged trees can persist for up to a year (Sullivan et al., 2003). Furthermore, *Ophiostoma ips* is more successful after burns or in drier conditions, both because it is vectored to more trees and because it thrives in drier wood (Hood & Ramsden, 1997).

Drought is another serious risk factor, especially in arid regions as it can affect entire plantations and is difficult to mitigate when freshwater resources are limited. In Australia, *I. grandicollis* attacks are common during drought conditions (Yousuf et al., 2014), and trees are especially vulnerable after dry winters (Abbott, 1993). A 1970 study in Western Australia found that 70% of 1,900 radiata pine showed signs of drought stress, with 12% of these trees attacked by *I. grandicollis* - typically in the lower 3 m of the tree (Abbott, 1993). Among the healthy trees, only 1% showed evidence of attack. In another study comparing live and dead standing trees in 1988, 70.9% of the dead standing trees were attacked, but only 0.4% of the live trees (McGrath et al., 1990).

Windthrow events are also known to cause bark beetle population booms within healthy forests (Griffin & Symonds, 2021). Although healthy trees are typically resistant to *I. grandicollis*, dead or damaged branches can provide suitable breeding sites (Abbott, 1993). Wind damage has a sizable impact on planted forests in New Zealand, with approximately 63,000 ha of planted forests damaged by wind between 1945 and 2011, though the total impact on the net stocked area averaged 0.2% (Moore et al., 2013). Climate change is associated with an increased frequency of such environmental disturbances, with outbreaks of current and future bark and wood-boring insects likely to become increasingly common.

Severe defoliation caused by biotic factors is another disturbance strongly linked to *I. grandicollis* attack (Wallin & Raffa, 2001). Damage to needles alters the composition and concentration of monoterpenes produced by the host, which can attract bark beetles for an initial attack (Wallin & Raffa, 1999). At high concentrations, monoterpenes may become insecticidal and inhibit colonisation, but they can be overcome during mass attack (Coyne & Lott, 1976). Severe bark beetle attacks and increased mortality risk are also strongly correlated with prior defoliations caused by other insect outbreaks (Wallin & Raffa, 2001). Consequently, defoliating insects in plantation forests may facilitate *I. grandicollis* outbreaks.

Stressed trees are not only more susceptible to bark beetle attack, but also infection from opportunistic foliar pathogens such as *Dothistroma septosporum* (Roberts et al., 2020). As bark beetles and tree pathogens both cause stress, and are more successful on stressed trees, theoretically the presence of one may facilitate establishment of the other. However, bark beetle outbreaks have not typically been associated with symptomatic tree disease, with most research attributing climate-related stress to the increased frequency of both bark beetle and disease outbreaks (Murdock et al., 2013; Wyka et al., 2018).

Human activities such as felling, thinning, and pruning host trees can also facilitate *I. grandicollis* attacks (Fettig et al., 2007). Felled trees and stumps create breeding grounds for large populations to build and, when populations are high, pruning wounds may be used as novel attack sites on otherwise healthy trees. It has thus been recommended that pruning be avoided from September to May in the Southern Hemisphere when *I. grandicollis* is most active (Abbott, 1993).

High-density planting of *P. radiata* could pose risks given predicted decreases in rainfall and increases in hot-dry days. Elevated drought stress in young pine plantations has been a cause of extensive tree mortality in Australia, either directly or indirectly, as drought weakens trees and makes them more susceptible to pests and diseases including bark beetles (*I. grandicollis*), the sirex wood wasp, and *Diplodia* canker. Reducing stand density through thinning has been recommended as a strategy to moderate drought effects by reducing competition for water and nutrients (Aussenac & Granier, 1988). However, thinning may come at the expense of optimising densities based on other factors like wood volume, genotype traits, site conditions, and cost structures (Hanewinkel et al., 2011).

High-density planting is often necessary to optimise short-term production, but it can exacerbate the effects of drought stress, increasing vulnerability to bark beetles, woodboring insects, and other biotic and abiotic damage. In short-rotation forestry, where plantations are grown for less than 20 years at a high stocking rate (~1,000 stems per hectare), careful management is crucial to mitigate environmental stress and optimise plantation growing conditions (Jones et al., 2023).

Recommendations for alternative forestry management types in New Zealand – including increased stocking regimes - could draw on recommended best practices for *P. radiata* plantations in Australia, such as avoiding low-elevation sites (<600m) or areas with poor water retention capacity, and considering drought-tolerant genotypes (Stone et al., 2012).

4.3 Blue staining

The primary economic issue associated with *I. grandicollis* is the damage to timber quality caused by the vectored fungus *Ophiostoma* (formerly *Ceratocystis*) *ips*, which leads to blue staining, also known as sap staining, in affected wood (Figure 7). *Ophiostoma ips* colonises xylem tissue within live trees, restricting water flow through the stem and drying the wood, which creates ideal conditions for the growth of the fungi. While trees may somewhat compensate by increasing water flow through the healthy sapwood (Fernández et al., 2004), the fungus typically spreads to the xylem unless the tree's induced resinosis mechanisms contain it within the phloem, preventing blue staining (Wallin & Raffa, 2001).



Figure 7: Blue stain fungus (*Ophiostoma ips*) affecting wood of *Pinus* sp. Source: Ronald F. Billings, Texas Forest Service, USA, Bugwood.org.

Both live trees and harvested material are susceptible to blue staining. The damage caused by *O. ips* following the 1994 bushfires in Queensland is estimated to have cost the Australian forestry industry several million dollars (Wylie et al., 1999). A common practice during this period to reduce sap-staining was to regularly apply water sprays (e.g., 150 mm/day) to recently harvested logs, which maintains a high water content and limits oxygen available for the fungi (Stone & Simpson, 1987). Wylie et al. (1999) found that while water spraying decreased the incidence and severity of blue staining, it did not prevent attacks from other bark beetles or the establishment of saprophytic fungi. Therefore, they recommended that logs not be stored under a water spray for more than six months.

A single beetle can introduce *O. ips* into an uninfected tree, but the severity of blue staining increases with higher beetle densities (Lombardero et al., 2006). A field study of low inoculation densities achieved artificially through subcortical applications of cultured *O. ips*, showed that trees may be able to restrict the spread of *O. ips* by increasing resin flow to the inoculated areas (Wallin & Raffa, 2001). However, at high inoculation densities, the tree's defences are overwhelmed. Inoculations above 400 inoculi/m² typically reduced tree vigour, and at 800 inoculi/m², tree mortality is highly likely after three months (Fernández et al., 2004). For *P. sylvestris*, healthy conductive sapwood can reduce from 85% to 35% within three months when artificially inoculated at 800 inoculi/m².

Artificial inoculations can serve as a proxy for bark beetle attacks, as each beetle introduction of *O. ips* to the attack site can be quantified. It is predicted that ~800 *I. grandicollis* attacks/m² will result in tree mortality. Although the critical attack density required to overcome tree defences has not been field-tested for *I. grandicollis*, an attack density of 850 attacks/m² has been estimated for *I. acuminatus* vectoring *O. brunneociliatum* through experimental mass inoculations of a young *P. sylvestris* forest in France (Guérard et al., 2000).

4.4 Relationship to *Sirex noctilio* biological control

Sirex noctilio is an invasive species of woodwasp that established in Tasmania, Australia in 1952 and has since spread within Australia to Victoria, South Australia, New South Wales, and Queensland (Gitau et al., 2013). In 1970, the Sopron strain of the parasitic nematode (*Deladenus siricidicola*) was introduced to Australia from Hungary to control *S. noctilio* populations (Bedding & Akhurst, 1974). This strain of *D. siricidicola* is highly virulent in its parasitic form and maintained a parasitism rate 90-100% for many years. However, its efficacy in the field was often much lower than anticipated. Eventually, researchers found an association between poor *S. noctilio* control and *I. grandicollis* presence (Yousuf et al., 2014).

Sirex noctilio vectors the fungus *Amylostereum areolatum*, which is fed on by the woodwasp and by *D. siricidicola* when in its mycetophagous form (Bedding, 1972). *Amylostereum areolatum* grows slower than *O. ips* and is outcompeted when wood conditions are dry (Yousuf, Carnegie, et al., 2014). In artificial wood media, the presence of *O. ips* inhibited the growth of the nematode, which was ultimately unable to survive (Yousuf et al., 2018). Furthermore, *I. grandicollis* is attracted to the trap trees where the nematode is introduced for biological control, so it is common to find *I. grandicollis* where these efforts are applied. Trap trees attacked by both *S. noctilio* and *I. grandicollis* and were found to have much lower nematode parasitism rates (7-44%) than trees only attacked by *S. noctilio* (Carnegie & Loch, 2010). Efforts were made in Australia to interrupt the attraction of *I. grandicollis* to the trap trees but were unsuccessful (Dodds & Miller, 2010).

Sirex noctilio has been present in New Zealand since at least 1900 (Miller & Clark, 1935), and is currently held in check primarily by introduced biological control agents and changes in silvicultural regimes, though it may outbreak under conditions such as drought (Bain et al., 2012). *Deladenus siricidicola* is widespread in New Zealand but it is unclear what level of control it has on *S. noctilio* populations. An increased frequency of drought associated with climate change and/or

establishment *I. grandicollis* and *O. ips* in New Zealand may further affect pine tree susceptibility to *S. noctilio* by creating drier wood conditions unsuitable for *D. siricidicola*.

5. Diagnostics

5.1 Attack symptoms

Observable symptoms of *I. grandicollis* attacks on standing pine trees include an accumulation of red dust from boring in bark crevices and at the base of the tree. Numerous emergence holes in wood can be observed on trees that have been infested for some time. Similar symptoms can be observed on logs, large branches and stumps. On live hosts, the needles above the attack sites begin to turn red, followed by the entire crown turning red and then brown as the tree dies (CABI, 2019). Peeling away the bark to expose the phloem near frass accumulations can reveal nuptial chambers and brood galleries with adults and developing progeny during the early and middle stages of attack. Later, when the bark is riddled with emergence holes, the bark can be pulled off easily, and at this stage, most of the young adults will be gone (CABI, 2019). Similar symptoms can be associated with infestations by several other species of aggressive or opportunistically aggressive pine bark beetles. In New Zealand, live pine trees are rarely attacked by bark beetles already present here, and thus reddened needles and an accumulation of boring dusts on live pine trees would be indicative of *I. grandicollis* or other similarly behaving exotic species.

5.2 Trap-based sampling

Flying adults can be collected using traps baited with semiochemical lures (e.g., Fettig & Hilszczański, 2015). The aggregation pheromone for *I. sexdentatus*, ipsenol, is the most effective lure for capturing this beetle (Dodds & Miller, 2010; Miller & Allison, 2011). However, adding other bark beetle pheromones to these lures, such as ipsdienol (attractive to other *Ips* species) and/or lanierone (attractive to *Dendroctonus*), should be approached with caution if the objective of deploying these traps is specifically to capture *I. grandicollis*. These compounds have been shown to reduce catches for *I. grandicollis* (Allison et al., 2012; Aukema & Raffa, 2005; Birgersson et al., 2012; Chase et al., 2018; Miller, 2020). Similarly, ethanol and other host volatiles, such as alpha-pinene, have minimal effect on attracting *I. grandicollis* or other *Ips* species, and when combined with ipsenol, may even have antagonistic effects (Appendix A, Chase et al., 2018; Miller, 2023; Miller et al., 2011).

The most common methods for trapping adult bark beetles include multiple funnel traps and flight intercept panel traps. These traps typically consist of a series of funnels, or panels, designed to intercept beetles attracted to lure(s) placed on the trap (Figure 8). Simpler and more affordable versions of these traps have also been developed, making them suitable for wider-scale deployment, including citizen surveillance (Grégoire et al., 2022; Poland & Rassati, 2019). Trap modifications, such as the application of lubricants (Sweeney et al., 2023) or the use of different colours or reflective paints (Giuseppe Morgante, pers. comm., 2025) can further improve capture rates. All types of interception traps feature a collection cup at the bottom, usually filled with a preservative or insecticide, and are suspended at the desired height. However, while some species may have higher catch rates in the canopy or understory, catch rates for *I. grandicollis* do not appear to be affected by trap height (Miller et al., 2020).

Interception traps are generally low maintenance, making them ideal for research, monitoring, or small-scale management. However, they are not effective for mass trapping once an outbreak has occurred (Sweeney et al., 2023). The same is valid for trap trees (trees artificially stressed via chemical or mechanical methods or by pheromones to initiate beetle colonisation). The only viable solution for managing outbreaks is clear-cutting and the destruction of infested timber (Bakke, 1982).

Light traps, while useful for detecting and monitoring many insect species, are not considered effective for trapping most bark beetles. Trials with *Ips* species have shown very low capture rates using light traps (Marchioro et al., 2020).



Figure 8: Multiple funnel (Lindgren) traps(a), intercept panel traps (b) are commonly used to capture bark beetles and woodborers. Malaise traps (c) are used for bark beetles and other taxa, while bucket traps are primarily used to capture Lepidoptera (d) (Sweeney et al., 2023).

5.3 Collections on infested wood material

On trees, logs, and other infested wood products (see section 6.2), all *Ips* life stages can be found and collected immediately under the bark or in the phloem. The wood underneath the bark can be inspected for typical “H” or “Y” shape galleries (Figure 5), and inspected with a magnifying lens for adults, pupae, larvae, and eggs. It is generally best to use soft forceps to collect individuals. These can be placed immediately in 70% ethanol for preservation, or adults may be killed by freezing. For longer-term preservation, larvae should be placed in boiling water for 30 – 60 seconds before placement in ethanol. For DNA analysis, specimens should be preserved in 95% ethanol, or propylene glycol. Adults should be collected, if possible, since they have important diagnostic characteristics.

5.4 Morphological and molecular identification

Experienced personnel can identify dry, clean adult specimens using a diagnostic key, such as that provided in the ISPM 27 Diagnostic protocol for *Ips* spp. (IPPC, 2025). Since the genus *Ips* is not present in New Zealand, any beetle collected in the country with the genus morphological characters (see section 3.2) should be of high concern and identified to species. Life stages other than adults, however, cannot be used for the identification of *Ips* species morphologically. However, final instar larvae may be able to be morphologically distinguished as not being *Ips* using a key with reference to other Scolytinae (IPPC, 2025).

Molecular identifications can also help to identify all life stages to the genus and species level. Diagnostic sequences for the mitochondrial cytochrome oxidase subunit 1 (COI) gene (DNA barcoding) of *I. grandicollis* have been published (Bold Systems, 2024), but validated protocols for universal DNA identification of *Ips* species are not well developed. The “universal” Folmer primers, commonly used for DNA identification of insects (Folmer et al., 1994). can be problematic for amplifying *Ips* DNA, because the DNA of associated organisms, such as nematodes, may be preferentially amplified when present (Becker et al., 2021). Becker et al. (2021) describe alternative primers and a PCR protocol that works well to distinguish *I. typographus* and *I. duplicatus*. To the best of our knowledge, this has not yet been tested with *I. grandicollis*. Having adult specimens available for morphological analysis therefore remains the preferred option for identification.

6. Risk of *Ips grandicollis* to New Zealand

6.1 Global spread and current distribution

The native range of *I. grandicollis* is from southern Manitoba and Quebec in Canada to Florida in the United States and the Gulf of Mexico, concentrated on the eastern side of North America (Wood, 1982). Increased global lumber trade over the past two hundred years has likely facilitated the spread of *I. grandicollis* outside of its native range, including to the Caribbean (Jamaica), Asia (China), and Oceania (Australia) (EPPO, 2024) (Figure 9).

Ips grandicollis was first recorded in Australia in 1943, from Wirrabara, South Australia (Abbott, 1993). However, the first outbreak wasn't reported until 1952 when it was found in two plantations (Collier and Somerville) near Perth, Western Australia. It was presumed to have spread there via a shipment of infested material to Fremantle. By 1962, *I. grandicollis* was present in almost all *P. pinaster* and *P. radiata* plantations in Western Australia. The beetle is now present in all Australian states with pine plantations (except Tasmania), where it retains its pest status despite control efforts (Gitau et al., 2013).

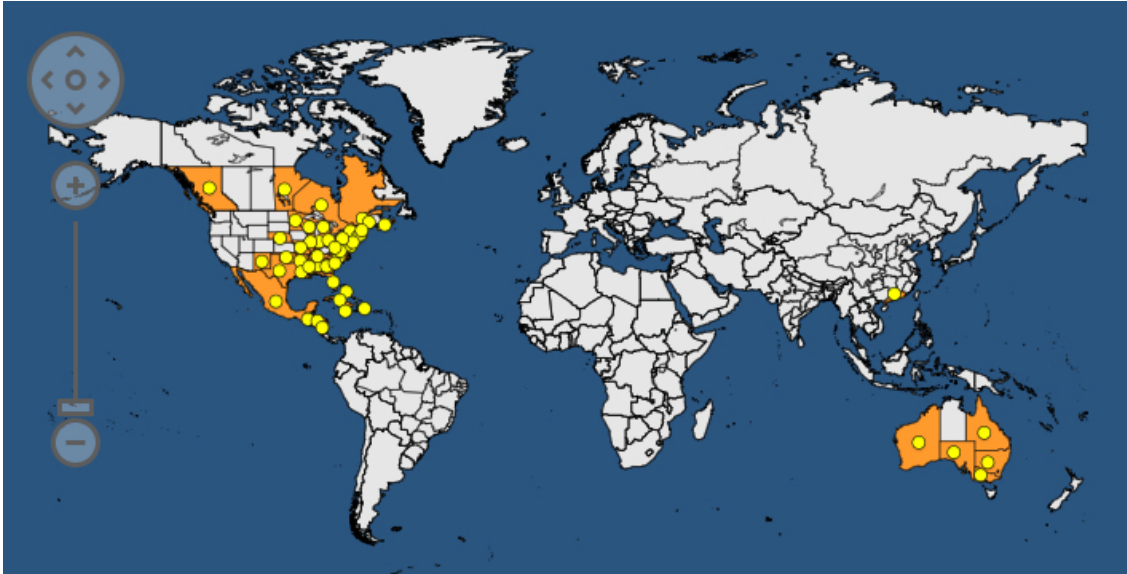


Figure 9: Global distribution of *Ips grandicollis*. Source: EPPO (2024). *Ips grandicollis* (IPSXGR)[World distribution] EPPO Global Database.

Reports of *I. grandicollis* in Central America are from as early as 1970 when it was found in Cuba (Nunberg, 1974), and later in Honduras (Wood, 1977), Jamaica (Garraway & Freeman, 1990), the Dominican Republic (Billings, 1985; Wood, 1982), Haiti (Billings, 1985), and Guatemala (Haack & Paiz-Schwartz, 1997). However, it is currently unknown whether *I. grandicollis* is native to these regions or if it has been introduced. It is generally accepted that *I. grandicollis* and the closely related *I. cribricollis* are sympatric throughout Central America, though it is difficult to verify the exact distribution of each species as they have been challenging to differentiate historically, and some reports may have been subject to misidentification (Yousuf et al., 2014). There have been no reports of *I. grandicollis* spreading to South America.

Ips grandicollis was first recorded in Asia in 2016 (Li et al., 2021). Adult specimens were repeatedly found in ethanol traps in Zhuhai, China, from 2016 to 2018 during a regional survey to investigate the extent of exotic bark beetle establishment. The gut contents of collected specimens consisted of planted exotic host species only, and it is still unclear whether *I. grandicollis* poses a biosecurity risk to native pine forests in Asia.

In 2014, *I. grandicollis* was collected in Spain during surveillance trapping in forests near ports using *Ips* DeGeer lures. However, ongoing trapping did not yield any further specimens, and it is therefore not considered to be established (Mas & Johnson, 2023).

6.2 Potential entry pathways for *Ips grandicollis* into New Zealand

Aside from natural spreading by flight, *I. grandicollis* is most commonly introduced into new regions via unseasoned sawn wood and solid wooden packing material containing attached bark (CABI, 2019). In New Zealand, material occasionally reported to retain bark includes wooden crates, dunnage, cases, pallets, skids, packages and cartons (Bulman, 1992). Bark with potential to sustain bark beetles has also been found in imported furniture, for example, in imported sofas from China (Thompson et al., 2007). Scion's BUGS database (with records from 1950-2000) contains 49 occurrences of *I. grandicollis* interceptions in New Zealand, in dunnage, casewood and pallets from North America and Australia.

6.3 Spread pathways for *Ips grandicollis* within New Zealand

Readily available host plants, *Pinus* spp., near points of entry and throughout New Zealand's landscape, increase the risk of establishment. Natural dispersal of *I. grandicollis* occurs by adult flight. When resources are plentiful, adults are unlikely to disperse far from the immediate area of infestation, and spread occurs relatively slowly (see section 3.3.4). However, when resources become scarce, adults are likely to be capable of flying several kilometres in search of new host trees.

Human-mediated spread occurs through the movement of infested material, and rapid spread throughout the country is plausible. Harvested wood containing bark or bark fragments could be moved throughout the North Island or South Island while being transported to processing areas or ports, and these movements are not well-mapped (P. Hall, pers. comm., 2025). Depending on external temperatures and the phenology of *I. grandicollis*, it's conceivable that adults could emerge from wood during transport or short-term storage. The movement of firewood also represents a significant risk, because of the presence of bark and typical longer-term storage.

7. Control methods and risk management options

The Ministry for Primary Industries (MPI) has identified nursery stock, timber, wood products, and wood packaging as the primary pathways for bark and wood-boring beetles, with the risk from nursery stock being well-managed by insecticide treatments, mandatory inspections, and post-entry quarantine, and risks from wood/timber, wood products, and wood packaging managed by treatment (heat, fumigation, or chemical preservation), processing, and inspection protocols. Biosecurity NZ and the forestry sector also support these efforts through their post-border surveillance programmes, which aim to detect risk organisms early to prevent establishment. These programmes include general surveillance, which encourages public reporting of suspicious organisms, targeted surveillance focusing on specific pests, and pathway surveillance at high-risk sites like seaports and airports.

7.1. Import health standards

New Zealand's 'Import health standard: wood packaging material from all countries', introduced in 2006 and most recently revised in 2023 (Biosecurity New Zealand, 2023), is based on the International Standard for Phytosanitary Measures (ISPM) No. 15 (IPPC, 2019). It specifically lists *I. grandicollis* and other *Ips* species as regulated pests potentially associated with wood. Established in 2002 and implemented globally in subsequent years, ISPM 15 mandates that wood packaging material (WPM), such as pallets, crates, and dunnage (commonly used to support and protect cargo), be treated to eliminate live wood-boring and bark-boring insects, while also requiring the debarking of the wood. However, the efficacy of the ISPM 15 has been debated, particularly regarding dunnage (Lovett & Davila, 2021). Critics argue that treatments may not be fully effective and may be improperly applied, or WPM may be fraudulently marked by trading partners. Such concerns were notably highlighted in a 2005–2006 Australian study (Zahid et al., 2008), which found that about one-third of ISPM 15-stamped materials were noncompliant, with 10% still containing bark.

In a long-term USA investigation (2003–2020), Haack et al. (2022) reported a 36–61% decrease in borer detection rates for WPM entering through various cargo routes after the standard was implemented. However, this reduction has diminished over time, with occasional increases in detection rates associated with specific imports (e.g., tiles from Italy between 2015–2018). This trend occurred despite updates to ISPM 15, such as requirements for mandatory debarking, limits on bark patch sizes, debarking before fumigation, and longer fumigation periods. These USA findings included *Ips* and other bark beetle species, which was an unexpected result, given that ISPM 15 should be particularly effective against pests of live or freshly cut trees (as opposed to drywood pests, which are expected to re-infest treated material). One potential explanation for this

ongoing issue, which remains largely understudied, is the reuse and repair of pallets and dunnage, making them vulnerable to re-infestation.

For New Zealand, no similar study directly compares infestation rates before and after the adoption of ISPM 15. A 4.3% borer detection rate was recorded for WPM in randomly selected maritime consignments entering New Zealand between 1989 and 1991, before ISPM 15 (Bulman, 1992). Current phytosanitary measures established by MPI/Biosecurity New Zealand include that all WPM be declared via a Sea Container Quarantine Declaration (QD) before arrival. Full Container Loads are electronically assessed, and if the WPM is not ISPM certified, Biosecurity NZ's Target Evaluation Team (TET) may direct further inspection or treatment. For Limited Container Loads, which may contain both compliant and non-compliant packaging, WPM is assessed at transitional facilities by an Accredited Person. Additionally, Biosecurity NZ inspects 1% of sea containers through its General Sea Container Assurance programme.

7.2 Surveillance

Surveillance is a cornerstone of early detection and management for invasive species in New Zealand. The country employs a range of surveillance approaches across its land, freshwater, and marine ecosystems to enable early detection of new or emerging diseases, support claims of freedom from specific pests or diseases, and investigate potential new threats (Acosta et al, 2020). MPI plays a leading role in these efforts, overseeing large-scale surveillance programmes for high-risk pests such as fruit flies (Tephritidae) and spongy moth (*Lymantria* spp.) (Ministry for Primary Industries [MPI], 2024b).

In forestry pest surveillance, New Zealand has shifted from a historical focus on large production forests to a more risk-based approach that tailors surveillance efforts according to varying risk levels (Stevens, 2008). The current Forest Biosecurity Surveillance System combines four key components, providing extensive coverage with a focus on high-risk areas (Appendix D; New Zealand Forest Owners Association [FOA], 2022). Central to this system are visual surveys, where trained staff perform direct field observations to identify pest life stages, damage on host trees, and other infestation indicators. Through labour-intensive, visual surveys provide valuable data on pest presence and damage. These surveys are typically conducted via walk transects around target trees in urban areas or a combination of walk and drive transects in pine plantations. Aerial surveys from fixed-wing aircraft, combined with ground truthing, occasionally supplement these efforts to monitor larger or less accessible areas.

In addition to visual surveys, insect traps provide an effective surveillance tool, particularly for bark and wood-boring beetles. Traps use chemical attractants, light, or colour to capture insects, offering a more efficient alternative to visual surveys and enabling real-time monitoring of pest populations (Brockerhoff, Corley, et al., 2023). The value of trap-based surveillance has been recognised in an external evaluation of New Zealand's Forest Health Surveillance Programme, commissioned by the Forest Owners Association (Liebhold & Callan, 2007). This evaluation recommended the implementation of a nationwide trap network, which could improve early detection and enhance eradication efforts.

Trials conducted by the Ministry of Agriculture and Forestry (MAF) between 2002 and 2005 aimed to detect invasive wood-boring bark beetles (WBBB) that could threaten New Zealand's conifer plantations and native forests. The programme sought to serve as an early-warning system, test various lures for exotic species, and assess the effects of trap placement and proximity to host trees on trap efficiency. A total of 580 funnel traps baited with different attractants were placed at high-risk sites, including seaports, airports, and forests near these areas (Brockerhoff et al., 2006). Over 27,000 beetles were caught during the survey, including 12 species of Scolytinae (including specimens of all four known species of introduced bark beetles), but no new species establishments were detected. Traps were baited with either generalist attractive mixtures (alpha-pinene, or beta-pinene, and ethanol) or specific bark beetle pheromones (frontalin and ipsdienol). While the programme was successful in its monitoring role, full-scale implementation of a nationwide trap network has not yet occurred. However, efforts to reinstate it are currently

underway, with 40 traps placed at forest locations in Auckland, Bay of Plenty, and Canterbury by SPS Biota as of 2023. Additionally, 55 traps have been set up in Auckland and Waikato to monitor the spread of *Scolytus multistriatus*, a bark beetle vector of Dutch elm disease.

Though surveillance trapping is an investment-intensive approach, it can significantly reduce the financial burden of pest outbreaks by detecting infestations earlier, minimising spread, and lowering eradication and containment costs. Cost-benefit analyses support this, showing that early detection through surveillance can substantially reduce pest control costs, including eradication and crop loss, particularly when focused on high-risk trade and urban centres. For example, updating previous calculations (Brockerhoff et al. 2012; Epanchin-Niell et al., 2014), we estimate that a dedicated surveillance programme would yield positive economic returns across all scenarios considered. Such a programme could enhance detection, eradication, and control efforts while mitigating long-term damage to forest and urban environments. Over a 30-year timeframe, high-investment surveillance strategies could reduce control costs and invasion damages to urban and plantation forests by approximately 39%, with additional benefits from investment in research to improve trap technology, standardise monitoring protocols, enhance diagnostics, and improve eradication success. The deployment of 200–1000 traps at a national scale, for instance, is projected to generate NZ\$0.37–0.61 billion in economic returns over 30 years in a high-damage scenario (where biosecurity measures fail to prevent significant forest invaders from spreading). Estimated benefits could increase to NZ\$1.39–1.46 billion over the same period in a scenario where biosecurity management is more efficient (reducing spread and impacts). These estimates demonstrate a return that more than doubles typical cost-benefit ratios for biosecurity research (e.g. 30:1 return on investment) (Dodd et al. 2020).

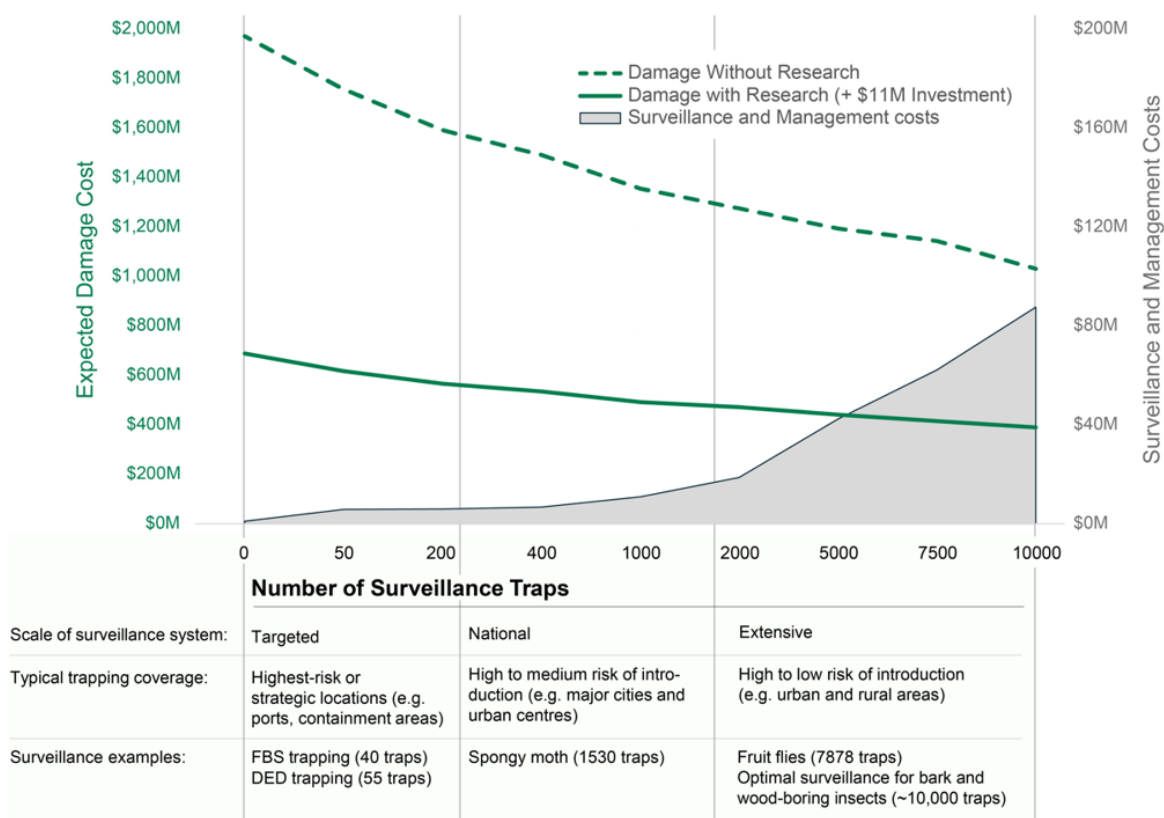


Figure 10: Expected benefit of research for managing bark and woodboring beetle invasions for various levels of biosecurity surveillance. Costs include surveillance (trapping operations and diagnostics) and potential management costs (e.g., for eradication and/or long-term control). Calculations are based on Epanchin-Niell et al. (2014), with research benefits corresponding to the difference between the high and low-damage scenarios for urban and plantation forests.

Successful trap-based surveillance for bark and wood-boring beetles already exists in Europe, North America, and Australia. While New Zealand has national trapping for other pests, it remains limited for bark and wood-boring beetles as part of the Forest Biosecurity Surveillance (FBS) and Dutch Elm Disease (DED) monitoring programmes. Recent advances in molecular methods, such as environmental DNA (eDNA) and metabarcoding, offer a highly sensitive, non-invasive surveillance tool. eDNA refers to genetic material shed by organisms into the environment, which can be collected from soil, water, or air samples to detect the presence of pests even in the absence of visible signs, thus enhancing early detection efforts.

Additionally, remote sensing and aerial surveys offer a valuable means of monitoring large areas, especially in regions that are difficult to access on the ground. These technologies are crucial for tracking insect damage across expansive forest landscapes, enabling timely detection of threats in hard-to-reach locations and even the possibility of pre-symptomatic detection of infested trees.

7.2 Eradication programmes

Examples of successful eradications of introduced bark beetles and other forest insects are extremely rare, and there is currently only one species of Scolytinae referenced in the global eradication and response database (the ambrosia beetle *Xylosandrus crassiusculus*) (Kean et al., 2024). Another recent example is the eradication of *I. typographus*, which was first discovered in the UK in 2018. With multiple outbreak sites in southeast England, all were presumed to be the result of natural dispersal events across the Channel from the continent (Blake et al., 2024). Although still present at several sites, *I. typographus* is now considered eradicated from the first known outbreak location, and continued efforts have prevented further dispersal from all known outbreak sites (see Appendix B for map). The current success of the management programme tells us that eradication efforts can be worthwhile if detected early enough so that the infested area is small.

In the case of *I. typographus*, the outbreak area was divided into four zones, where spruce trees were either cut down and destroyed or inspected and removed if they appeared to be at risk (Blake et al., 2024). The originally infested stand was cut down in 2019, and most of the leftover woody debris was destroyed. The remaining beetles emerging from the site were trapped using pheromone traps, billet piles, and trap trees. These immediate measures successfully eradicated the breeding population, but a few adult *I. typographus* were still captured on the outbreak site in 2020 and 2021. All spruce within a 1 km radius were located and checked, and any that appeared stressed or were in poor condition (>30 % loss in crown density), or were dying or dead, were felled, inspected and destroyed. An extended monitoring programme was also developed over a buffer zone expanding from 1 km to 100 km around the originally infested stand. All public spruce stands in that zone were visited, and trees showing signs of dieback, top death or general decline were felled and inspected for *I. typographus*.

Following the original response in 2019, extensive trap networks were deployed, and new site infestations were detected in 2021, 2022 and 2023-2024 (Appendix B; Inward et al., 2024). Ground surveys for *I. typographus* are undertaken by collecting bark panels and confirmed breeding sites are deemed eradication sites and are assessed for severity. At eradication sites, unhealthy spruce trees are immediately removed, and eventually, all spruce within a defined area at each site are removed. Trapping is undertaken for monitoring purposes to 'soak up' remaining beetles from harvesting residue or those that had overwintered in the soil. Besides trapping, ongoing monitoring includes aerial surveillance combined with targeted ground inspections and a wider network of traps, including a Great Britain-wide trapping programme through the Forest Trapping Network.

With natural dispersal across the Channel being the suspected entry pathway (34 km at the narrowest point), dedicated coastal trapping networks have been established on both sides of the North Sea, with modelling being used to understand the potential for combined outbreaks on the continent and specific weather patterns to influence dispersal (Inward et al., 2024). Tests are also being undertaken to assess attractiveness and breeding success on Sitka spruce as a second host species in addition to the primary host, Norway spruce (Forestry Commission, 2024).

7.3 “Slow the spread” programmes

Slow the spread programmes are enacted when eradication is deemed unfeasible, to isolate the invasive species to prevent further spread and damage. Quickly removing susceptible materials, such as recently wind-thrown and felled timber, along with localised sanitation felling in poorly growing or water-stressed stands, is crucial for effectively managing the spread and outbreak patterns of *Ips* and other bark beetles (Fettig & Hilszczański, 2015). If present, inspections should take place in affected areas before transporting the material away.

In response to the *I. typographus* incursion in England, a demarcated area is now also in place to restrict the felling and movement of potentially infested host material (Appendix B). The new policy requires anyone felling or moving spruce trees within the specified extended demarcation area to inform the Forestry Commission in writing before undertaking any actions, such that inspections may take place. Affected landowners are instructed to remove and destroy infected and neighbouring spruce trees, using a risk-based approach that adheres to biosecurity protocols yet attempts to maximize the amount of wood that can be removed as roundwood. Landowners can receive funding for felling and infrastructure where the sale of timber does not cover their operational costs. In some cases, predicted climate change has resulted in proactive management whereby spruce has been removed to minimise the risk of future outbreaks (Forestry Commission, 2024). A shift away from planting and growing spruce in southern England is being considered (Inward et al., 2024).

7.4 Silvicultural practices

Ips grandicollis is highly opportunistic and can undergo rapid population growth when suitable hosts are plentiful (Neumann & Morey, 1984). One of the most effective management strategies to prevent outbreaks in plantations is therefore the rapid removal of forestry slash, typically within 24 hours of felling (Abbott, 1993). Alternatively, the slash can be left on-site but destroyed before the adult beetles emerge through methods such as roller chopping or controlled burning (Gitau et al., 2013; McNichol et al., 2019). Promptly removing or destroying slash leads to significant reductions in source beetle populations and lowers the risk of an outbreak in surrounding forests (Yousuf et al., 2014). This method is particularly effective for maintaining healthy forests where slash is the primary host material. Trees damaged by fire, lightning or windstorms should also be salvaged immediately as they are susceptible to attack (e.g., Wylie, 2000). However, in the case of severe disturbances, such as large windthrows, there may not be enough time for clearing of affected areas. On-site debarking is a potential alternative to the removal or destruction of damaged stems (Wermelinger, 2004), and this method could become more widespread with the increasing use of machine felling heads equipped with effective debarking capabilities.

Attacks on healthy trees are more common when *I. grandicollis* abundance is high (Mason, 1970; Werner, 1972a). Other silvicultural activities that reduce tree stress, such as appropriate thinning to reduce moisture stress during drought periods, can be applied to minimise outbreak risks (Fettig et al., 2007). Practices that increase susceptibility to attacks, like pruning and thinning, should be timed to avoid coinciding with beetle activity or stress-inducing disturbances, such as fire (Fettig et al., 2007). Additionally, adjusting the timing of silvicultural operations can reduce beetle pressure by ensuring that susceptible material is not available during critical periods of beetle activity. For example, conducting operations just after the flight period of pest species, allowing time for wood decay, can reduce the attractiveness of the material to beetles. In Norway, studies showed stumps generated in autumn were less attractive to spring-colonising *I. typographus* than fresh stumps, likely due to decay (Schroeder et al., 1999).

7.5 Chemical control

Research on the chemical control of *I. grandicollis* has primarily focused on the use of insecticides and semiochemicals to induce mortality or prevent attacks through deterrents or pheromone interruptants.

7.5.1 Insecticides

Effective tree protection treatments include systemic insecticides such as emamectin benzoate and fipronil. When injected into the stem, emamectin benzoate can provide near-complete protection from *I. grandicollis* attack four weeks from application to at least five months after application (Grosman & Upton, 2006). During this period, colonising males are either deterred from boring into the bark or killed upon attack, and the cessation of aggregation pheromone production by males prevents female establishment. Fipronil is similarly effective, but it requires approximately three months to disperse within the tree and provide complete protection (Grosman & Upton, 2006). However, these methods are costly and involve treating individual trees, making them unsuitable for a large-scale application in commercial forests.

To prevent population explosions of *I. grandicollis*, especially after disturbances like storms or fires, applications of non-systemic insecticides can be implemented to control beetle activity. One possible approach is a prophylactic spray treatment applied directly to logs via the mechanical feller head when harvesting takes place. This method protects the logs right after felling, as bark beetles, including *I. grandicollis*, are active during the daytime when harvesting occurs. A broad-spectrum insecticide could be used in this prophylactic spray, with the application technology later adaptable for distributing other treatments, such as bio-based insecticides like fungal sprays or repellents.

Non-systemic insecticides that act through contact or ingestion have proven effective against *I. grandicollis*, but their use is limited due to toxicity concerns. For example, trees treated with carbaryl had attack levels reduced by a factor of four or five compared to control trees (Burke et al., 2012), but its use was discontinued in Australia because of its high toxicity to honey bees and aquatic invertebrates (Yousuf et al., 2014). Similarly, the pyrethroid insecticide bifenthrin has proven efficacy against *Ips* species but is classified as a 'restricted-use' pesticide by the U.S. Environmental Protection Agency due to its ecological toxicity and possible carcinogenicity (Burke et al., 2012; Grosman & Upton, 2006). Other non-systemic insecticides have had variable success in demonstrated efficacy. Stone and Simpson (1987) found that permethrin was only moderately effective against *I. grandicollis* attacks and that it had lower efficacy than another pyrethroid, deltamethrin, and the organophosphate, chlorpyrifos-methyl. In contrast, other authors have found that permethrin works well to prevent bark beetle attacks (Grosman & Upton, 2006; Strom et al., 2015). In New Zealand, synthetic pyrethroids have been applied at wood-processing sites as a risk management measure, with sprays used around building perimeters and storage areas to manage the cerambycid *Arhopalus ferox* (Pawson & Meurisse, 2015).

Ecotoxicity of three commonly used pyrethroids (bifenthrin, cypermethrin, and deltamethrin) has been tested, with cypermethrin found to be the least toxic (Rivera-Dávila et al., 2021). Ineffective treatments include fenitrothion (Stone & Simpson, 1987), dinotefuran (Grosman & Upton, 2006), and imidacloprid products (Grosman & Upton, 2006; Strom et al., 2015).

Chemical treatments can also be used to reduce blue staining damage. In early efforts to prevent blue staining in Australia, it was found that the extent of blue stain damage in *P. elliotii* could be reduced by 75% in billets treated with Gamma-BHC compared to control billets (Stone & Simpson, 1987). However, this chemical was later found to be ecotoxic. Even a single *I. grandicollis* individual vectoring *Ophiostoma ips* is enough to cause undesirable blue staining, which worsens with the establishment of more beetles. Furthermore, any method aimed at deterring *I. grandicollis* from colonising recently felled logs should be conducted within 24 hours to prevent the initial establishment of colonising males.

7.5.2 Semiochemicals

Bark beetle aggregation pheromones can act as attractants or deterrents for different bark beetle species. In *I. grandicollis*, the pheromone ipsenol is emitted by pioneering males to attract conspecifics (and other bark beetles), and by doing so aids in overwhelming host defences. Ipsenol is attractive to bark beetles in the genus *Ips*, such as *I. grandicollis* and *I. avulsus* (Miller, 2023), but also other bark beetles and even cerambycids in the genus *Monochamus* (Smith et al., 2021). It can thus be used as an effective tool for monitoring these species. Other bark beetle pheromones can act as attractants for some species but deter other species. As such, they function to regulate resource competition by signalling that a host is already occupied by a competing species.

Ipsdienol, for example has been shown to have a deterrent effect on *I. grandicollis* (Allison et al., 2012; Birgersson et al., 2012; Kohnle et al., 1994), though this effect was not found by Carnegie and Loch (2010). Lanierone is another semiochemical that has been found to deter *I. grandicollis* (Birgersson et al., 2012) but had no effect in other work (Miller et al., 2005).

Semiochemicals termed “interruptants” reduce the efficacy of attractants when used concurrently, rather than deterring the target completely. In one study in the early 1970s, the *D. frontalis* aggregation pheromone frontalin was combined with trans-verbenol interrupted ipsenol, and reduced *I. grandicollis* attack, while equal concentrations of frontalin with methyl chavicol or (-) α -pinene had a deterrent effect on 100% of *I. grandicollis* females (Werner, 1972a). In contrast, Aukema and Raffa (2005) found that frontalin with (-) α -pinene was a deterrent for *I. pini* but was an attractant for *I. grandicollis*. Dickens et al. (1992) found hexanal alone to be the most useful interruptant for *I. grandicollis*.

When used in forest pest management, repellents can be used for “pushing” insects away from the trees or timber resources and attractants used simultaneously for “pulling” these insects towards traps that kill them. This is often referred to as a “push-pull” strategy. Afzal et al. (2023) conducted a meta-analysis of 863 experiments on the interactions between bark beetles and various semiochemicals. Some *Ips* species, such as *I. perturbatus*, were managed very successfully using this technique, having populations reduced by an average of 94% across studies (e.g., Fettig et al., 2013). However, data on *I. grandicollis* were mixed and it was concluded that further research would be needed to validate the efficacy of this technique in managing *I. grandicollis* populations (Afzal et al. 2023a, 2023b).

7.6 Biological control

7.6.1 Parasitoids

The management of *I. grandicollis* using biological control agents has been carried out in Australia. Several natural enemies were imported to the Waite Institute of Agricultural Research in South Australia from North America in the early 1980s to investigate their potential as biocontrol agents (Abbott, 1993). Two parasitoids and two predators were subsequently introduced into pine plantations in Australia in 1981 (Table 2). Establishment was confirmed only for *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae). Three other parasitoid species were later released in South Australia but failed to establish, presumably due to low release numbers (Waterhouse & Sands, 2001). These included *Coeloides sympitus*, *Dinotiscus dendroctoni*, and *Rhopalicus pulcheripennis*.

Roptrocerus xylophagorum is a parasitic wasp native to North America and Europe, where it specialises in the parasitism of bark beetle larvae; late instar larvae are preferred hosts but pupae may also be parasitised (Samson, 1984). This species is abundant throughout its native range, and is recognized as an important natural enemy of economically significant bark beetles, including *D. frontalis* and *I. grandicollis*, among others (Mills, 1983; Moore, 1972).

Table 2: Parasitoids and predators introduced into Australia as a biological control component in the integrated control of *Ips grandicollis* (Morgan, 1989).

Species	Family	Control type	Establishment status	Preliminary control assessment (1988)
<i>Roptrocercus xylophagorum</i>	Pteromalidae	Parasitoid	Widespread	25%
<i>Dendrosoter sulcatus</i>	Braconidae	Parasitoid	Doubtful*	–
<i>Thanasimus dubius</i>	Cleridae	Predator	Doubtful*	–
<i>Temnochila virescens</i>	Trogossitidae	Predator	Doubtful*	–

* Breeding in field release sites recorded.

In South Australia adult *R. xylophagorum* were introduced into plantations in 1982, and establishment was confirmed by 1988 (Abbott, 1993). In Western Australia, just under 3,000 parasitoids were introduced over three release seasons (1984, 1988, 1989). The first cohort established quickly (by the following year) and spread to nearby plantations where it had not been released. The 1988 and 1989 releases were conducted to supplement the established populations with increased genetic diversity. Laboratory studies found that each adult female *R. xylophagorum* survived for an average of 24 days at 24°C and could parasitise up to 11 *I. grandicollis* larvae each (Samson, 1984). In the field, the average parasitism rate of *R. xylophagorum* across surveyed sites that contained radiata pine was 5.2% (max 16.4%) of the total *I. grandicollis* population, which was similar to results from laboratory studies (Samson & Smibert, 1986). Waterhouse and Sands (2001) found that *I. grandicollis* populations reduced by 25-70% on average after the introduction of *R. xylophagorum*, with greater control outcomes at sites where good *Ips* management strategies (de-barking, promptly removing slash, etc.) were being used concurrently with biological control.

7.6.2 Predators

Thanasimus dubius (Coleoptera: Cleridae) is commonly cited as the main predator of *I. grandicollis* in North America and much research has been conducted on its life history, host specificity, and dispersal ability (Aukema & Raffa, 2005). It has been shown to have reasonable host specificity, preying only on phloem feeding beetles within the trunk a few metres above ground level, which reduces the risk of non-target impacts (Erbilgin & Raffa, 2001b). Adults have also been shown to have greater dispersal ability than their prey, though unlike *I. grandicollis* they are confined to forested areas (Costa et al., 2013). Furthermore, it was shown that they could easily be mass-reared using artificial diet without impacting their feeding preferences (Reeve et al., 2003). Despite this, *T. dubius* failed to establish when introduced to South Australia for biological control in 1983, as did the predator *Temnoscheila* (= *Temonchila*) *virescens* (Coleoptera: Trogossitidae) which was introduced in 1984 and 1990 (Lawson & Morgan, 1992). It is unclear why these biological control attempts were unsuccessful, though some possible explanations include predator-prey asynchrony in Australia or climate incompatibility (Yousuf et al., 2014).

7.6.3 Natural enemies already in New Zealand

Several natural enemies of bark beetles are already present in New Zealand that may provide some control over newly established species. From 1975-1977 the Pteromalid parasitoid *Rhopalicus tutela* (Walker) was introduced to New Zealand to control the black pine bark beetle *Hylastes ater* (Paykull), though establishment was not confirmed until 2015 (Romo et al., 2017). Though *I. grandicollis* has never been an observed host of this species, several other *Ips* have, including *I. typographus*, *I. duplicatus*, and *I. cembrae*, among other bark beetles (CABI, 2019).

The palearctic bark beetle predator *Thanasimus formicarius* was imported from Austria and introduced to both North Island and South Island pine forests in New Zealand between 1977 and

1987 for control of *H. ater* and *Hylurgus ligniperda*. This predator was recovered in the field only from Whakarewarewa Forest, but was presumed likely to be established in other localities as well (Cameron et al., 1989). To our knowledge, *T. formicarius* has not been collected for many years. However, if it is still present in New Zealand, it has the potential to predate upon *I. grandicollis*, which would be a more suitable host than already established pine bark beetles such as *H. ater* or *H. ligniperda*.

7.6.4 Other potential biological control agents

Several other natural enemies have already been summarised as potential biocontrol agents in Australia (Appendix C). The most attractive candidates tend to be the ones most commonly associated with *I. grandicollis* in its native range. Some of these include *Platysoma cylindrica* (Coleoptera: Histeridae), *P. parallelum*, and the predatory long-legged fly *Medetera bistrata* (Diptera: Dolichopodidae) (Erbilgin & Raffa, 2002). Common predators have evolved to locate *I. grandicollis* by detecting various semiochemicals, including ipsenol, the Ips-specific aggregation pheromone produced by the adult beetles when colonising new host trees (Erbilgin & Raffa, 2001a). Specialist predators like *T. dubius* and *P. cylindrica* are attracted to semiochemicals produced only by bark beetles that feed a few metres from the ground, and evidence suggests these predators may have co-evolved alongside *I. grandicollis*, as well as *I. pini* (Erbilgin & Raffa, 2001b). On the other hand, more generalist predators like *Tenebroides collaris* (Coleoptera: Trogossitidae) are attracted to bark beetles that feed in various sections of the tree, including species such as *D. valens*, which often feed on the lower stem.

7.7 RNA interference

Gene silencing through RNA interference (RNAi) to control wood boring beetles is still an advancing area of research, with challenges such as the development of reliable delivery methods (Joga et al., 2021). However, laboratory studies have validated RNAi as a promising solution for *Dendroctonus* spp. (Kyre & Rieske, 2022; Kyre et al., 2019), and even more recently Wallace and Rieske (2023) have made progress in characterising the RNAi pathway for *I. calligraphus*. Future research will seek to develop mass deployment strategies, investigate the potential to exploit symbiotic fungi as vectors to target bark beetles, and assess the efficacy of alternate target genes. For instance, RNAi could cause pest reduction not only by mortality but could also be used to reduce fecundity or disrupt chemical communication (Kyre et al., 2020). One of the primary benefits of RNAi is its highly specific nature, meaning non-target effects are unlikely (Kyre & Rieske, 2022).

8. Recommendations for further readiness work

8.1. Preparedness

We recommend that the forestry sector collaborates across the whole supply chain (forest to port) and with MPI to develop comprehensive readiness plans and tools that will guide response activities effectively. These plans should address the key actions outlined in Section 7, which includes control methods and risk management options such as import health standards, surveillance, eradication, and asset management programmes.

8.1.1 Management of risk pathways

Given that the highest risk of entry for bark beetles and wood borers is through wood and sawn timber products, New Zealand must implement rigorous management of these pathways. To mitigate residual risks, it is essential to verify and enforce the correct application of phytosanitary treatments for all timber products, including wood packaging material and dunnage. Currently, MPI

relies on audits without objective sampling to verify the efficacy of risk management practices. We recommend that MPI strengthens its approach by reinstating inspections of wood packaging material to assess the effectiveness of ISPM 15 standards. Additionally, regular independent assessments of high-risk pathways could be conducted, for example, every five years. These assessments would raise biosecurity awareness and recommend good practices, such as the proper disposal of dunnage and other risk materials at ports.

8.1.2 Surveillance programmes

To further enhance biosecurity, we recommend the establishment of a broader national biosecurity surveillance programme targeting bark and ambrosia beetles (Curculionidae: Scolytinae and Platypodinae), longhorn beetles (Cerambycidae) and jewel beetles (Buprestidae), particularly around potential entry locations. The absence of such a programme in New Zealand is a notable gap in our biosecurity efforts and regrettably sets us apart from other countries. Currently, bark beetle detections principally rely on chance encounters during non-targeted inspections or public reporting. A comprehensive, ongoing surveillance system would also provide evidence of areas of pest freedom, supporting the continued export of logs and wood products.

8.1.3 Incursion responses

Dedicated equipment and protocols for specific surveys targeting *I. grandicollis* (or other species) should be identified and secured in advance, ensuring readiness for deployment in the case of an incursion response. This preparation must include all necessary equipment to support pest delimitation, such as traps and lures. Dodds et al. (2024) provide recommendations for both generic and species-specific surveys, should a target pest be detected and further trapping be required to delineate the affected area. Similarly, identification tools such as taxonomic keys and molecular diagnostic protocols should be prepared in advance. Key personnel should also be identified and trained in performing collections and diagnostics in an emergency context to ensure a swift and efficient response.

To support surveillance and response operations, mapping of *Pinus* species in urban areas near points of entry is recommended. This would provide broader benefits and could accelerate response efforts, as seen in Australia with the control of giant pine scale. Additionally, the ability to track the movement of felled trees in New Zealand would be valuable for implementing controlled area notices during large-scale response operations.

8.1.4 Licence to operate

Sectoral and public awareness campaigns should be developed to inform relevant stakeholders about potential scenarios during a biosecurity incursion. Educating sectoral managers, workers, and the public about the necessity of restricting the movement of infested wood will help mitigate resistance or conflict when such measures are necessary (Carnegie & Grant, 2025). These actions may involve the destruction of commodities and other wood material at ports, transitional facilities and warehouses, as well as infested standing trees during an incursion. Furthermore, clear communication and understanding is needed regarding the availability of permits and licences – including official (e.g., EPA), industrial (e.g., ports), and societal (e.g., residents and communities) – for the use of chemicals (e.g., attractants, repellents, and insecticides) for monitoring and control purposes.

8.2. Research

8.2.1. Development of DNA Analysis Protocol

We recommend developing an optimised DNA analysis protocol for key bark beetles, and in particular, *I. grandicollis*, based on the methodology developed for other *Ips* species by Becker et al. (2021). This diagnostic tool would facilitate the rapid identification of all life stages, enhancing the speed and accuracy of pest detection during biosecurity responses.

8.2.2. Improved traps for surveillance and monitoring

We suggest investigating the enhancement of trapping systems to improve the detection and monitoring of *I. grandicollis* and other wood-boring pests. Research could focus on refining trap design, attractants, and placement strategies to optimise effectiveness in both forested and urban environments.

8.2.3. Assessment of dispersal and efficacy of biosecurity measures

The pathways and biosecurity measures involved as logs move through forests to ports or processing yards influence regional and national spread risk. The duration that material remains exposed to infestations while awaiting processing is currently under-documented. We recommend a comprehensive study to assess these pathways and the effectiveness of current biosecurity measures, particularly focusing on exposure times and their impact on pest dispersal.

8.2.4. Testing susceptibility of pine hybrids and other conifers

Consideration should be given to testing the susceptibility of *Pinaceae* species grown in New Zealand, including *Pinus* hybrids, as well as native New Zealand conifers. While *Pinus* species are the primary hosts for *I. grandicollis*, other conifers have been reported to be attacked when principal hosts are unavailable (IPPC, 2024). Understanding the vulnerability of other conifers will help assess risks to New Zealand's forestry industry and biodiversity.

8.2.5. Modelling of climate and silvicultural management risks

We recommend developing predictive models to assess the risks posed by climate change, extreme events, and silvicultural practices on *I. grandicollis* and other potentially aggressive bark beetle species that could be introduced to New Zealand. Climate models should examine how changes in temperature, precipitation, and seasonal patterns affect beetle growth, reproduction, and dispersal, while silvicultural models can explore how forest management practices, such as high-density, short-rotation systems, influence beetle-host interactions and forest vulnerability. An integrated model that includes factors like disturbance events, such as large-scale windthrows or droughts, would improve forecasting of potential beetle outbreaks.

8.2.6. Investigation of biological control

The potential for utilising safe and effective biological control agents, such as the parasitoid *R. xylophagorum*, should be further explored. This investigation should include a review of host specificity testing conducted in Australia, an assessment of risks to New Zealand's native species, and an evaluation of whether importation for additional host testing is warranted. Biological control may offer a sustainable solution to managing *I. grandicollis* populations.

8.3. Future proofing

8.3.1. Land use

Given that severe weather events, such as droughts and windthrows are primary drivers of bark beetles and other pest outbreaks, risk models should be employed to inform decisions regarding the adoption of alternative forest plantation species or land uses. Forest mixtures could be considered as an option, as they appear to be more resistant than monocultures to specialised insect herbivores, fire, and windthrow events (Jactel et al., 2017; Jactel et al., 2021), notably during pest invasions (Rigot et al., 2014). However, certain species within the mixtures may also be more vulnerable to droughts, which can predispose them to attacks by specific pests, like bark beetles. Therefore, the potential benefits of mixed-species plantations or mosaics of tree species within the landscape should be carefully balanced with the risks, and the operational and commercial practicality of diversifying forest systems.

8.3.2. Silvicultural practices

Further evaluation is needed of the impacts of silvicultural practices, such as high stocking densities and chemical thinning, on forest vulnerability to pest attacks. The abundance of resources in these systems may trigger pest outbreaks, particularly for species like *I. grandicollis*, which can rapidly grow in numbers in the absence of density-dependent regulation by natural enemies. Modelling resource availability and pest dynamics in response to different stocking regimes and thinning practices would provide valuable insights into strategies that minimise forest susceptibility to infestations.

8.3.3. Sanitation practices

Research has demonstrated that removing forestry slash within 24 hours of felling in areas where *I. grandicollis* is present is an effective management strategy (Abbott, 1993). We recommend revising forest sanitation policies to reduce the risk of pest outbreaks, not only for *I. grandicollis* but also for other insect pests such as *Sirex noctilio* and *Hylastes ater*. Prompt sanitation following logging activities is critical for mitigating these risks and ensuring a rapid response to potential pest infestations. Additionally, the increasing risks associated with wilding pine forests, such as the overstocked *Pinus contorta* stands in Marlborough, which are entering high-stress states, need to be considered as these could contribute increased biosecurity risks in the future.

8.3.4. Policies

We recommend the development of policies focused on sanitation following natural disaster events such as cyclones, windthrow, wildfires, and extreme drought conditions. These events create favourable conditions for pest outbreaks, and policies should ensure rapid response measures to limit the spread of pests in affected areas. However, these policies should be tailored to specific events. For example, the 5000-hectare windthrow event near Taupo, which took over 12 months to recover from, involved significant health and safety concerns that should be considered when designing policy responses. Ensuring rapid, region-specific interventions will be essential to preventing pest spread during post-disaster recovery.

Acknowledgements

The authors would like to thank Carl Wardhaugh, Andrew Cridge, Brendan Gould, Bill Dyck and Andrew Pugh for reviewing earlier and later drafts of this document. Melissa Welsh contributed the economic analyses. This work was requested by the New Zealand Forest Owners Association on behalf of the FOA/FFA Forest Biosecurity Committee and was funded by the Forest Growers Levy Trust.

References

- Abbott, I. (1993). Review of the ecology and control of the introduced bark beetle *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) in Western Australia, 1952-1990. *CALMScience*, 1(1), 36-46. <https://library.dbca.wa.gov.au/static/Journals/080273/080273-01.003.pdf>
- Acosta, H., Earl, L., Growcott, A., MacLellan, R., Marquetoux, N., Pecock, L., Phiri, B. J., Stanislawek, W., Stevens, P., Tana, T., van Andel, M., Watt, J., & Gould, B. (2020). *Atlas of Biosecurity surveillance—January 2020* (pp. 1–90). Ministry for Primary Industries. <https://www.mpi.govt.nz/dmsdocument/39674-Atlas-of-Biosecurity-2019>
- Afzal, S., Nahrung, H. F., Lawson, S. A., & Hayes, R. A. (2023). How Effective Are Push–Pull Semiochemicals as Deterrents for Bark Beetles? A Global Meta-Analysis of Thirty Years of Research. *Insects*, 14(10), 812. <https://doi.org/10.3390/insects14100812>
- Allison, J. D., McKenney, J. L., Miller, D. R., & Gimmel, M. L. (2012). Role of ipsdienol, ipsenol, and cis-verbenol in chemical ecology of *Ips avulsus*, *Ips calligraphus*, and *Ips grandicollis* (Coleoptera: Curculionidae: Scolytinae). *Journal of Economic Entomology*, 105(3), 923-929. <https://doi.org/10.1603/EC12078>
- Atkinson, T. H. (2024). Bark and ambrosia beetles of the Americas. Retrieved 9 April 2025 from <http://www.barkbeetles.info>
- Aukema, B. H., & Raffa, K. F. (2005). Selective manipulation of predators using pheromones: Responses to frontalin and ipsdienol pheromone components of bark beetles in the Great Lakes region. *Agricultural and Forest Entomology*, 7(3), 193-200. <https://doi.org/10.1111/j.1461-9555.2005.00250.x>
- Aussenac, G., & Granier, A. (1988). Effects of thinning on water stress and growth in Douglas-fir. *Canadian Journal of Forest Research*, 18(1), 100-105. <https://doi.org/10.1139/x88-015>
- Ayres, B. D., Ayres, M. P., Abrahamson, M. D., & Teale, S. A. (2001). Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera: Scolytidae). *Oecologia*, 128(3), 443-453. <https://doi.org/10.1007/s004420100665>
- Bain, J., Sopow, S. L., & Bulman, L. S. (2012). The sirex woodwasp in New Zealand: history and current status. In B. Slippers, P. de Groot, & M. J. Wingfield (Eds.), *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest* (pp. 167-173). Springer. https://doi.org/10.1007/978-94-007-1960-6_13
- Bakke, A. (1982). Mass trapping of the spruce bark beetle *Ips typographus* in Norway as part of an integrated control program. *Insect suppression with controlled release pheromone systems*, 2, 17-25.
- Bauhus, J., Forrester, D. I., Pretzsch, H., Felton, A., Pyttel, P., & Benneter, A. (2017). Silvicultural Options for Mixed-Species Stands. In H. Pretzsch, D. I. Forrester, & J. Bauhus (Eds.), *Mixed-Species Forests* (pp. 433–501). Springer. https://doi.org/10.1007/978-3-662-54553-9_9
- Becker, M., König, S., & Hoppe, B. (2021). A simple PCR-based approach for rapid detection of *Ips typographus* and *Ips duplicatus* in the presence of (associated) symbionts and parasites. *Journal of Plant Diseases and Protection*, 128(2), 527-534. <https://doi.org/10.1007/s41348-020-00388-w>
- Bedding, R. (1972). Biology of *Deladenus siricidicola* (Neotylenchidae) an entomophagous-mycetophagous nematode parasitic in siricid woodwasps. *Nematologica*, 18, 482–493. <https://doi.org/10.1163/187529272X00098>
- Bedding, R., & Akhurst, R. (1974). Use of the nematode *Deladenus siricidicola* in the biological control of *Sirex noctilio* in Australia. *Australian Journal of Entomology*, 13(2), 129-135. <https://doi.org/10.1111/j.1440-6055.1974.tb02163.x>
- Bedding, R. (1993). Biological control of *Sirex noctilio* using the nematode *Deladenus siricidicola*. In R.A. Bedding, H.K. Kaya, & R. Akhurst (Eds.), *Nematodes and the Biological Control of Insect Pests* (pp. 11–20). Csiro Publishing. <https://doi.org/10.1071/9780643105218>
- Billings, R. (1985). Evaluation of pine tree mortality in Haiti. Unpublished report submitted to the USDA Forest Service, International Forestry Office, Washington, DC.
- Biosecurity New Zealand. (2023). Import health standard: wood packaging material from all countries. Ministry for Primary Industries, New Zealand. Retrieved 3 April 2025 from <https://www.mpi.govt.nz/dmsdocument/1212-wood-packaging-material-from-all-countries-import-health-standard>
- Birgersson, G., Dalusky, M. J., Espelie, K. E., & Berisford, C. W. (2012). Pheromone production, attraction, and interspecific inhibition among four species of *Ips* bark beetles in the Southeastern USA. *Psyche (London)*. <https://doi.org/10.1155/2012/532652>

- Blake, M., Straw, N., Kendall, T., Whitham, T., Manea, I. A., Inward, D., Jones, B., Hazlitt, N., Ockenden, A., Deol, A., Brown, A., Ransom, E., Smith, L., & Facey, S. (2024). Recent outbreaks of the spruce bark beetle *Ips typographus* in the UK: Discovery, management, and implications. *Trees, Forests and People*, 16. <https://doi.org/10.1016/j.tfp.2024.100508>
- Bold Systems. (2024). Barcode of Life Data System. Retrieved 9 April 2025 from <https://www.boldsystems.org/>
- Brockhoff, E. G., Epanchin-Niell, R., Kean, J.M. & Turner, J.A. (2012). Cost-Benefit Analysis of Surveillance for Wood Borers and Bark Beetles. Confidential report for the New Zealand Forest Owners Association and the Forest Biosecurity Council. Scion (the NZ Forest Research Institute), Rotorua, New Zealand. 68pp.
- Brockhoff, E. G., Corley, J. C., Jactel, H., Miller, D. R., Rabaglia, R. J., Sweeney, J., Allison, J. D., Paine, T. D., Slippers, B., & Wingfield, M. J. (2023). Monitoring and surveillance of forest insects. In: J.D. Allison, T.D. Payne, B. Slippers, & M.J. Wingfield (Eds). *Forest entomology and pathology*, 1, 669-705. <https://doi.org/10.1007/978-3-031-11553-0>
- Brockhoff, E. G., Gresham, B. A., Meurisse, N., Nahrung, H. F., Perret-Gentil, A., Pugh, A. R., Sopow, S. L., & Turner, R. M. (2023). Pining away and at home: global utilisation of *Pinus radiata* by native and non-native insects. *NeoBiota*, 84, 137-167. <https://doi.org/10.3897/NEOBIOTA.84.95864>
- Brockhoff, E. G., Jones, D. C., Kimberley, M. O., Suckling, D. M., & Donaldson, T. (2006). Nationwide survey for invasive wood-boring and bark beetles (Coleoptera) using traps baited with pheromones and kairomones. *Forest Ecology and Management*, 228(1-3), 234-240. <https://doi.org/10.1016/j.foreco.2006.02.046>
- Bulman, L. S. (1992). Forestry quarantine risk of cargo imported into New Zealand. *New Zealand Journal of Forestry Science*, 22, 32-38. <https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=f04bd6418f1a3cad7017c401d691127f1dbb75ed>
- Burke, J. L., Hanula, J. L., Horn, S., Audley, J. P., & Gandhi, K. J. (2012). Efficacy of two insecticides for protecting loblolly pines (*Pinus taeda* L.) from subcortical beetles (Coleoptera: Curculionidae and Cerambycidae). *Pest Management Science*, 68(7), 1048-1052. <https://doi.org/10.1002/ps.3266>
- CABI. (2019). *Ips grandicollis* (five-spined bark beetle). CABI Compendium. Retrieved 25 Mar 2024 from <https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.28825#sec-12>
- Cameron, P. J., Hill, R. L., Bain, J., & Thomas, W. P. (1989). *A review of biological control of invertebrate pests and weeds in New Zealand 1874-1987*. CAB International, 424 pp.
- Carnegie, A. J., & Grant, A. (2025). Social licence to eradicate invasive pests of trees in urban landscapes: A review to prepare for the next incursion. *Urban Forestry & Urban Greening*, 106. <https://doi.org/https://doi.org/10.1016/j.ufug.2025.128722>
- Carnegie, A. J., & Loch, A. D. (2010). Is *Ips grandicollis* disrupting the biological control of *Sirex noctilio* in Australia? In: K.A. McManus, K.W. Gottschalk (Eds.). Proceedings. 21st U.S. Department of Agriculture interagency research forum on invasive species, 12-15 January 2010. Annapolis, MD. USDA-FS, Northern Research Station, 3pp: 8-10.
- Chase, K. D., Kelly, D., Liebhold, A. M., Bader, M. K. F., & Brockhoff, E. G. (2017). Long-distance dispersal of non-native pine bark beetles from host resources. *Ecological Entomology*, 42(2), 173-183. <https://doi.org/10.1111/een.12371>
- Chase, K. D., Stringer, L. D., Butler, R. C., Liebhold, A. M., Miller, D. R., Shearer, P. W., & Brockhoff, E. G. (2018). Multiple-Lure Surveillance Trapping for *Ips* Bark Beetles, *Monochamus* Longhorn Beetles, and *Halyomorpha halys* (Hemiptera: Pentatomidae). *Journal of Economic Entomology*, 111(5), 2255-2263. <https://doi.org/10.1093/jeet/toy190>
- Chénier, J. V. R., & Philogène, B. J. R. (1989). Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. *Journal of Chemical Ecology*, 15(6), 1729-1745. <https://doi.org/10.1007/BF01012261>
- Cognato, A. I. (2015). Biology, Systematics, and Evolution of *Ips*. In F.E.V.W. Hofstetter (Ed.), *Bark Beetles: Biology and Ecology of Native and Invasive Species* (pp. 351–370). Academic Press. <https://doi.org/10.1016/B978-0-12-417156-5.00009-5>
- Costa, A., A. M., Boone, C. K., Kendrick, A. P., Murphy, R. J., Sharpee, W. C., Raffa, K. F., & Reeve, J. D. (2013). Dispersal and edge behaviour of bark beetles and predators inhabiting red pine plantations. *Agricultural and Forest Entomology*, 15(1), 1-11. <https://doi.org/10.1111/j.1461-9563.2012.00585.x>
- Coyne, J., & Lott, L. (1976). Toxicity of substances in pine oleoresin to southern pine beetles.
- Denham, S. O., Coyle, D. R., Oishi, A. C., Bullock, B. P., Heliövaara, K., & Novick, K. A. (2019). Tree resin flow dynamics during an experimentally induced attack by *Ips avulsus*, I.

- calligraphus*, and *I. grandicollis*. *Canadian Journal of Forest Research*, 49(1), 53-63.
<https://doi.org/10.1139/cjfr-2018-0024>
- Dickens, J. C., Billings, R. F., & Payne, T. L. (1992). Green leaf volatiles interrupt aggregation pheromone response in bark beetles infesting southern pines. *Experientia*, 48(5), 523-524.
<https://doi.org/10.1007/BF01928180>
- Dodd, A., Stoeckl, N., Baumgartner, J., & Kompas, T. (2020). Key result summary: Valuing Australia's biosecurity system. Centre of Excellence for Biosecurity Risk Analysis (CEBRA) Report, 41 pp.
https://cebra.unimelb.edu.au/__data/assets/pdf_file/0020/3535013/CEBRA_Value_Docs_KeyResultSummary_v0.6_Endorsed.pdf
- Dodds, K. J., & Miller, D. R. (2010). Test of nonhost angiosperm volatiles and verbenone to protect trap trees for *Sirex noctilio* (Hymenoptera: Siricidae) from attacks by bark beetles (Coleoptera: Scolytidae) in the northeastern United States. *Journal of Economic Entomology*, 103(6), 2094-2099. <https://doi.org/10.1603/EC10225>
- Dodds, K. J., Sweeney, J., Francese, J. A., Besana, L., & Rassati, D. (2024). Factors affecting catches of bark beetles and woodboring beetles in traps. *Journal of Pest Science*.
<https://doi.org/10.1007/s10340-024-01774-1>
- Eichhoff, W. J. (1867). Neue amerikanische Borkenkäfer-Gattungen und Arten. *Berliner entomologische Zeitschrift*, 11(3-4), 399-402. <https://doi.org/10.1002/mmnd.18670110320>
- Eichhoff, W. J. (1868). Neue Borkenkäfer. *Berliner Entomologische Zeitschrift*, 12(3-4), 273.
- Eickwort, J., & Mayfield III, A. E. (2018). Featured Creatures: *Ips engraver* beetles. University of Florida.
- Epanchin-Niell, R. S., Brockerhoff, E. G., Kean, J. M., & Turner, J. A. (2014). Designing cost-efficient surveillance for early detection and control of multiple biological invaders. *Ecological Applications*, 24(6), 1258-1274. <https://doi.org/10.1890/13-1331.1>
- EPPO. (2024). European Plant Protection Organization Global Database, *Ips grandicollis*, . Retrieved 9 April 2025 from <https://gd.eppo.int/taxon/IPSXGR/hosts>
- Erbilgin, N., & Raffa, K. F. (2001a). Kairomonal range of generalist predators in specialized habitats: Responses to multiple phloeophagous species emitting pheromones vs. host odors. *Entomologia Experimentalis et Applicata*, 99(2), 205-210.
<https://doi.org/10.1046/j.1570-7458.2001.00818.x>
- Erbilgin, N., & Raffa, K. F. (2001b). Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. *Oecologia*, 127(3), 444-453.
<https://doi.org/10.1007/s004420000606>
- Erbilgin, N., & Raffa, K. F. (2002). Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens. *Forest Ecology and Management*, 164(1-3), 221-236.
[https://doi.org/10.1016/S0378-1127\(01\)00596-5](https://doi.org/10.1016/S0378-1127(01)00596-5)
- Fernández, M., Garcia, A., & Lieutier, F. (2004). Effects of various densities of *Ophiostoma ips* inoculations on *Pinus sylvestris* in north-western Spain. *Forest Pathology*, 34(4), 213-223.
- Fettig, C. J., Burnside, R. E., Hayes, C. J., Kruse, J. J., Lisuzzo, N. J., McKelvey, S. R., Mori, S. R., Nickel, S. K., & Schultz, M. E. (2013). Factors influencing northern spruce engraver colonization of white spruce slash in interior Alaska. *Forest Ecology and Management*, 289, 58-68. <https://doi.org/10.1016/j.foreco.2012.09.040>
- Fettig, C. J., & Hilszczański, J. (2015). Management Strategies for Bark Beetles in Conifer Forests. In F.E.V.W. Hofstetter (Ed.), *Bark Beetles: Biology and Ecology of Native and Invasive Species* (pp. 555–584). Academic Press.
<http://www.sciencedirect.com/science/article/pii/B9780124171565000149>
- Fettig, C. J., Klepzig, K. D., Billings, R. F., Munson, A. S., Nebeker, T. E., Negrón, J. F., & Nowak, J. T. (2007). The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management*, 238(1-3), 24-53.
- Field, E., Hector, A., Barsoum, N., & Koricheva, J. (2025). Tree diversity reduces pathogen damage in temperate forests: a systematic review and meta-analysis. *Forest Ecology and Management*, 578, 122398.
- Flamm, R. O., Pulley, P. E., & Coulson, R. N. (1993). Colonization of disturbed trees by the southern pine bark beetle guild (Coleoptera: Scolytidae). *Environmental Entomology*, 22(1), 62-70. <https://doi.org/10.1093/ee/22.1.62>
- Flechtmann, C. A. H., Dalusky, M. J., & Berisford, C. W. (1999). Bark and ambrosia beetle (Coleoptera: Scolytidae) responses to volatiles from aging loblolly pine billets. *Environmental Entomology*, 28(4), 638-648. <https://doi.org/10.1093/ee/28.4.638>

- Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular marine biology and biotechnology*, 3(5), 294-299.
- FOA. (2022). Forest Biosecurity News March 2022. New Zealand Forest Owners Association (FOA), Wellington, New Zealand, 6pp. Retrieved 9 April 2025 from [https://www.nzffa.org.nz/system/assets/7655/FGT_4277_Newsletter_P5_V4_\(1\).pdf](https://www.nzffa.org.nz/system/assets/7655/FGT_4277_Newsletter_P5_V4_(1).pdf)
- FOA. (2023). Facts & Figures 2022/23 -New Zealand Plantation forest industry. New Zealand Forest Owners Association (FOA), Wellington, New Zealand, 35pp. Retrieved 9 April 2025 from https://www.nzfoa.org.nz/images/stories/pdfs/Facts_Figures_2016_%C6%92a_web_version_v3.pdf
- Forestry Commission. (2024). 'Behind the Scenes' at the Forestry Commission: Managing *Ips typographus*.....five years on. Forestry Commission. Retrieved 9 April 2025 from <https://forestrycommission.blog.gov.uk/2023/10/10/behind-the-scenes-at-the-forestry-commission-managing-ips-typographus-five-years-on/>
- Forsse, E., & Solbreck, C. (1985). Migration in the bark beetle *Ips typographus* L.: duration, timing and height of flight. *Zeitschrift für Angewandte Entomologie*, 100(1-5), 47-57. <https://doi.org/10.1111/j.1439-0418.1985.tb02756.x>
- Gandhi, K. J. K., & Hofstetter, R. W. (2021). *Bark Beetle Management, Ecology, and Climate Change*. Elsevier. <https://doi.org/10.1016/C2019-0-04282-3>
- Garraway, E., & Freeman, B. E. (1990). The population dynamics of *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) in Jamaica. *The Canadian Entomologist*, 122(2), 217-227. <https://doi.org/10.4039/Ent122217-3>
- Gitau, C. W., Carnegie, A. J., Nicol, H. I., Bashford, R., Poynter, C., & Gurr, G. M. (2013). Incidence of *Ips grandicollis* (Coleoptera: Scolytinae) in trap trees prepared for biological control of *Sirex noctilio* (Hymenoptera: Siricidae) in Australia: Influence of environment and silviculture. *Forest Ecology and Management*, 310, 865-874. <https://doi.org/10.1016/j.foreco.2013.09.035>
- Grégoire, J. C., Caili, E., Hasbroucq, S., Molenberg, J. M., & Willenz, S. (2022). When the Beetles Hit the Fan: The Fan-Trap, an Inexpensive, Light and Scalable Insect Trap under a Creative Commons License, for Monitoring and Experimental Use. *Insects*, 13(12). <https://doi.org/10.3390/insects13121122>
- Griffin, M. J., Holwell, G. I., & Symonds, M. R. E. (2020). Sex ratio and female allocation to harems in a polygynous bark beetle. *Austral Entomology*, 59(1), 149-155. <https://doi.org/10.1111/aen.12440>
- Griffin, M. J., & Symonds, M. R. E. (2021). Environment and local substrate availability effects on harem formation in a polygynous bark beetle. *Insects*, 12(2), 1-13. <https://doi.org/10.3390/insects12020098>
- Grosman, D. M., & Upton, W. W. (2006). Efficacy of systemic insecticides for protection of loblolly pine against southern pine engraver beetles (Coleoptera: Curculionidae: Scolytinae) and wood borers (Coleoptera: Cerambycidae). *Journal of Economic Entomology*, 99(1), 94-101. [https://doi.org/10.1603/0022-0493\(2006\)099\[0094:EOSIFP\]2.0.CO;2](https://doi.org/10.1603/0022-0493(2006)099[0094:EOSIFP]2.0.CO;2)
- Guérard, N., Dreyer, E., & Lieutier, F. (2000). Interactions between Scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (Math.): estimation of the critical thresholds of attack and inoculation densities and effects on hydraulic properties in the stem. *Annals of Forest Science*, 57(7), 681-690. <http://dx.doi.org/10.1051/forest:2000149>
- Haack, R. A., Hardin, J. A., Caton, B. P., & Petrice, T. R. (2022). Wood borer detection rates on wood packaging materials entering the United States during different phases of ISPM 15 implementation and regulatory changes. *Frontiers in Forests and Global Change*, 5. <https://doi.org/10.3389/ffgc.2022.1069117>
- Haack, R. A., & Paiz-Schwartz, G. (1997). Bark beetle (Coleoptera: Scolytidae) outbreak in pine forests of the Sierra de las Minas biosphere reserve, Guatemala. *Entomological News*, 108(1), 67-76. <https://www.biodiversitylibrary.org/item/55164#page/8/mode/1up>
- Hanewinkel, M., Hummel, S., & Albrecht, A. (2011). Assessing natural hazards in forestry for risk management: a review. *European Journal of Forest Research*, 130, 329-351. <https://doi.org/10.1007/s10342-010-0392-1>
- Hertel, G. D., Hain, F. P., & Anderson, R. F. (1969). Response of *Ips grandicollis* (Coleoptera: Scolytidae) to the attractant produced by attacking male beetles. *The Canadian Entomologist*, 101(10), 1084-1091. <https://doi.org/10.4039/Ent1011084-10>
- Hood, I. A., & Ramsden, M. (1997). Sapstain and decay following fire in stands of *Pinus elliottii* var. *elliottii* near beerburum, south east queensland. *Australian Forestry*, 60(1), 7-15. <https://doi.org/10.1080/00049158.1997.10674693>

- International Plant Protection Convention. (2019). International Plant Protection Convention International Standard for Phytosanitary Measures 15, Regulation of wood packaging material in international trade. Food and Agriculture Organization of the United Nations, Rome, Italy, 24pp. Retrieved 9 April 2025 from https://www.ippc.int/static/media/files/publication/en/2019/02/ISPM_15_2018_En_WoodPackaging_Post-CPM13_Rev_Annex1and2_Fixed_2019-02-01.pdf
- International Plant Protection Convention. (2025). International Plant Protection Convention International Standard for Phytosanitary Measures 27. Diagnostic protocols for regulated pests - DP 27: *Ips* spp. Food and Agriculture Organization of the United Nations, Rome, Italy, 39 pp. Retrieved 9 April 2025 from https://assets.ippc.int/static/media/files/publication/en/2025/03/DP_27_Ips_Rev_2025-03-10_No-Covers.pdf
- Inward, D. J. G., Caiti, E., Barnard, K., Hasbroucq, S., Reed, K., & Grégoire, J. C. (2024). Evidence of cross-channel dispersal into England of the forest pest *Ips typographus*. *Journal of Pest Science*. <https://doi.org/10.1007/s10340-024-01763-4>
- Isitt, R., Økland, B., Krokene, P., Sweeney, J., Heard, S. B., & Pureswaran, D. S. (2023). Successful colonization of novel spruce hosts by European and North American spruce bark beetles can favour trans-Atlantic range expansion. *Forestry*, *96*(5), 631-638. <https://doi.org/10.1093/forestry/cpad015>
- Jackson, P. L., Straussfogel, D., Lindgren, B. S., Mitchell, S., & Murphy, B. (2008). Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk.(Coleoptera: Scolytidae) in flight above the forest canopy. *Canadian Journal of Forest Research*, *38*(8), 2313-2327. <https://doi.org/10.1139/X08-066>
- Jactel, H. (1991). Dispersal and flight behaviour of *Ips sexdentatus* (Coleoptera: Scolytidae) in pine forest. *Annales des Sciences Forestieres*, *48*(4), 417-428. <https://doi.org/10.1051/forest:19910405>
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J. R., Koricheva, J., Meurisse, N., & Brockerhoff, E. G. (2017). Tree diversity drives forest stand resistance to natural disturbances. *Current Forestry Reports*, *3*, 223-243. <https://doi.org/10.1007/s40725-017-0064-1>
- Jactel, H., & Marini, L. (2021). Free evolution of forests and control of the health risk associated with conifer bark beetles. *Revue forestiere francaise*, *73*(2-3), 383-390. <https://doi.org/10.20870/revforfr.2021.5477>
- Jactel, H., Moreira, X., & Castagneyrol, B. (2021). Tree diversity and forest resistance to insect pests: patterns, mechanisms, and prospects. *Annual Review of Entomology*, *66*(1), 277-296. <https://doi.org/10.1146/annurev-ento-041720-075234>
- Joga, M. R., Mogilicherla, K., Smagghe, G., & Roy, A. (2021). RNA Interference-Based Forest Protection Products (FPPs) Against Wood-Boring Coleopterans: Hope or Hype? *Frontiers in Plant Science*, *12*. <https://doi.org/10.3389/fpls.2021.733608>
- Jones, A. G., Adusei-fosu, K., Bartlett, M., Dobbie, K., Grant, A., McLay, E., Sopow, S., & Withers, T. (2023). Assessment and mitigation of biophysical and social risk for short rotation bioenergy forestry. Internal confidential report. Scion, Rotorua, New Zealand, 79pp.
- Kausrud, K., Økland, B., Skarpaas, O., Grégoire, J.-C., Erbilgin, N., & Stenseth, N. Chr. (2012). Population dynamics in changing environments: The case of an eruptive forest pest species. *Biological Reviews*, *87*(1), 34–51. <https://doi.org/10.1111/j.1469-185X.2011.00183.x>
- Kean, J. M., Suckling, D. M., Sullivan, N. J., Tobin, P. C., Stringer, L. D., Smith, G. R., Kimber, B., Lee, D. C., Flores Vargas, R., Fletcher, J., Macbeth, F., McCullough, D. G., Herms, D. A., & al., e. (2024). Global eradication and response database. Retrieved 5 August 2024 from <http://b3.net.nz/gerda>.
- Kinn, D. N. (1971). The life cycle and behavior of *Cercoleipus coelonotus* (Acarina: Mesostigmata). Including a survey of phoretic mite associates of California Scolytidae. *University of California Publications in Entomology*, *65*, 1-59. <https://www.biodiversitylibrary.org/partpdf/179966>
- Kinn, D. N. (1986). *Studies on the flight capabilities of Dendroctonus frontalis and Ips calligraphus: preliminary findings using tethered beetles* (Vol. 324). US Department of Agriculture, Forest Service, Southern Forest Experiment Station, 3pp. <https://doi.org/10.2737/SO-RN-324>
- Kirkendall, L. R., Biedermann, P. H. W., & Jordal, B. H. (2015). Evolution and Diversity of Bark and Ambrosia Beetles. In F.E.V.W. Hofstetter (Ed.), *Bark Beetles: Biology and Ecology of Native and Invasive Species* (pp. 85–156). Academic Press. <https://doi.org/10.1016/B978-0-12-417156-5.00003-4>

- Kohnle, U., Vité, J. P., Meyer, H., & Francke, W. (1994). Response of four American engraver bark beetles, *Ips* spp. (Col., Scolytidae), to synthetic racemates of chiral pheromones. *Journal of Applied Entomology*, 117(1-5), 451-456. <https://doi.org/10.1111/j.1439-0418.1994.tb00761.x>
- Krokene, P. (2015). Conifer Defense and Resistance to Bark Beetles. In F.E.V.W. Hofstetter (Ed.), *Bark Beetles: Biology and Ecology of Native and Invasive Species* (pp. 177-207). Academic Press. <https://doi.org/10.1016/B978-0-12-417156-5.00005-8>
- Kyre, B. R., Bentz, B. J., & Rieske, L. K. (2020). Susceptibility of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) to gene silencing through RNAi provides potential as a novel management tool. *Forest Ecology and Management*, 473. <https://doi.org/10.1016/j.foreco.2020.118322>
- Kyre, B. R., & Rieske, L. K. (2022). Using RNAi to silence heat shock protein has congeneric effects in North America's *Dendroctonus* bark beetles. *Forest Ecology and Management*, 520. <https://doi.org/10.1016/j.foreco.2022.120367>
- Kyre, B. R., Rodrigues, T. B., & Rieske, L. K. (2019). RNA interference and validation of reference genes for gene expression analyses using qPCR in southern pine beetle, *Dendroctonus frontalis*. *Scientific Reports*, 9(1). <https://doi.org/10.1038/s41598-019-42072-6>
- LaBonte, J. R., & Valley, S. A. (2011). Illustrated key to the species of *Ips*, *Orthotomicus*, and *Pseudips* of North America (or spines, spines, and more spines). Version 05-04-11. Oregon Department of Agriculture, Salem, Oregon. Accessed 9 April 2025, <https://conference.ifas.ufl.edu/npdn/Docs/Workshop%20Materials/Ips%20050411.pdf>
- Lantschner, M. V., Atkinson, T. H., Corley, J. C., & Liebhold, A. M. (2017). Predicting North American Scolytinae invasions in the Southern Hemisphere. *Ecological Applications*, 27(1), 66-77. <https://doi.org/10.1002/eap.1451>
- Lantschner, M. V., Corley, J. C., & Liebhold, A. M. (2020). Drivers of global Scolytinae invasion patterns. *Ecological Applications*, 30(5). <https://doi.org/10.1002/eap.2103>
- Latty, T. M., Magrath, M. J. L., & Symonds, M. R. E. (2009). Harem size and oviposition behaviour in a polygynous bark beetle. *Ecological Entomology*, 34(5), 562-568. <https://doi.org/10.1111/j.1365-2311.2009.01103.x>
- Lawson, S. A. (1993). Overwintering mortality of *Ips grandicollis* Eichh. (Col., Scolytidae) and its parasitoid, *Roptrocerus xylophagorum* Ratz. (Hym., Pteromalidae), in South Australia. *Journal of Applied Entomology*, 115(1-5), 240-245. <https://doi.org/10.1111/j.1439-0418.1993.tb00385.x>
- Lawson, S. A., & Morgan, F. D. (1992). Rearing of two predators, *Thanasimus dubius* and *Temnochila virescens*, for the biological control of *Ips grandicollis* in Australia. *Entomologia Experimentalis et Applicata*, 65(3), 225-233. <https://doi.org/10.1111/j.1570-7458.1992.tb00675.x>
- Li, Y., Johnson, A. J., Gao, L., Wu, C., & Hulcr, J. (2021). Two new invasive *Ips* bark beetles (Coleoptera: Curculionidae) in mainland China and their potential distribution in Asia. *Pest Management Science*, 77(9), 4000-4008. <https://doi.org/10.1002/ps.6423>
- Liebhold, A., & Callan, B. (2007). New Zealand Forest Health Surveillance Review. Unpublished report commissioned by the New Zealand Forest Owners Association, 16pp..
- Lombardero, M. J., Ayres, M. P., & Ayres, B. D. (2006). Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. *Forest Ecology and Management*, 225(1-3), 349-358. <https://doi.org/10.1016/j.foreco.2006.01.010>
- Lombardero, M. J., Ayres, M. P., Ayres, B. D., & Reeve, J. D. (2000). Cold tolerance of four species of bark beetle (Coleoptera: Scolytidae) in North America. *Environmental Entomology*, 29(3), 421-432. <https://doi.org/10.1603/0046-225X-29.3.421>
- Lovett, G., & Davila, D. (2021). *A novel approach for keeping pests out of wood packaging material*. Cary Institute of Ecosystem Studies. Retrieved 9 April 2025 from <https://www.caryinstitute.org/news-insights/feature/novel-approach-keeping-pests-out-wood-packaging-material>
- Marchioro, M., Battisti, A., & Faccoli, M. (2020). Light traps in shipping containers: A new tool for the early detection of insect alien species. *Journal of Economic Entomology*, 113(4), 1718-1724. <https://doi.org/10.1093/jee/toaa098>
- Mas, H., & Johnson, A. J. (2023). First Reported Detection of *Ips calligraphus* (Germar) and *Ips grandicollis* (Eichhoff)(Coleoptera: Curculionidae) in a Port of Entry and its Surrounding Forest in Spain. *The Coleopterists Bulletin*, 77(4), 501-506. <https://doi.org/10.1649/0010-065X-77.4.501>
- Mason, R. R. (1970). Comparison of flight aggregation in two species of southern *Ips* (Coleoptera: Scolytidae). *The Canadian Entomologist*, 102(8), 1036-1041. <https://doi.org/10.4039/Ent1021036-8>

- McGrath, J. F., Ward, D. J., & Davison, E. M. (1990). *Pine deaths in the Blackwood Valley plantations: a recurrent problem*. Department of Conservation and Land Management. Retrieved 9 April 2025 from <https://library.dbca.wa.gov.au/static/FullTextFiles/009663.pdf>
- McNichol, B. H., Montes, C. R., Barnes, B. F., Nowak, J. T., Villari, C., & Gandhi, K. J. K. (2019). Interactions between southern Ips bark beetle outbreaks, prescribed fire, and loblolly pine (*Pinus taeda* L.) mortality. *Forest Ecology and Management*, 446, 164-174. <https://doi.org/10.1016/j.foreco.2019.05.036>
- Mead, D. J. (2013). *Sustainable management of Pinus radiata plantations*. MFAO Forestry Paper No. 170. Food and Agriculture Organization of the United Nations (FAO), Rome, 265pp. Retrieved 9 April 2025 from <https://www.fao.org/4/i3274e/i3274e.pdf>
- Mead, D. J., & Burdon, R. D. (2023). Lessons from Insect and Disease Impacts on Radiata Pine (*Pinus radiata* D. Don) Plantations in New Zealand over the Last Hundred Years. *International Forestry Review*, 25(3), 335-357. <https://doi.org/10.1505/146554823837586221>
- Meurisse, N., & Pawson, S. (2017). Quantifying dispersal of a non-aggressive saprophytic bark beetle. *PLoS ONE*, 12(4). <https://doi.org/10.1371/journal.pone.0174111>
- Miller, D., & Clark, A. (1935). *Sirex noctilio* (Hym.) and its parasite in New Zealand. *Bulletin of Entomological Research*, 26(2), 149-154. <https://doi.org/10.1017/S000748530003813X>
- Miller, D. R. (2020). Effects of Ethanol and α -Pinene in a Generic Trap Lure Blend for Pine Bark and Wood-Boring Beetles in Southeastern United States. *Journal of Entomological Science*, 55(3), 310-320. <https://doi.org/10.18474/0749-8004-55.3.310>
- Miller, D. R. (2023). Should Ipsdienol and Ipsenol Lures be Retained in a Generic Trap Lure Blend for Pine Bark and Woodboring Beetles (Coleoptera) in the Southeastern United States? *Journal of Entomological Science*, 58(2), 230-241. <https://doi.org/10.18474/JES22-41>
- Miller, D. R., & Allison, J. D. (2011). Variation in enantiospecific attraction of *Ips avulsus* (Coleoptera: Curculionidae) to the pheromone ipsdienol in Georgia. *Journal of Economic Entomology*, 104(3), 895-900. <https://doi.org/10.1603/EC10405>
- Miller, D. R., Asaro, C., & Berisford, C. W. (2005). Attraction of southern pine engravers and associated bark beetles (Coleoptera: Scolytidae) to ipsenol, ipsdienol, and lanierone in Southeastern United States. *Journal of Economic Entomology*, 98(6), 2058-2066. <https://doi.org/10.1093/jee/98.6.2058>
- Miller, D. R., Asaro, C., Crowe, C. M., & Duerr, D. A. (2011). Bark beetle pheromones and pine volatiles: Attractant kairomone lure blend for longhorn beetles (Cerambycidae) in pine stands of the Southeastern United States. *Journal of Economic Entomology*, 104(4), 1245-1257. <https://doi.org/10.1603/EC11051>
- Miller, D. R., Crowe, C. M., & Sweeney, J. D. (2020). Trap height affects catches of bark and woodboring beetles (Coleoptera: Curculionidae, Cerambycidae) in baited multiple-funnel traps in southeastern United States. *Journal of Economic Entomology*, 113(1), 273-280. <https://doi.org/10.1093/jee/toz271>
- Mills, N. (1983). The natural enemies of scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. *Biocontrol News and Information*, 4(4), 303-326.
- MPI. (2024a). Forestry and wood processing data. Ministry for Primary Industries (MPI), Wellington, New Zealand. Retrieved 9 April 2025 from <https://www.mpi.govt.nz/forestry/forest-industry-and-workforce/forestry-wood-processing-data/>
- MPI. (2024b). Surveillance 2023 annual report. *Ministry for Primary Industries*, 51(3), 190. Ministry for Primary Industries (MPI), Wellington, New Zealand, 190pp. Retrieved 9 April from <https://www.mpi.govt.nz/dmsdocument/65409-Surveillance-Magazine-Annual-report-Volume-51.-No-3.-September-2024>
- Moore, G. E. (1972). Southern pine beetle mortality in North Carolina caused by parasites and predators. *Environmental Entomology*, 1(1), 58-65.
- Moore, J. R., Manley, B. R., Park, D., & Scarrott, C. J. (2013). Quantification of wind damage to New Zealand's planted forests. *Forestry*, 86(2), 173-183. <https://doi.org/10.1093/forestry/cps076>
- Morgan, F. D. (1989). Forty years of *Sirex noctilio* and *Ips grandicollis* in Australia. *New Zealand Journal of Forestry Science*, 19(2-3), 198-209. https://www.scionresearch.com/_data/assets/pdf_file/0006/59991/NZJFS192-and-31989MORGAN198_209.pdf
- Murdock, T. Q., Taylor, S. W., Flower, A., Mehlenbacher, A., Montenegro, A., Zwiars, F. W., Alfaro, R., & Spittlehouse, D. L. (2013). Pest outbreak distribution and forest management impacts

- in a changing climate in British Columbia. *Environmental Science and Policy*, 26, 75-89. <https://doi.org/10.1016/j.envsci.2012.07.026>
- Neumann, F., & Morey, J. (1984). Studies on the introduced bark beetle *Ips grandicollis* (Eichhoff) in Victorian radiata pine plantations. *Australian forest research*, 14(4), 283-300.
- Neumann F. G., & Morey J. L. (1984). Studies on the introduced bark beetle *Ips grandicollis* (Eichhoff) in Victoria radiata pine plantations. *Australian Forest Research*, 14, 283-300.
- Neumann, F. G. (1987). Introduced bark beetles on exotic trees in Australia with special reference to infestations of *Ips grandicollis* in pine plantations. *Australian Forestry*, 50(3), 166-178. <https://doi.org/10.1080/00049158.1987.10674513>
- Nunberg, M. (1974). The occurrence of *Ips grandicollis* (Eichh.)(Coleoptera, Scolytidae) in Cuba. *Polskie Pismo Entomologiczne*, 44(4), 735-736.
- Page, M., Nelson, L. J., Blomquist, G. J., & Seybold, S. J. (1997). Cuticular hydrocarbons as chemotaxonomic characters of pine engraver beetles (*Ips* spp.) in the grandicollis subgeneric group. *Journal of Chemical Ecology*, 23(4), 1053-1099. <https://doi.org/10.1023/B:JOEC.0000006388.92425.ec>
- Paine, T. D., Birch, M. C., & Švihra, P. (1981). Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia*, 48(1), 1-6. <https://doi.org/10.1007/BF00346980>
- Palmer, J. G., Watt, M. S., Kimberley, M. O., Hock, B. K., Payn, T. W., & Lowe, D. J. (2010). Mapping and explaining the productivity of *Pinus radiata* in New Zealand.
- Pawson, S., Williams, N., Gear, I., & Armstrong, J. (2014). Reducing biosecurity business risks for logs and timber. *New Zealand Journal of Forestry*, 59, 23. <https://nzif.org.nz/nzif-journal/publications/article/22800>
- Pawson, S. M., & Meurisse, N. (2015). *Evaluation of potential risk reduction strategies to decrease the infestation of export logs by insects*. Confidential report to Stakeholders in Methyl Bromide Reduction (STIMBR) and Ministry for Primary Industries (MPI). Scion, Rotorua, New Zealand.
- Poland, T. M., & Rassati, D. (2019). Improved biosecurity surveillance of non-native forest insects: a review of current methods. *Journal of Pest Science*, 92(1), 37-49. <https://doi.org/10.1007/s10340-018-1004-y>
- Reeve, J. D., Rojas, M. G., & Morales-Ramos, J. A. (2003). Artificial diet and rearing methods for *Thanasimus dubius* (Coleoptera: Cleridae), a predator of bark beetles (Coleoptera: Scolytidae). *Biological Control*, 27(3), 315-322. [https://doi.org/10.1016/S1049-9644\(03\)00021-5](https://doi.org/10.1016/S1049-9644(03)00021-5)
- Reid, M. L. (1999). Monogamy in the bark beetle *Ips latidens*: ecological correlates of an unusual mating system. *Ecological Entomology*, 24(1), 89-94. <https://doi.org/10.1046/j.1365-2311.1999.00168.x>
- Rigot, T., Van Halder, I., & Jactel, H. (2014). Landscape diversity slows the spread of an invasive forest pest species. *Ecography*, 37(7), 648-658. <https://doi.org/10.1111/j.1600-0587.2013.00447.x>
- Rimes, G. (1959). Insect pest and their control - The bark beetle. *Journal of the Department of Agriculture, Western Australia*. 8(3), 353-355. https://library.dpird.wa.gov.au/journal_agriculture3/vol8/iss3/16
- Rivera-Dávila, O. L., Sánchez-Martínez, G., & Rico-Martínez, R. (2021). Ecotoxicity of pesticides and semiochemicals used for control and prevention of conifer bark beetle (*Dendroctonus* spp.) outbreaks. *Chemosphere*, 263. <https://doi.org/10.1016/j.chemosphere.2020.128375>
- Roberts, M., Gilligan, C. A., Kleczkowski, A., Hanley, N., Whalley, A., & Healey, J. R. (2020). The effect of forest management options on forest resilience to pathogens. *Frontiers in Forests and Global Change*, 3, 7. <https://doi.org/10.3389/ffgc.2020.00007>
- Romo, C. M., Early, J. W., & Massart, X. (2017). 'Unestablished' biological control agent found in Canterbury 40 years later. *New Zealand Entomologist*, 40(1), 16-21. <https://doi.org/10.1080/00779962.2017.1307164>
- Safranyik, L., & Wilson, B. (2007). The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia. 304 p. Retrieved 9 April 2025 from <https://ostrnrcan-dostrncan.canada.ca/handle/1845/222361>
- Samson, P. R. (1984). The biology of *Roptrocerus xylophagorum* [Hym.: Torymidae], with a note on its taxonomic status. *Entomophaga*, 29(3), 287-298. <https://doi.org/10.1007/BF02372116>
- Samson, P. R., & Smibert, J. (1986). Preliminary studies on the efficacy and establishment of *Roptrocerus xylophagorum* [Hym.: Torymidae], a parasitoid of *Ips grandicollis* [Col.:

- Scolytidae], in Australia. *Entomophaga*, 31(2), 173-182.
<https://doi.org/10.1007/BF02372368>
- Santoro, A. E., Lombardero, M. J., Ayres, M. P., & Ruel, J. J. (2001). Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecology and Management*, 144(1-3), 245-254. [https://doi.org/10.1016/S0378-1127\(00\)00389-3](https://doi.org/10.1016/S0378-1127(00)00389-3)
- Schroeder, L. M., Weslien, J., Lindelöw, A., & Lindhe, A. (1999). Attacks by bark- and wood-boring Coleoptera on mechanically created high stumps of Norway spruce in the two years following cutting. *Forest Ecology and Management*, 123(1), 21-30.
[https://doi.org/10.1016/S0378-1127\(99\)00013-4](https://doi.org/10.1016/S0378-1127(99)00013-4)
- Six, D. L. (2012). Ecological and evolutionary determinants of bark beetle - Fungus symbioses. *Insects*, 3(1), 339-366. <https://doi.org/10.3390/insects3010339>
- Smith, Z. M., Chase, K. D., Takagi, E., Kees, A. M., & Aukema, B. H. (2021). Colonization and reproduction of potential competitors with mountain pine beetle in baited logs of a new host for mountain pine beetle, jack pine. *Forest Ecology and Management*, 497.
<https://doi.org/10.1016/j.foreco.2021.119455>
- Sopow, S. L., Bader, M. K. F., & Brockerhoff, E. G. (2015). Bark beetles attacking conifer seedlings: Picking on the weakest or feasting upon the fittest? *Journal of Applied Ecology*, 52(1), 220-227. <https://doi.org/10.1111/1365-2664.12368>
- Stevens, P. (2008). High risk site surveillance (HRSS): an example of best practice plant pest surveillance. In *Surveillance for biosecurity: Pre-border to pest management*. New Zealand Plant Protection Society (pp. 127-134). New Zealand Plant Protection Society.
https://nzpps.org/_oldsite/books/2008_Surveillance/Surveillance.pdf
- Stoate, T. N. (1953). *Report on the operations of the forests department for the year ended 30th June, 1953*. Forests Department of Western Australia.
- Stone, C., Penman, T., & Turner, R. (2012). Managing drought-induced mortality in *Pinus radiata* plantations under climate change conditions: a local approach using digital camera data. *Forest Ecology and Management*, 265, 94-101.
<https://doi.org/10.1016/j.foreco.2011.10.008>
- Stone, C., & Simpson, J. A. (1987). Influence of *Ips grandicollis* on the incidence and spread of bluestain fungi in *Pinus elliotii* billets in north-eastern New South Wales. *Australian Forestry*, 50(2), 86-94. <https://doi.org/10.1080/00049158.1987.10674500>
- Strom, B. L., Oldland, W. K., Meeker, J. R., & Dunn, J. (2015). Evaluation of general-use insecticides for preventing host colonization by New Jersey southern pine beetles. *Arboriculture and Urban Forestry*, 41(2), 88-102. <https://doi.org/10.48044/jauf.2015.010>
- Sullivan, B. T., Fettig, C. J., Otrosina, W. J., Dalusky, M. J., & Berisford, C. W. (2003). Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. *Forest Ecology and Management*, 185(3), 327-340.
[https://doi.org/10.1016/S0378-1127\(03\)00223-8](https://doi.org/10.1016/S0378-1127(03)00223-8)
- Sullivan, B. T., Munro, H. L., Barnes, B. F., McNichol, B. H., Shepherd, W. P., & Gandhi, K. J. K. (2024). Potential for a minor pine bark beetle pest, *Dendroctonus terebrans* (Coleoptera: Curculionidae: Scolytinae), to mediate host location by a major pine killer, *Dendroctonus frontalis*. *Journal of Economic Entomology*, 117(3), 1010-1021.
<https://doi.org/10.1093/jee/toae054>
- Swaine, J. M. (1916). New species of the family Ipidae (Coleoptera): Part III. *The Canadian Entomologist*, 48(6), 181-192. <https://doi.org/doi:10.4039/Ent48181-6>
- Swaine, J. M. (1924). The allies of *Ips confusus* LeC. in western America Family Ipidae, Coleoptera. *The Canadian Entomologist*, 56(3), 69-72. <https://doi.org/doi:10.4039/Ent5669-3>
- Sweeney, J., Dodds, K. J., Fettig, C. J., & Carnegie, A. J. (2023). IPM: the forest context. Springer. In: J.D. Allison, T.D. Payne, B. Slippers, & M.J. Wingfield (Eds). *Forest entomology and pathology, Volume 1: Entomology* (pp. 581-646).
https://doi.org/10.1007/978-3-031-11553-0_19
- Thompson, G., Froud, K., Tohovaka, S., & Allison, V. (2007). Unwanted pests arrive in comfort (Biosecurity monitoring survey: imported furniture). *Biosecurity Magazine*, 79, 8-9.
<https://www.nzffa.org.nz/farm-forestry-model/the-essentials/forest-health-pests-and-diseases/biosecurity/unwanted-pests-arrive-in-comfort/>
- Tillman, J. A., Lu, F., Goddard, L. M., Donaldson, Z. R., Dwinell, S. C., Tittiger, C., Hall, G. M., Storer, A. J., Blomquist, G. J., & Seybold, S. J. (2004). Juvenile hormone regulates de novo isoprenoid aggregation pheromone biosynthesis in pine bark beetles, *Ips* spp., through transcriptional control of HMG-CoA reductase. *Journal of Chemical Ecology*, 30(12), 2459-2494. <https://doi.org/10.1007/s10886-004-7945-z>

- Toft, F. (2023). 'Behind the Scenes' at the Forestry Commission: Managing *Ips typographus*..... five years on. *Forestry commission*. Retrieved 9 April 2025 from <https://forestrycommission.blog.gov.uk/2023/10/10/behind-the-scenes-at-the-forestry-commission-managing-ips-typographus-five-years-on/>
- Vega, F. E., & Hofstetter, R. W. (2014). *Bark beetles: biology and ecology of native and invasive species*. Academic Press, 640 pp. <https://doi.org/10.1016/C2013-0-04752-4>
- Vité, J. P., & Renwick, J. A. A. (1971). Population aggregating pheromone in the bark beetle, *Ips grandicollis*. *Journal of Insect Physiology*, 17(9), 1699-1704. [https://doi.org/10.1016/0022-1910\(71\)90065-5](https://doi.org/10.1016/0022-1910(71)90065-5)
- Wallace, M., & Rieske, L. K. (2023). Ingestion of Species-Specific dsRNA Alters Gene Expression and Can Cause Mortality in the Forest Pest, *Ips calligraphus*. *Forests*, 14(2). <https://doi.org/10.3390/f14020422>
- Wallin, K. F., & Raffa, K. F. (1999). Altered constitutive and inducible phloem monoterpenes following natural defoliation of jack pine: Implications to host mediated interguild interactions and plant defense theories. *Journal of Chemical Ecology*, 25(4), 861-880. <https://doi.org/10.1023/A:1020853019309>
- Wallin, K. F., & Raffa, K. F. (2001). Effects of folivory on subcortical plant defenses: Can defense theories predict interguild processes? *Ecology*, 82(5), 1387-1400. [https://doi.org/10.1890/0012-9658\(2001\)082\[1387:EOFOSP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1387:EOFOSP]2.0.CO;2)
- Waterhouse, D. F., & Sands, D. P. A. (2001). *Classical biological control of arthropods in Australia*.
- Weed, A. S., Ayres, M. P., & Bentz, B. J. (2015). Population Dynamics of Bark Beetles. In *Bark Beetles: Biology and Ecology of Native and Invasive Species* (pp. 157-176). Academic press. <https://doi.org/10.1016/B978-0-12-417156-5.00004-6>
- Wermelinger, B. (2004). Ecology and management of the spruce bark beetle *Ips typographus* - A review of recent research. *Forest Ecology and Management*, 202(1-3), 67-82. <https://doi.org/10.1016/j.foreco.2004.07.018>
- Werner, R. A. (1972a). Aggregation behaviour of the beetle *Ips grandicollis* in response to insect-produced attractants. *Journal of Insect Physiology*, 18(5), 1001-1013. [https://doi.org/10.1016/0022-1910\(72\)90037-6](https://doi.org/10.1016/0022-1910(72)90037-6)
- Werner, R. A. (1972b). Response of the beetle, *Ips grandicollis*, to combinations of host and insect produced attractants. *Journal of Insect Physiology*, 18(7), 1403-1412. [https://doi.org/10.1016/0022-1910\(72\)90268-5](https://doi.org/10.1016/0022-1910(72)90268-5)
- Witanachchi, J. P. (1986). Response of *Ips grandicollis* (Eichhoff) adults (Coleoptera:Scolytidae) to sites in bark initiated by others of the same species. *Australian Journal of Entomology*, 25(1), 41-46. <https://doi.org/10.1111/j.1440-6055.1986.tb01067.x>
- Witanachchi, J. P., & Morgan, F. D. (1981). Behaviour of the bark beetle, *Ips grandicollis*, during host selection. *Physiological Entomology*, 6(2), 219-223. <https://doi.org/10.1111/j.1365-3032.1981.tb00644.x>
- Wood, S. L. (1977). Introduced and exported american Scolytidae (Coleoptera). *The Great Basin Naturalist*, 67-74. <https://scholarsarchive.byu.edu/gbn/vol37/iss1/5>
- Wood, S. L. (1982). The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs*, 1359 pp. Retrieved 9 April 2025 from <https://archive.org/details/biostor-239409>
- Wyka, S. A., Munck, I. A., Brazee, N. J., & Broders, K. D. (2018). Response of eastern white pine and associated foliar, blister rust, canker and root rot pathogens to climate change. *Forest Ecology and Management*, 423, 18-26. <https://doi.org/10.1016/j.foreco.2018.03.011>
- Wylie, F. R., Peters, B., DeBaar, M., King, J., & Fitzgerald, C. (1999). Managing attack by bark and ambrosia beetles (Coleoptera: Scolytidae) in fire-damaged Pinus plantations and salvaged logs in Queensland, Australia. *Australian Forestry*, 62(2), 148-153. <https://doi.org/10.1080/00049158.1999.10674776>
- Wylie, R. (2000). Integrated pest management in tropical forestry. In: Proceedings of the International Conference on timber plantation development held from 7–9 November 2000, Manila, Philippines. Retrieved 9 April from <https://www.fao.org/4/ac781e/ac781e07.htm>
- F., Carnegie, A. J., Bashford, R., Bedding, R. A., Nicol, H. I., & Gurr, G. M. (2014). Bark beetle (*Ips grandicollis*) disruption of woodwasp (*Sirex noctilio*) biocontrol: Direct and indirect mechanisms. *Forest Ecology and Management*, 323, 98-104. <https://doi.org/10.1016/j.foreco.2014.03.009>
- Yousuf, F., Carnegie, A. J., Bashford, R., Nicol, H. I., & Gurr, G. M. (2018). The fungal matrices of *Ophiostoma ips* hinder movement of the biocontrol nematode agent, *Deladenus siricidicola*, disrupting management of the woodwasp, *Sirex noctilio*. *BioControl*, 63(5), 739-749. <https://doi.org/10.1007/s10526-018-9897-1>

- Yousuf, F., Gurr, G. M., Carnegie, A. J., Bedding, R. A., Bashford, R., & Gitau, C. W. (2014). Biology of the bark beetle *Ips grandicollis* Eichhoff (Coleoptera: Scolytinae) and its arthropod, nematode and microbial associates: A review of management opportunities for Australia. *Austral Entomology*, 53(3), 298-316. <https://doi.org/10.1111/aen.12077>
- Yousuf, F., Gurr, G. M., Carnegie, A. J., Bedding, R. A., Bashford, R., Gitau, C. W., & Nicol, H. I. (2014). The bark beetle, *Ips grandicollis*, disrupts biological control of the woodwasp, *Sirex noctilio*, via fungal symbiont interactions. *FEMS Microbiology Ecology*, 88(1), 38-47. <https://doi.org/10.1111/1574-6941.12267>
- Zahid, M. I., Grgurinovic, C. A., & Walsh, D. J. (2008). Quarantine risks associated with solid wood packaging materials receiving ISPM 15 treatments. *Australian Forestry*, 71(4), 287-293. <https://doi.org/10.1080/00049158.2008.10675047>
- Zimmermann, C. (1868). Synopsis of the Scolytidae of America North of Mexico. *Transactions of the American Entomological Society*, 1, 141-178. <https://www.jstor.org/stable/pdf/25076203.pdf>

Appendix A

Literature comparisons of captures of *Ips grandicollis* and other bark beetles species using traps baited with different combinations of host semiochemicals and bark beetle pheromones as attractants.

Tested semiochemical blends include:

- i. the host-produced primary attractants α -pinene and ethanol, which are broadly attractive to many bark and wood boring beetles, especially those attacking Pinaceae;
- ii. the bark beetle pheromone ipsenol, which attracts *I. grandicollis* and *I. avulsus*, synergises attraction for *I. calligraphus*, but acts as an anti-aggregation signal (inhibitor) for *I. pini*;
- iii. the bark beetle pheromone ipsdienol, which is attractive to most *Ips* species attacking pines, but acts as an anti-aggregation signal (inhibitor) for *I. grandicollis*;
- iv. the bark beetle pheromone lanierone, which synergises attraction of certain *Ips* species, like *I. pini*, to traps baited with ipsdienol; and
- v. the cerambycid monochemical (2-undecyloxy-1-ethanol), identified as a pheromone for longhorn beetles in the genus *Monochamus*.

Example 1.

Study details are provided in Miller et al. (2011)

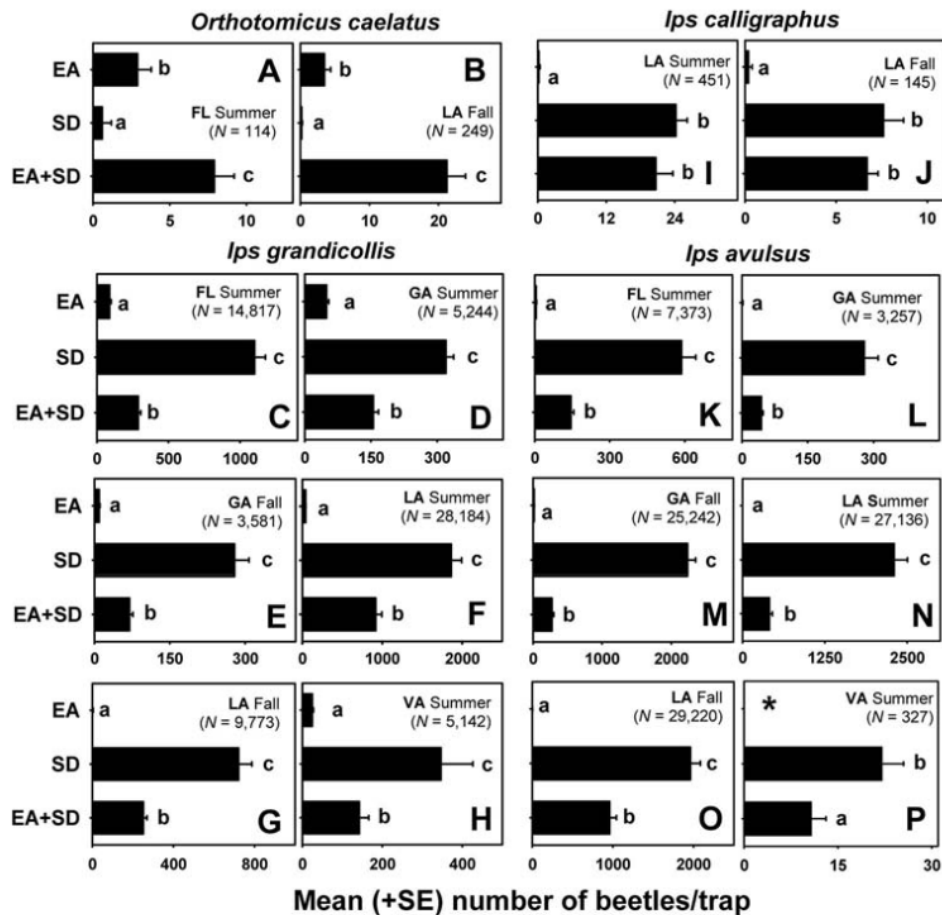


Fig. 4. Effects of ethanol + α -pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) on trap catches of *O. caelatus* (A and B) *I. grandicollis* (C-H), *I. calligraphus* (I and J), and *I. avulsus* (K-P) in the southeastern United States. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm-Sidak test [A-M, O, P] or t -test [N]; see text). Treatment with an asterisk had zero catches.

Example 2.

Study details are provided in Chase et al. (2018).

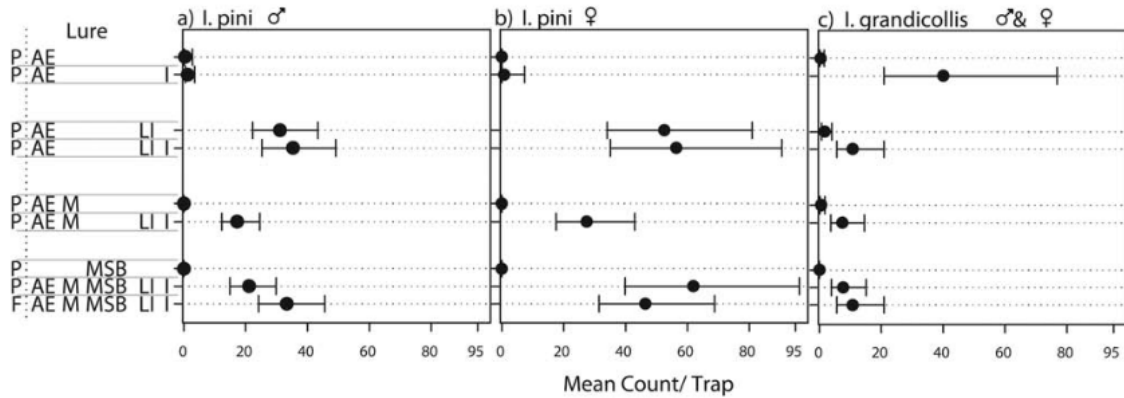


Fig. 4. Estimated mean trap capture (based on a hierarchical generalized linear model) of *Ips pini* (male [a] and female [b]) and *I. grandicollis* (c) per trap baited with each combination of lures. Trap types: P, panel trap; F, funnel trap. Lures: AE, α -pinene/ethanol; M, monochamol; LI, lanierone/ipdienol; I, ipsenol; MSB, Bisaboladienol & MDT. See Table 1 for more explanation of the lure codes. Error bars show 95% confidence limits.

Example 3.

Study details are provided in Miller (2023)

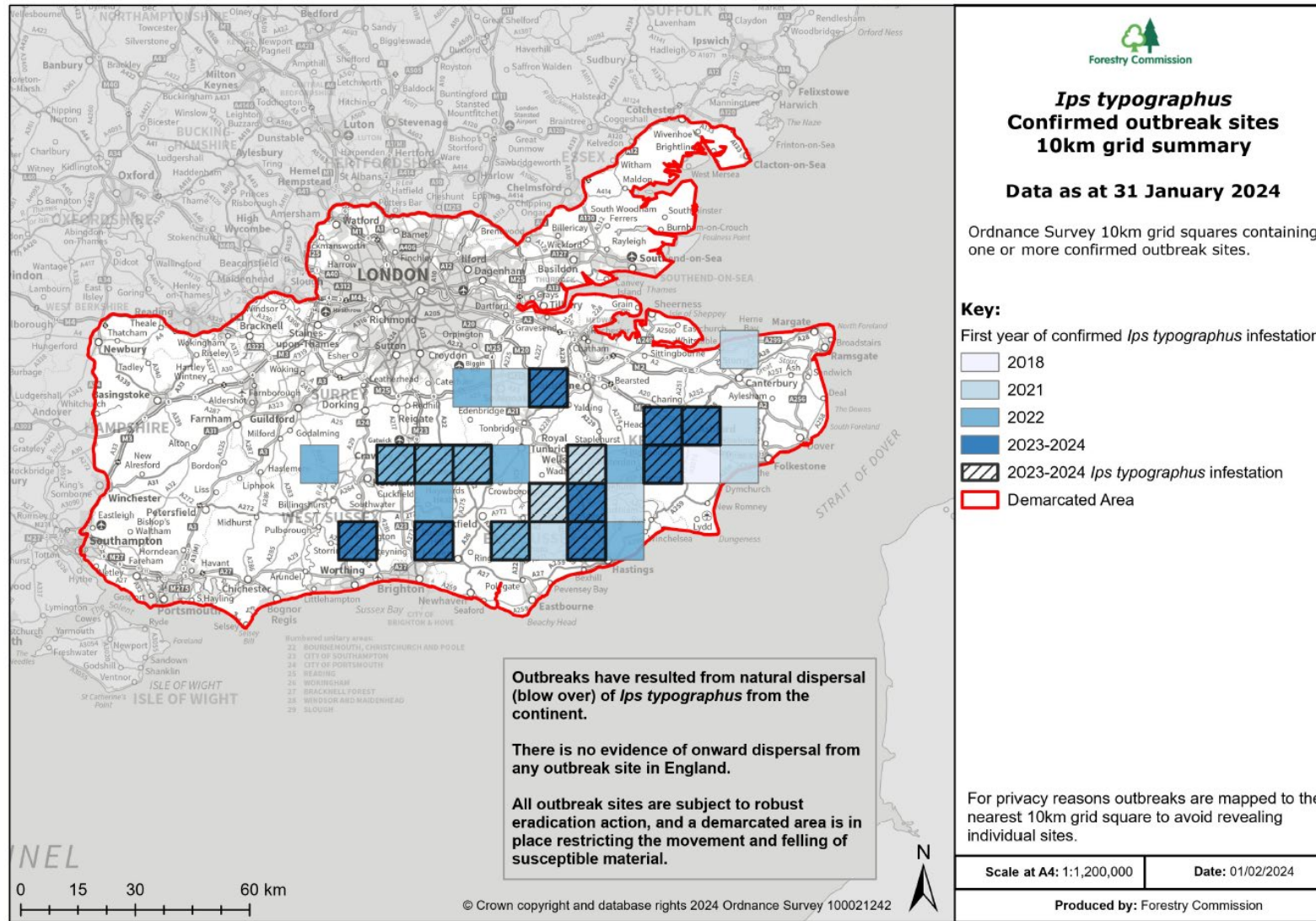
Table 3. Mean (\pm SE) catches of beetles in traps baited with ethanol + α -pinene (EA), with or without ipsenol (S) and/or ipsdienol (D), in northcentral Georgia in 2007 ($n = 10$). * (—) indicates none captured.

Family and Species	EA	EA + D	EA + S	EA + D + S
Cerambycidae				
<i>Acanthocinus obsoletus</i>	0.7 \pm 0.3a	7.0 \pm 2.0b	7.0 \pm 2.1b	8.8 \pm 2.1b
<i>Monochamus titillator</i>	2.2 \pm 0.8a	17.9 \pm 2.9b	23.4 \pm 4.7b	22.5 \pm 2.7b
Cleridae				
<i>Thanasimus dubius</i>	0.4 \pm 0.2a	0.7 \pm 0.3a	1.9 \pm 0.5b	0.2 \pm 0.1a
Curculionidae				
<i>Hylastes salebrosus</i>	9.2 \pm 1.0ab	10.5 \pm 1.8b	11.6 \pm 1.2b	5.4 \pm 0.8a
<i>Ips avulsus</i>	1.8 \pm 0.9a	10.1 \pm 1.5b	15.4 \pm 1.8	44.1 \pm 7.3c
<i>Ips calligraphus</i>	0.7 \pm 0.2a	7.1 \pm 1.7c	2.1 \pm 0.4b	8.8 \pm 1.0c
<i>Ips grandicollis</i>	32.3 \pm 3.2a	26.1 \pm 3.0a	152.3 \pm 19.8b	131.4 \pm 19.4b
<i>Orthotomicus caelatus</i>	2.2 \pm 0.4a	9.8 \pm 1.3b	3.1 \pm 0.7a	4.2 \pm 0.8a
Histeridae				
<i>Platysoma</i> spp.	4.2 \pm 1.1a	16.5 \pm 2.4b	72.4 \pm 5.4d	48.3 \pm 2.4c
Trogossitidae				
<i>Temnoscheila virescens</i>	23.1 \pm 3.1a	52.9 \pm 6.7b	54.6 \pm 7.6b	58.5 \pm 6.1b
Zopheridae				
<i>Aulonium tuberculatum</i>	—	1.7 \pm 0.5a	9.7 \pm 2.1b	9.1 \pm 1.4b
<i>Lasconotus</i> spp.	57.6 \pm 8.1a	39.4 \pm 8.4a	141.2 \pm 24.3b	63.2 \pm 15.7a

* Means in row followed by different lowercase letters are significantly different at $P < 0.05$ (Holm-Sidak test).

Appendix B

Ips typographus outbreak sites in the United Kingdom, 2024 (Toft, 2023).



Ips typographus Confirmed outbreak sites 10km grid summary

Data as at 31 January 2024

Ordnance Survey 10km grid squares containing one or more confirmed outbreak sites.

Key:

First year of confirmed *Ips typographus* infestation

- 2018
- 2021
- 2022
- 2023-2024
- 2023-2024 *Ips typographus* infestation
- Demarcated Area

For privacy reasons outbreaks are mapped to the nearest 10km grid square to avoid revealing individual sites.

Scale at A4: 1:1,200,000

Date: 01/02/2024

Produced by: Forestry Commission

Appendix C

Biocontrol agents that could be considered for introduction into Australia to control *Ips grandicollis* (Yousuf et al., 2014).

© 2014 Australian Entomological Society
Table 1 Biological control agents that could be considered for introduction into Australia to control *Ips grandicollis*

Taxon	Potential biocontrol species	Order: family	Present host/target	Present range	References
Bacteria	<i>Pseudomonas fluorescens</i>	Pseudomonadales: Pseudomonadaceae	<i>I. sexdentatus</i> (Boemer)	Europe	Sevim <i>et al.</i> 2012
	<i>Serratia liquefaciens</i>	Enterobacteriales: Enterbacteriaceae	<i>I. typographus</i> (L.)	Europe	Muratoğlu <i>et al.</i> 2011
Fungi	<i>Wolbachia</i> spp.	Hypocreales: Cordycipitaceae	<i>I. typographus</i> , <i>P. calcographus</i> (L.)	Europe	Stauffer <i>et al.</i> 1997; Arthofer <i>et al.</i> 2010
	<i>Beauveria bassiana</i> (Bals.-Criv.) Vuill		<i>Ips</i> spp.	Europe	Kreutz <i>et al.</i> 2004; Hallet & Grégoire 1994
	<i>Isaria farinose</i> (Holm.) Fr.	Eurotiales: Trichocomaceae	<i>I. typographus</i> ; <i>I. sexdentatus</i>	Europe	Zimmermann 2008; Draganova <i>et al.</i> 2007
	<i>Lecanicillium lecanii</i> (Zimmerman, Zare and Gams)	Hypocreales: Clavicipitaceae	<i>I. sexdentatus</i> and <i>I. acuminatus</i> (Gyll.)	Europe	Draganova <i>et al.</i> 2007
	<i>Metarhizium anisopliae</i> (Metsch.) Sorokin	Hypocreales: Clavicipitaceae	<i>I. typographus</i>	Europe	Draganova <i>et al.</i> 2007
Insects (predators)	<i>Platysoma cylindrica</i> Paykull	Coleoptera: Histeridae	<i>I. pini</i> and <i>I. grandicollis</i>	North America	Aukema <i>et al.</i> 2000a; Erbilgin & Raffa 2001; Aukema & Raffa 2004
	<i>Platysoma parallelum</i> Say	Coleoptera: Histeridae	<i>I. pini</i> and <i>I. grandicollis</i>	North America	Aukema <i>et al.</i> 2000a; Erbilgin & Raffa 2001
	<i>Plegaderus transversus</i> (Say)	Coleoptera: Histeridae	<i>D. frontalis</i> and <i>Ips</i> spp. including <i>I. grandicollis</i>		Shepherd & Goyer 2005
	<i>Enoclerus lecontei</i> (Wolcott)	Coleoptera: Cleridae	<i>I. pini</i>	North America	Raffa & Dahlsten 1995
	<i>Thanasimus formicarius</i> L.	Coleoptera: Cleridae	<i>I. typographus</i> , <i>I. acuminatus</i> , <i>I. sexdentatus</i>	Europe	Westien & Regnander 1992
	<i>Rhizophagus depressus</i> F.	Coleoptera: Rhizophagidae	<i>Tomiscus piniperda</i> (L.)	Europe	Herard & Mercadier 1996
	<i>Medetera bistrigata</i> Parent	Diptera: Dolichopodidae	<i>I. pini</i>	North America	Aukema & Raffa 2004
	<i>Tennochila chlorodia</i> Mannerheim	Coleoptera: Trogositidae	<i>I. pini</i>	North America	Seybold <i>et al.</i> 1992; Raffa & Dahlsten 1995
Parasitoids	<i>Coeloides bostrichorum</i> Giraud	Hymenoptera: Braconidae	<i>Ips amitinus</i> , <i>I. typographus</i> and <i>Ptyokteines curvidens</i> Gemar	Belgium and Czech Republic	Lozan & Zelený 2002; Hougardy & Grégoire 2004; Ünal 2010
	<i>Coleoides pissodes</i> Ashmead	Hymenoptera: Braconidae	<i>Dendroctonus frontalis</i> Zimmerman	US A	Moore 1972
	<i>Dendrosoter chaenopachoides</i> Rusch	Hymenoptera: Braconidae	<i>Phrynobatrachus calcaratus</i> Orthotomicus erosus, <i>I. lipperi</i>	Turkey	Thompson 1953
	<i>Dendrosoter hartigii</i> Ratzeburg	Hymenoptera: Braconidae	<i>P. calcaratus</i> , <i>O. erosus</i> , <i>Carphoborus minimus</i> , <i>I. acuminatus</i> and other <i>Ips</i> spp.	Europe, Israel	Thompson 1953; Mendel & Halperin 1981
	<i>Dendrosoter prouberans</i> (Nees)	Hymenoptera: Braconidae	<i>Ptyogenes</i> spp.		
	<i>Ropalophorus clavicornis</i> (Wesmael)	Hymenoptera: Braconidae	<i>Hylesinus varius</i> , <i>Phloeotribus scarabaeoides</i> Bernard and <i>I. sexdentatus</i>	Spain, Turkey	Lozano <i>et al.</i> 2000; Ünal 2010
	<i>Cheilopachus quadrum</i>	Hymenoptera: Pteromalidae	<i>I. typographus</i>	Czech Republic, Bulgaria	Lozan & Zelený 2002
	<i>Dinotiscus eupterus</i> Waker	Hymenoptera: Pteromalidae	<i>Phloeotribus scarabaeoides</i>	Spain	Campo & Lozano 1994
	<i>Heydenia unika</i> Cook and Davis	Hymenoptera: Pteromalidae	<i>I. typographus</i> , <i>I. amitinus</i> and <i>Ptyogenes chalcographus</i>	Poland	Hilszczański <i>et al.</i> 2007
	<i>Rhopalkus tutela</i> (Walker)	Hymenoptera: Pteromalidae	<i>Pisodes strobil</i> (Peck), <i>I. pini</i> and other <i>Ips</i> spp.	USA and Canada	Williams & Langor 2002; Boone <i>et al.</i> 2008
	<i>Tomiscobia setneri</i> (Ruschka)	Hymenoptera: Pteromalidae	<i>I. typographus</i> (L.), <i>I. amitinus</i> and <i>Ptyogenes chalcographus</i>	Poland	Hilszczański <i>et al.</i> 2007
	<i>Tomiscobia tibialis</i>	Hymenoptera: Pteromalidae	<i>I. typographus</i> , <i>I. amitinus</i> and other <i>Ips</i> spp.	Europe	Faccoli 2000, 2001; Georgiev & Takov 2005
	<i>Dolichomitus terebrans</i> Ratzeburg	Hymenoptera: Ichneumonidae	<i>I. pini</i>	Canada	Senger & Roitberg 1992
			<i>P. castaneus</i> DeGeer	Europe	Kenis & Mills 1994

Appendix D

The four components of the Forest Biosecurity Surveillance system (based on New Zealand's forest biosecurity surveillance system, article featured in Forest Biosecurity News, Issue #1 March 2022, Forst Owners Association, Wellington, New Zealand).

Surveillance Programme	Funder	Description
High Risk Site Surveillance Programme (HRSS)	Biosecurity New Zealand	<p>This programme is designed to monitor trees, shrubs and wood in areas (predominantly urban) that are endpoints for significant pathways and/or high-risk establishment sites for exotic organisms. These largely comprise active sea and airports, vegetation-rich urban areas, transitional facilities and tourist sites, but also some industrial and military sites that receive large volumes of imported goods.</p> <p>Surveillance effort is largely allocated using a specifically designed Bayesian risk allocation and resource optimisation model.</p> <p>The main objective of the HRSS programme is to detect new plant pests and diseases that may pose a biosecurity risk, negatively impacting on native forests, urban trees, plantation forests and other trees.</p>
Forest Biosecurity Surveillance programme – model allocated surveillance effort (FBS)	Biosecurity New Zealand / Forest Owners Association on behalf of the Forest Growers Levy Trust	<p>This programme is similar to the HRSS programme, however, it specifically targets commercial plantation forest species in areas (predominantly urban) that are endpoints for significant pathways and/or high-risk establishment sites for exotic organisms that are considered a risk to plantation forests.</p> <p>Surveillance effort is also allocated using a specifically designed Bayesian risk allocation and resource optimisation model.</p> <p>The main objective of the FBS programme is to detect new forest pests and pathogens that may pose a biosecurity risk, negatively impacting on forest production species.</p>
Forest Biosecurity Surveillance programme – non model allocated surveillance effort (NMA)	Forest Owners Association on behalf of the Forest Growers Levy Trust	<p>This is a component of the FBS, which also targets commercial plantation species, but where the FBS focuses primarily on areas that are endpoints for significant pathways and/or high-risk establishment sites for exotic organisms (predominantly urban areas), the NMA focuses effort toward high risk areas and pathways within and around plantation forests. Effort is not allocated using the model used in the FBS but utilises various risk information, experience, invasion biology and knowledge of internal risk pathways as mechanisms for spread.</p> <p>This shares the same objectives as the FBS.</p>
Forest Health Assessments (FHA)	Forest Companies	<p>These surveys fulfil a wide range of outcomes for forest growers, a key one of which is to understand the health of their forests and to provide early detection of any biosecurity threat, or other issues that may affect the health of their forests. These also provide for early detection of biosecurity threats (new or established) as well as monitoring the spread of established pests and pathogens throughout New Zealand.</p> <p>These surveys are undertaken within commercial forest plantations.</p>
New Zealand's general surveillance system	Biosecurity New Zealand	<p>Biosecurity New Zealand maintains a general (passive) surveillance system that comprises a free 24/7 Pest and Disease hotline (0800 80 99 66), specialist incursion investigators, diagnostics laboratories, a notifiable organisms list, an Unwanted Organisms register, legislative requirements to report suspect new to New Zealand organisms (Notifiable Organisms) or unwanted organisms, and an engaged and aware community (comprising industry staff, scientists, government staff, tangata whenua, and members of the public).</p> <p>This system encompasses all sectors and provides for broad geographic coverage and enables anyone in New Zealand to actively participate in the biosecurity surveillance system.</p> <p>All notifications made into this system are triaged by a call centre and allocated to specialist incursion investigators, or laboratory scientists, who follow these up with the aim of rapidly ascertaining or ruling out a potential biosecurity threat.</p>